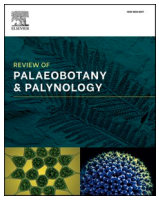
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Tracing 40,000 years of vegetation change in the Baetic-Rifan biodiversity hotspot

José S. Carrión [a,*], Juan Ochando [a,b], Fabrizio Michelangeli [b], Francisco Jiménez-Espejo [c], Fernando Ojeda [d], Gabriela Amorós [a,e], Manuel Munuera [f], Ana B. Marín-Arroyo [g], Penélope González-Sampériz [h], Joaquín Rodríguez-Vidal [i], Federico Di Rita [b], Donatella Magri [b]

[a] Department of Plant Biology (Botany Area), Faculty of Biology, University of Murcia, Campus de Espinardo, 30100 Murcia, Spain
[b] Sapienza University of Rome, Department of Environmental Biology, Piazzale Aldo Moro 5, 00185 Rome, Italy
[c] Instituto Andaluz de Ciencias de la Tierra (IACT), Armilla, Spain
[d] Departamento de Biología-IVAGRO, Universidad de Cádiz, Campus Río San Pedro, 11510 Puerto Real, Spain
[e] Department of Arts, Research Group ECCE HOMO, University of Murcia, Campus de Espinardo, Murcia, Spain
[f] Department of Agricultural Engineering, Polytechnic University of Cartagena, 30203 Cartagena, Spain
[g] Grupo I+D+i EvoAdapta (Evolución Humana y Adaptaciones durante la Prehistoria), Departamento Ciencias Históricas, University of Cantabria, Santander, Spain
[h] Instituto Pirenaico de Ecología-CSIC, Geoenvironmental Processes and Global Change Research, Av/ Montañana 1005, 50059 Zaragoza, Spain
[i] Department of Earth Sciences, Faculty of Experimental Sciences, University of Huelva, Campus del Carmen, Av. Tres de Marzo s/n, 21071 Huelva, Spain

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ABSTRACT

This study presents a 40,000-year-old pollen record from Los Tollos Lake in the Baetic-Rifan region of southernmost Spain. The data offer insights into the past ecosystems of a current biodiversity hotspot situated at the ecotone between the Atlantic and the Mediterranean. This new sequence encompasses Mediterranean and Ibero-North African sclerophylls, broad-leaf trees, conifers, and Tertiary relicts. The full-glacial abundance of mesothermophytes, particularly oaks, is among the highest recorded for the European Quaternary. Notably, the presence of ecologically significant pollen taxa, which are poorly dispersed and currently occur outside the study area, suggests that this biodiversity hotspot was more extensive in the Pleistocene. During the period of c. 40.8–36.5 ka, three *Artemisia* maxima at 40.6, 38.9, and 36.9 ka coincide with decreases in *Quercus*, indicating the spread of steppes in response to the abrupt coolings of the GS10, GS9 (HS4), and GS8 events. Similarly, increases in *Quercus* around 41, 40, and 37.2–38.3 ka parallel the GI10, GI9, and GI8 warm events. A forested period from 36.5–32 ka includes oak expansions during the GI7 and GI6 interstadials. From 32 to 19.2 ka, more xerophytic vegetation is observed, including the HS3, GS5-GS3, HS2, and GS2.1b-c cold spells, although the correlation with vegetation changes is not synchronous. As early as approximately 21 ka, *Artemisia* definitively declines, while the region was reforesting, likely due to the presence of stationary populations of broadleaf trees and conifers in the southern Baetic mountains. From approximately 12 ka onwards, the highest values of angiosperm trees are recorded, with oaks dominating throughout most of the Holocene. The pollen record and the correlation with marine records suggest a more intense hydrological regime during the first half of the Holocene, but there is also archaeobotanical evidence for human activity during the second half, resulting in a more open landscape, making it difficult to discriminate the impact of each factor. Some abrupt aridity events during the Holocene coincide with small variations in tree cover, particularly at 9.2, 8.2, 6.8, 5.5–4.8, 4.2, and 2.8 ka. Since the Neolithic and during the metallurgic stages, forest species, especially broad-leaf trees, experienced range retraction accompanied by population extinctions. The region's plant communities have been subject to fire regimes since the Pleistocene, seemingly dependent on the available tree biomass.

* Corresponding author.
E-mail address: carrion@um.es (J.S. Carrión).

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1. Introduction

Fundamental players in the exploration of paleoecosystems, pollen analysts often encounter the frustration of being unable to work on a desired study area due to one of the intrinsic features of paleontology: not all materials contain fossils, and deposits rich in pollen are frequently concentrated in regions beyond the project's scope. This issue is evident in a recent monographic study of the Iberian Peninsula and Balearic Islands, which has compiled and critically discussed paleobotanical information spanning the last 66 million years (Carrión et al.,

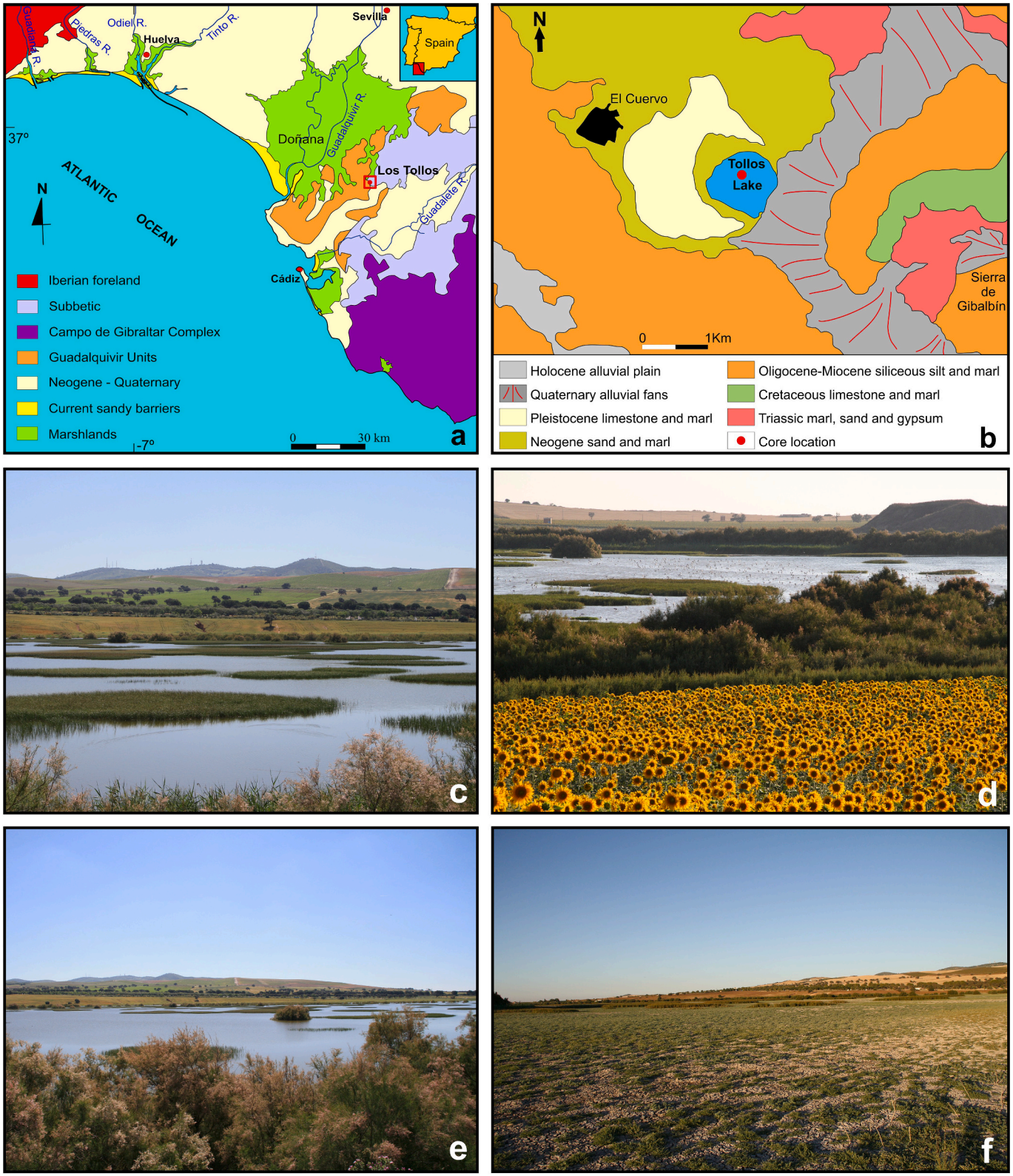


Fig. 1. a–b: Geological context of Los Tollos Lake (LT), Cádiz-Sevilla, southern Spain. c–f: Different panoramic views of the lake during inundation stages (c–d: winter 2014; e–f: winter 2023).

2024a, 2024b, 2024c: https://www.paleofloraiberica.org/). This limitation is not exclusive to palynologists, as the occurrence of plant macroremains is even more scarce. However, given the extraordinary floristic richness of the Iberian Peninsula, delving into the deep-time ecology of territories with a a highly emblematic natural heritage and a high degree of taxonomic, structural, and functional diversity such as the Strait of Gibraltar Region, is a compelling endeavor. Rodríguez-Sánchez et al. (2008) provided a comprehensive account of this region's biogeographical significance, which has separated the African and Iberian plates since the early Pliocene, showcasing high plant diversity and endemism. In such ecosystems, conservation strategies should be concentrated in a scenario marked by global change and the over-exploitation of natural resources.

While captivating the interest of botanists, ecologists, and biogeographers, the Strait of Gibraltar remains one of the least understood areas in Europe from a paleoecological perspective. This study presents a 40,000-year-old lacustrine palynological record that offers crucial insights into the Upper Pleistocene and Holocene vegetation of southern Iberia. The study site is situated close to a significant biodiversity hotspot within the western Mediterranean (Lobo et al., 2001; Rodríguez-Sánchez et al., 2008; Lavergne et al., 2013; Molina-Venegas et al., 2013; Molina-Venegas et al., 2015), at the interface between the Atlantic and the Mediterranean. It encompasses coastal platforms that include the Doñana National Park, the lower Guadalquivir valley, and the Baetic mountain range's westernmost extent, including the Grazalema, Aljibe, and Algeciras mountains.

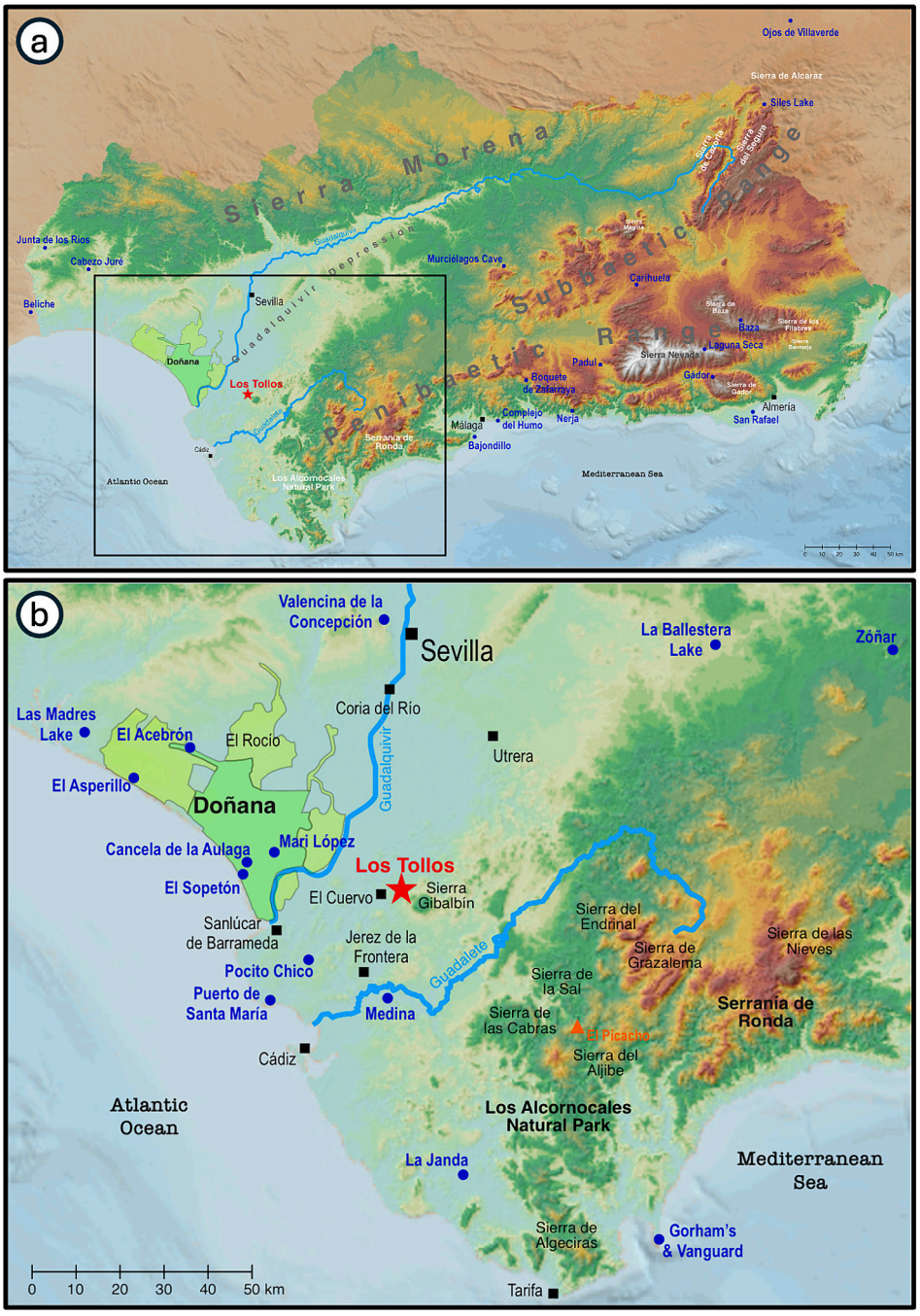


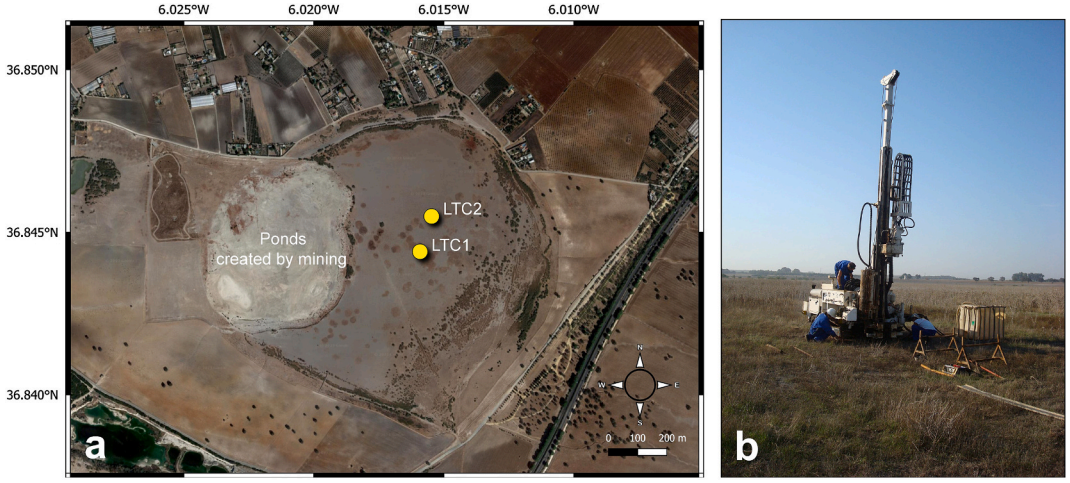
Fig. 2. Location of LT pollen site in the context of southern Iberian Peninsula, highlighting the surrounding orography (a) and the position of other paleoecological sites (in blue) mentioned in this paper (b). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

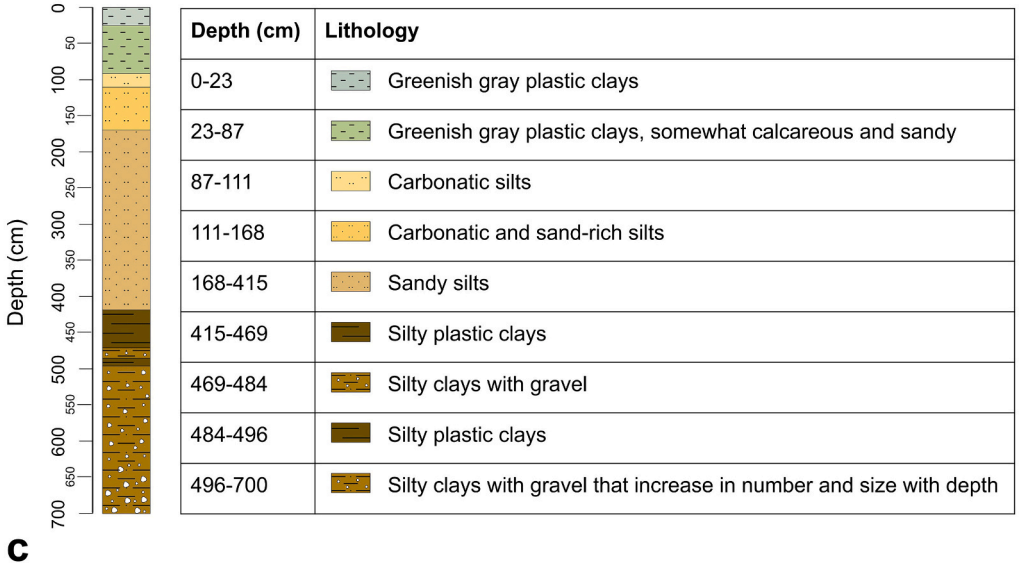
This investigation aims to elucidate the dynamics of vegetation changes within the context of prevailing abiotic and biotic stressors over time. While climatic change undoubtedly plays a significant role in inducing vegetation change, it is essential to clarify that our approach will not adhere strictly to conventional climatic determinism (Carrión, 2001). Similarly, we do not aim to establish "general trends" with predictive value for vegetation changes across southern Europe or even the southern Iberian Peninsula. Biological history is a complex tapestry of individual and site-specific narratives, each with its distinctive trajectory and lessons for future generations. This new sequence contributes to the extensive diversity of vegetational developments across the Mediterranean and southern Atlantic Iberia (Carrión et al., 2011), providing a platform for discussing the intricacies of biological complexity. This prompts us to question whether, due to the inherent limitations of pollen analysis and the often paucity of available data, palynologists might present oversimplified or over-speculative portrayals of the past. We may need to frequently reassess the scope of our paleoenvironmental inferences and contextualize the influences on vegetation within a historical-contingent framework. In a physiographically rugged region with such a dynamic geological history, rather than anticipating linear responses to climate change, what one can expect is a temporal and spatial puzzle of change, interaction, and stasis.

2. Lake Basin and recent disturbances

Los Tollos Lake (LT) (36° 50′ 43"N, 6° 0' 51"W, 68–70 m a.s.l.) is situated on the southern fringe of the Guadalquivir depression, marking the boundary between the municipalities of Jerez de la Frontera (Cádiz) and El Cuervo (Sevilla) in southern Spain (Figs. 1, 2). The lake basin displays characteristics of karstic morphogenesis, with the underlying bedrock exhibiting a geologic transition between the southern foothills of the Baetic Ranges (Subbaetic and Campo de Gibraltar Complex), the Guadalquivir Accretionary Complex (Guadalquivir Units), and the Neogene-Quaternary deposits of the Guadalquivir River Depression (Pérez-Valera et al., 2017) (Fig. 1). The prominent reliefs in the vicinity are situated to the southeast, encompassing the nearby Sierra de Gibalbín in Jerez de la Frontera (410 m) (Figs. 1, 2). Moving further east and southeast, larger massifs are found in the Sierras del Aljibe (1091 m), Las Cabras (673 m), La Sal (484 m), Sierra del Pinar (Torreón 1654 m, Cerezo 1600 m, Pico del Águila 1500 m), and Sierra del Endrinal (Simancón 1556 m, El Reloj 1535 m) among others within los Alcornocales and Sierra de Grazalema natural parks (Fig. 2).

Los Tollos Lake (LT) has functioned as an expansive wetland continuously since the mid-Pliocene, when the former coastal limit (sands) transformed into a coastal lagoon, which resembles the present pike of the Guadalquivir marsh, due to the topographic depression that originated (Oliveros et al., 2009). The lake receded during the





Depth (cm)	Lithology
0-23	Greenish gray plastic clays
23-87	Greenish gray plastic clays, somewhat calcareous and sandy
87-111	Carbonatic silts
111-168	Carbonatic and sand-rich silts
168-415	Sandy silts
415-469	Silty plastic clays
469-484	Silty clays with gravel
484-496	Silty plastic clays
496-700	Silty clays with gravel that increase in number and size with depth

Fig. 3. a–b: Drilling in Los Tollos, 2007; position of cores LT1 and LT2. The palynological study has been carried out on LT2. c: Lithology of LT2.

Pleistocene, with the LT basin accumulating silt, marl, and clay until its current configuration (Figs. 1, 3c). It seems probable that during several episodes of the late Quaternary, the current position of the lake lay across the emerged littoral of the so-called Tartessian Gulf-Lacus Ligustinus complex, a penetration of the Atlantic Ocean that would occupy a large part of what is today the marshlands of the final stretch of the Guadalquivir (García Fernández and García Vargas, 2010; Borja et al., 2018).

Currently, the primary water input into the lake is precipitation, with occasional supplementation from the 655-ha source basin, which carries sediments from the surrounding formations (Parra et al., 2013). This results in periodic flooding, covering up to 84 ha (Oliveros et al., 2009). Evapotranspiration is relatively high, and saline deposits, reminiscent of those observed in playa-lakes, are present in the vicinity (Durán-Valsero et al., 2003). The basin plays a significant ecological role in Andalusia due to its size and the abundance and diversity of threatened bird species that frequent it. The site serves as a wintering area and a crucial location for migratory avifauna from Europe to Africa (Birdlife International, 2023).

Between 1976 and 1997, mining activities resulted in the reduction and alteration of the lake's original surface, causing substantial disruption to its hydrology (Fig. 3). Historically, LT would have been a semi-permanent lake until the 1970s. During the mining years, groundwater extraction for urban supply brought two existing aquifers into contact. Given that one of them was permeable, filtrations made the lake hydrologically dependent on rainfall dynamics, streamflow, and evapotranspiration. The objective of mining was to extract a type of clay composed of magnesium and aluminum silicates with high absorbent power known as attapulgite (Moral et al., 2008). The exploration resulted in removing sedimentary sectors of the lake up to 25 m deep.

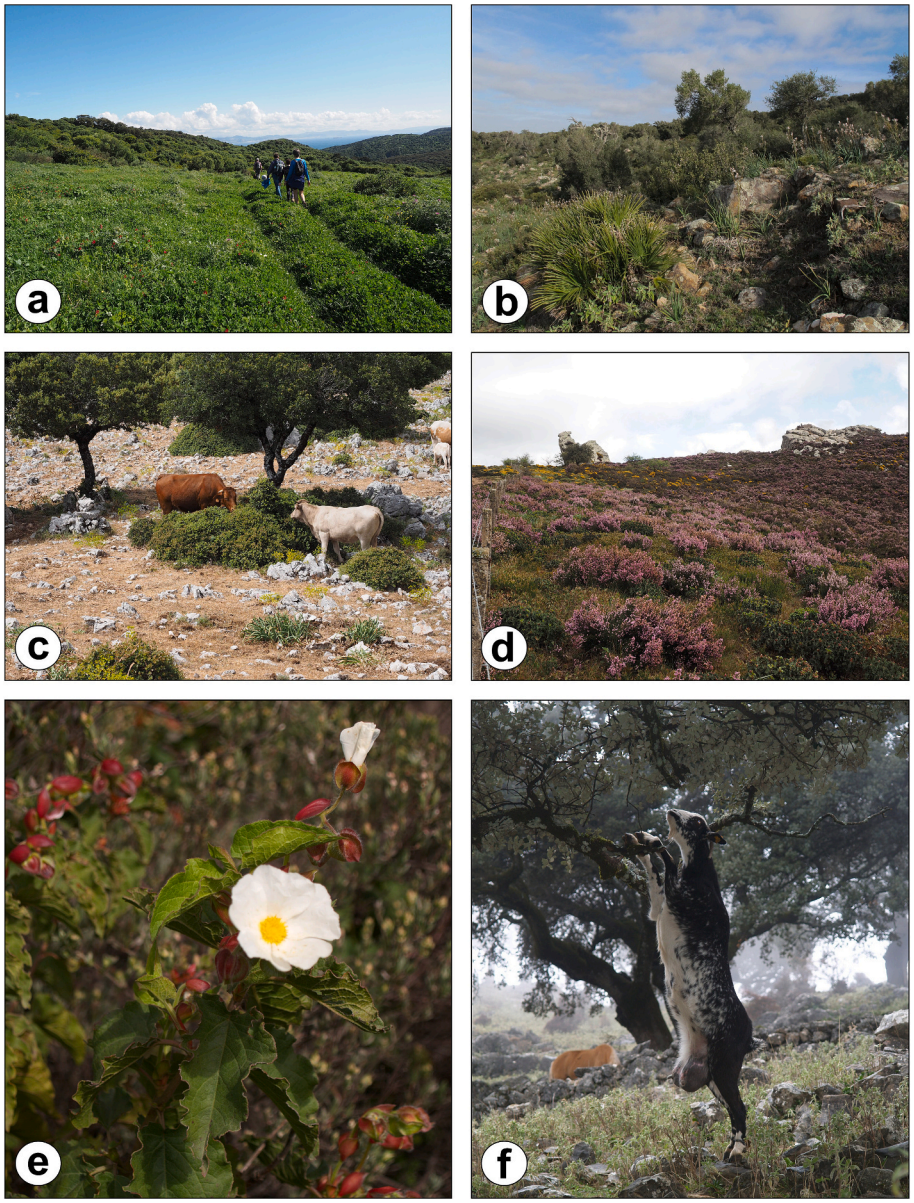


Fig. 4. a: Mediterranean grassland covering rolling hills on loamy soils (bujeos) near the Strait of Gibraltar. b: Mediterranean garrigue shrubland with dwarf palm (*Chamaerops humilis*) in the foreground and scattered *Olea europaea* trees in the background. c: Free range cattle browsing on clumps of *Quercus coccifera-Pistacia lentiscus* in a mountain holm-oak dehesa. d: Mediterranean heathland or herriza with *Erica australis* (pink) and *Pterospartum tridentatum* (yellow) in full bloom. e: *Cistus populifolius*, a characteristic species of the Mediterranean heathland or herriza. f: Goat reaching leaves of *Quercus ilex* subsp. *ballota* (Fagaceae) in a mountain holm-oak dehesa. Photographs: Fernando Ojeda. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Furthermore, the construction of illegal buildings was undertaken in and around the basin, with the introduction of plowing and the cultivation of crops, the use of heavy vehicles in the basin, the interruption of freshwater streams, and the establishment of a skeet shooting business within the basin itself (Oliveros et al., 2009). Local ecologists successfully advocated for the closure of mining activities and other disturbances, leading to the designation of Los Tollos as a protected area in the Natura 2000 Network (Oliveros et al., 2009). Since 2010, a process of conditioning, revegetation, infrastructure demolition, and waterproofing has been underway. Unfortunately, these actions involved not only filling mining holes with exogenous sediments but also the artificial restoration of the water network. These interventions, including water pumping and transfer from one area to another (Parra et al., 2013) and, more recently, fires, have ultimately altered the current ecosystem and the role of the previously unaltered bottom sediment as a paleoecological archive. Fortunately, the drilling from which our study derives took place a few years before all these disturbances, likely to have significantly impacted most of the lake stratigraphy.

3. Present-day climate and vegetation

The Strait of Gibraltar lies at the core of the Baetic-Rifan region (Ojeda et al., 2000), one of the ten plant biodiversity hotspots within the Mediterranean Region (Médail and Quézel, 1997; Devesa and Martínez-Sagarra, 2023) (Figs. 4, 5). Its outstanding levels of plant biodiversity and landscape heterogeneity are explained not only by its geographic position between two continents, but also by its edaphic miscellany and climatic singularity (Rodríguez-Sánchez et al., 2008) and, especially, by its unique geological history (Platt et al., 2013). The climate in the region is typically Mediterranean, with cool, moist winters and warm, dry summers. Mean annual temperature is about 18 °C and annual rainfall averages 800 mm. Local precipitation and temperature values based on the Trebujena station, located about 14 km from LT, provide an average yearly temperature of 18 °C and an average annual precipitation of 552 mm. Dominant soils are loamy to marly, neutral to basic pH, and moderate to high fertility (Arroyo and Marañón, 1990; Cowling et al., 1996; Porras et al., 2003). Such climatic and edaphic conditions explain this region's preponderance of garrigue-like shrublands and woodlands (Arroyo and Marañón, 1990). These are dominated by sclerophyllous (e.g. *Quercus rotundifolia*, *Q. coccifera*, *Olea europaea*, *Pistacia lentiscus*,

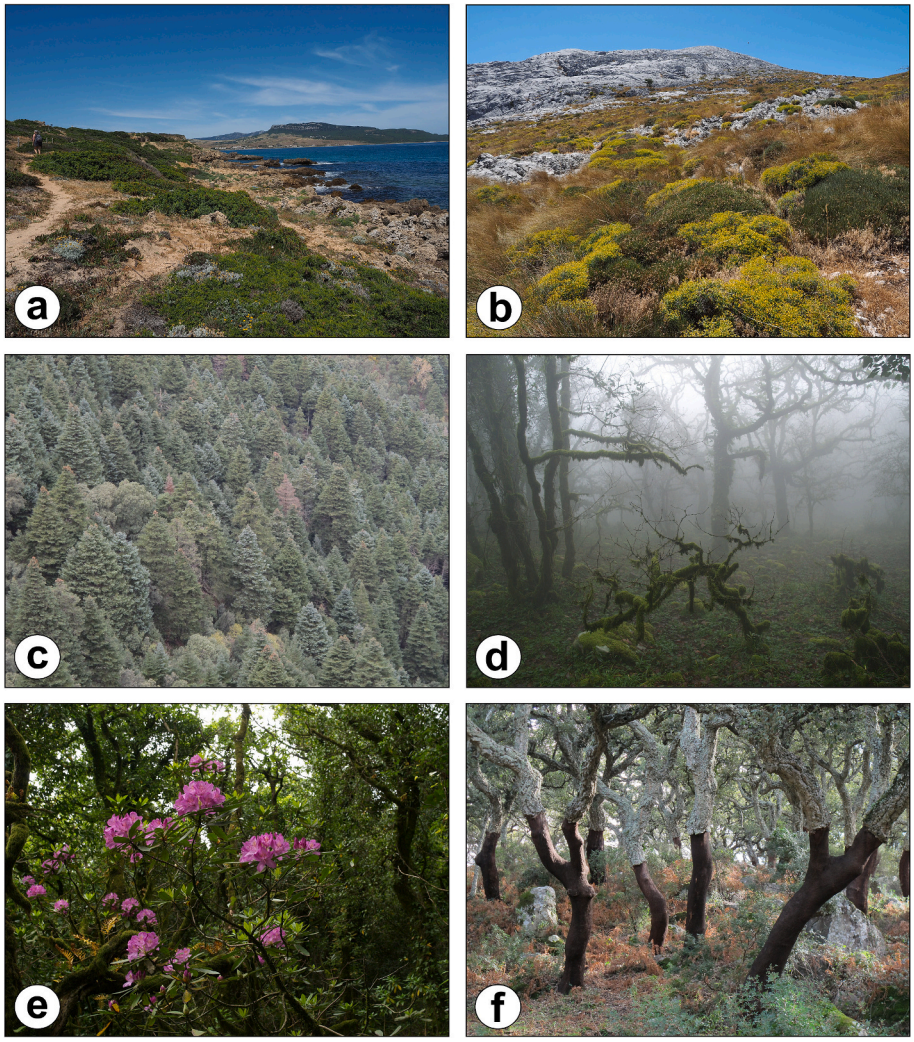


Fig. 5. a: Rocky coastal landscape in Cape Camarinal (Tarifa, Spain) dominated by wind-dwarfed *Juniperus phoenicea* shrubs. b: High mountain cushion-shrubland landscape dominated by *Bupleurum spinosum* (Apiaceae), *Erinacea anthyllis* (Fabaceae) and robust grasses (*Festuca* spp.). c: *Abies pinsapo* forest canopy. d: Bosque de niebla (mist forest) a striking example of warm-temperate forest at Sierra de Luna (Tarifa, Spain). Dominant tree species are semideciduous *Quercus canariensis*. e: *Rhododendron ponticum* (Ericaceae). Relict species abundant in canutos or warm-temperate forest patches found in moist sandstone gorges from the European side of the Strait of Gibraltar. f: Cork-oak (*Quercus suber*) woodland. The basal bark (cork) has been peeled off as a form of sustainable cork harvest (occurring every 8–10 years). Photographs: Fernando Ojeda.

Chamaerops humilis) and malacophyllous species (e.g. *Cistus* spp., *Phlomis purpurea*, *Salvia rosmarinus*) and represent the paradigm of Mediterranean vegetation in the Mediterranean Basin (Aparicio et al., 2001a). Owing to human disturbance, many of the shrublands and woodlands of the westernmost part of the Strait area, dominated by a hilly landscape, have been converted into pasture-grasslands with scattered trees (*dehesa* and *campiña* habitats) mainly for livestock grazing (Barbero et al., 1990) (Fig. 4).

Mountains further from the coastline are high (close to 1700 m on the European and over 2100 m on the southern African side, respectively) and dominated by Jurassic limestones and dolomites. Annual rainfall levels at high elevations increase markedly in these mountain ranges (above 2000 mm), and winters are much colder. Garrigue and *Quercus* woodlands are then replaced by coniferous forests of *Pinus* spp. (mostly *P. pinaster*), *Abies* spp. (*A. pinsapo* in the European and *A. maroccana* in the African) (Fig. 5c) and *Cedrus atlantica* (only in the African side) (Esteban et al., 2010). Exposed slopes and ridges of these high mountains are covered by dwarf vegetation with scattered *Juniperus* species (Lamrani and García-Novo, 1997). Mountains close to the Strait of Gibraltar region, by contrast, have lower elevations and are mostly composed of Oligo-Miocene siliceous sandstones (*Aljibe* sandstone formation) that produce highly acidic, nutrient-poor, sandy soils (Arroyo and Marañón, 1990; Ojeda et al., 1996). These infertile, acid soils appear as edaphic islands, surrounded by more fertile, non-acid, loamy or marly soils (Gil-López et al., 2017). Climate in these sandstone mountains is mild Mediterranean owing to the oceanic influence, with mean annual rainfall ranging from 800 to over 1500 mm. Prevailing southeastern winds, especially in summer, bring moisture from the sea to these sandstone mountains in the form of thick, low clouds and contribute to somewhat alleviating the severity of summer drought. Such contrasting climatic and edaphic features, together with its particular Plio-Pleistocene history (Rodríguez-Sánchez et al., 2008) explain the replacement of typical garrigue-like shrublands in these sandstone mountains by a distinct flora and vegetation. Extensive cork oak (*Quercus suber*) woodlands cover most sandstone middle slopes, their extension being favored in the last two centuries by the commercial exploitation of cork (Urbieta et al., 2008) (Fig. 5f). Moist semi-deciduous oak (*Quercus canariensis*) forests and lauroid forests, found in moist sandstone valleys and deep gorges, harbor a rich relict flora (Mejías et al., 2007) including pteridophytes of subtropical origin (Devesa and Martínez-Sagarra, 2023) (Fig. 5). The Mediterranean heathland or *herriza* (Fig. 4d) covers crests and ridges of these sandstone mountains. It is the most diverse subtype of European dry heathland (Ojeda, 2009) and, unlike other European heathlands, the herriza is highly diverse (Gil-López et al., 2018), being dominated by heath species such as *Erica australis* and *Calluna vulgaris*, the rockrose *Cistus populifolius* (Fig. 4e), gorses such as *Pterospartum tridentatum* or *Stauracanthus boivinii*, and the prostrated oak *Quercus lusitanica*. The herriza is also home to the carnivorous plant *Drosophyllum lusitanicum*, another Tertiary relict species (Martín-Rodríguez et al., 2020). Recurrent wildfires constitute a major selecting force in shaping the structure and function of many Mediterranean plant communities (Verdú and Pausas, 2007). Among them, the *herriza* outstands by its strong dependence on fire (Ojeda et al., 2010; Ojeda, 2020).

Finally, coastal habitats such as saltmarshes, dunes and rocky cliffs occupy the coastal boundary between terrestrial and marine ecosystems (Asensi and Díez-Garretas, 2017) (Fig. 5a). Saltmarshes are dominated by grasses such as *Spartina* spp., succulent chenopods (e.g. *Arthrocnemum macrostachyum*, *Salicornia* spp.) and halophytic shrubs such as *Limoniastrum monopetalum*. Sand dunes are characterized by the conspicuous presence of *Ammophila arenaria* and other species such as *Pancratium maritimum* and *Malcolmia littorea*. Gymnosperm shrubs such as *Juniperus* spp. are also found in sand dunes and contribute to stabilize them. There are also *Pinus pinea* stands in dune systems, but controversy exists as to whether they are ecologically native or planted (Bonari et al., 2017; Muñoz-Reinoso, 2021). Coastal rocky cliffs offer the harsher conditions for plant species and vegetation is sparse and scattered. Among the most frequent species are *Asteriscus maritimus*, *Limonium* spp., and *Armeria* spp.

Tamarix africana and *T. canariensis* colonize the lacustrine perimeter (Fig. 1). In the basinal vegetation, ephemeral formations of submerged macrophytes include abundant *Ruppia drepanensis* together with *Ranunculus peltatus, Zannichelia obtusifolia* and *Chara connivens*, this last covering the bottom of the basin with shallow water. The emerged species include *Scirpus maritimus* and *Scirpus lacustris, Salicornia ramosissima, Microcnemum coralloides, Suaeda splendens, S. albescens, S. spicata, S. vera, Halopeplis amplexicaulis, Phragmites australis* and grasslands of annual grasses (*Hordeum marinum, Polypogon maritimus*). When LT dries up, the presence of *Cressa cretica, Crypsis aculeata* and *Heliotropium supinum* is frequent. Farther from the water body is *Sarcocornia perennis*, which forms a dense fringe belt accompanied by stands of *Juncus subulatus, Juncus maritimus*, and *Frankenia laevis*. In the surrounding area there are dryland herbaceous crops interspersed with scattered holm oak (*Quercus rotundifolia*) trees, together with scrub patches containing *Asparagus* spp., *Quercus coccifera,* and *Chamaerops humilis*, among other species.

4. Material and methods

On September 25, 2007 two cores were obtained from the dry lake, LT1 (36° 50`42.7``N, 6° 1` 3.2``W, 10 m depth) and LT2 (36° 50`43.8``N, 6° 1`2.55W, 7 m depth) (Fig. 3). The drilling system was rotary, equipped with a piston to obtain continuous core sections within a 10 cm diameter liner, reaching a maximum length determined by the underlying bedrock. On fieldwork, core LT1 showed signs of sedimentary alteration, with frequent intrusions of the bedrock. This led us to drill for a second core, LT2, which was mainly made of silty and plastic clays alternating with carbonate silts (Fig. 3). This core was wrapped in cling-film in the field to prevent desiccation and stored in cool at 4 °C until sampling. Pollen samples were generally obtained every 1–4 cm with 1–2 cm in thickness. Samples for pollen in LT1, and those below 496 cm in LT2, were all sterile, although they occasionally contained a few fungal spores. The present study is based on the 495.5-cm depth section of LT2, including 147 polleniferous samples.

The chronological framework of LT2 is based on fourteen AMS radiocarbon dates performed on bulk sediment (Table 1). Raw AMS radiocarbon results were calibrated using the IntCal20 calibration curve (Reimer et al., 2020). The age-depth model was estimated following a Bayesian statistical approach using the R package rBacon 3.0.0 (Blaauw and Christen, 2022) (Fig. 6).

In the laboratory, the extraction of microfossils followed the conventional method of HCl, HF and KOH digestion and mineral separation with a heavy liquid density of 1.9 g/cm^{3}l, using $ZnCl_2$ (Moore et al., 1991) modified according to Carrión et al. (2008). Exotic *Lycopodium clavatum* tablets of a known concentration of spores (c. 12,542) were added to each sample at the beginning of the treatment to estimate pollen concentrations. After chemical and physical treatment, pollen identification and counting were carried out under a transmitted light microscope by comparison with the reference collection of the Laboratory of Palynology at the UMU. Occasionally, the identification of pollen types was aided by the Pollen Atlas of Western Andalusia (Valdés et al., 1987) and the study samples of pollen rain in the Alcornocales Natural Park (Gutiérrez, 2008). *Pinus pinaster* was palynologically distinguished from other pine palynotypes based on Carrión et al. (2000b). Three oak groups were palynologically distinguished according to the criteria detailed in Carrión et al. (2000a). This discrimination is illustrated in Reille's (1992) pollen atlas and mainly follows the work by Planchais (1962). The presence of an indeterminate *Quercus* pollen category in Los Tollos is due to the observation of transitional palynomorphs whose assignation to deciduous, evergreen, or cork oak palynotypes was uncertain. However, most doubtful pollen grains could rather fall into the cork oak and deciduous oak categories, so their curves might represent a

Table 1
Radiocarbon dates and relative mean calibrated ages used in the pollen diagrams of Los Tollos Lake, southern Spain.

Ref. Lab.	Depth cm	AMS ^{14}C age yr BP	AMS ^{14}C error	Mean age cal. yr BP
Poz-23,238	1	5	25	124
Poz-38,281	11	730	35	665
Poz-38,285	40	2465	35	2548
Poz-38,289	84	4885	35	5615
Poz-38,319	152	8990	60	9478
Poz-38,282	240	9890	60	11,332
Poz-23,239	291	10,070	50	12,277
Poz-38,320	299	10,370	70	12,499
Poz-38,321	332	19,150	150	22,878
Poz-38,286	367	21,350	230	26,019
Poz-38,287	388	27,940	240	31,675
Poz-28,038	434	32,890	360	36,764
Poz-38,242	458	33,390	340	38,341
Poz-23,240	494	35,200	600	40,834

conservative estimate of the past occurrence in the study area. Identification of non-pollen palynomorphs (NPPs) and counting charcoal particles higher than 10 μm were also carried out. In the case of NPPs, their identification was aided by the descriptions and microphotographs of van Geel et al. (1981, 1986, 1989) and Carrión and van Geel (1999), and the UMU's pollen collection.

A total of 100,543 palynomorphs were identified, 69,806 pollen grains and 30,737 spores were counted, excluding those not identified. Palynological results are expressed in relative percentages. Charcoal counts are expressed in concentration, calculated with reference to the *Lycopodium* counts. Along with cryptogam spores and NPPs, we excluded the pollen grains of Amaranthaceae, Asteroideae, and Cichorioideae from the total pollen sum because it is assumed that these pollen groups are overrepresented locally (Gutiérrez, 2008; Val-Peón et al., 2023a). The number of pollen types per sample varies between 17 and 64, with a total of 105 taxa being recognized. The counting of pollen, spores and NPPs was carried out until reaching a Pollen Base Sum (total of pollen grains, excluding the spores and NPPs) between 209 and 774 pollen grains per sample.

Pollen diagrams were plotted using *psimpoll.4.27* palaeoecological analysis program (Bennett, 2008) (Figs. 7–13). Constrained Cluster Analysis by Sum Squares (CONISS) was performed to identify the number of statistically significant pollen assemblage zones (hereinafter "zones"), using a dissimilarity matrix of Euclidean distances and involving all terrestrial pollen taxa. Six different pollen zones (LTP) were identified and numbered from the base upwards (Figs. 7–13). The pollen zone LTP1 is represented by 37 samples dated between c. 41,006–36,523 cal yr BP. The pollen zone LTP2 is formed by 12 samples dated between c. 36,523–32,009 cal yr BP. The pollen zone LTP3 is composed by 23 samples dated between c. 32,009–19,260 cal yr BP. The pollen zone LTP4 is represented by 16 samples dated between c. 19,260–12,276 cal yr BP. The pollen zone LTP5 consists of 38 samples dated between c. 12,276–5770 cal yr BP. The pollen zone LTP6 is composed of 20 samples dated between c. 5770–124 cal yr BP.

Principal Component Analyses (PCAs) were performed to summarize major patterns in palynological data and explore relationships between taxa (Figs. 14, 15). PCA was carried out on terrestrial pollen taxa with a maximum abundance higher than 2% and at least 10 occurrences in the dataset. Pollen percentages were first square root transformed to reduce the influence of dominant species. Microcharcoal concentration and selected NPPs were added passively to the analysis as supplementary variables and projected on the ordination plot using the R package "FactoMineR ver. 2.6" and "FactoExtra ver. 1.0.7". Pollen zones were added as qualitative supplementary variables and visualized in the scatter diagrams (Figs. 14, 15).

5. Palynological stratigraphy

5.1. Pollen zone LTP1 (41–36.5 cal kyr BP)

The pollen spectra from this zone are dominated by "arboreal" pollen (AP: woody component), which occasionally exceeds 70% (Figs. 7–13), with pine and oak pollen being the main contributors. *Pinus* is markedly fluctuating (17–44%), and there is indication of a continuous presence

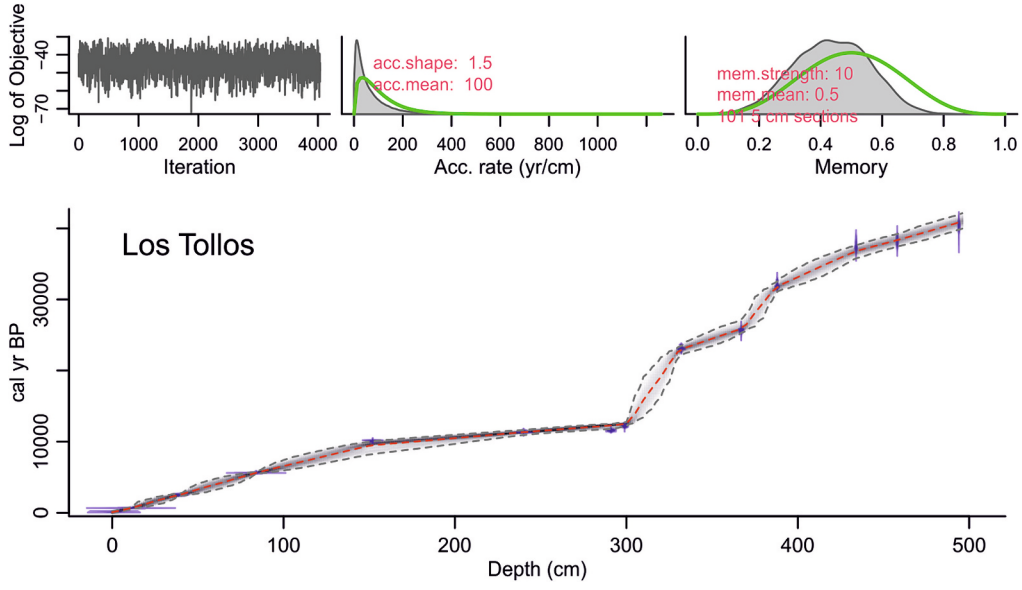


Fig. 6. Age-depth model of LT2 estimated following a Bayesian statistical approach using the R package rBacon 3.0.0 (Blaauw and Christen, 2022).

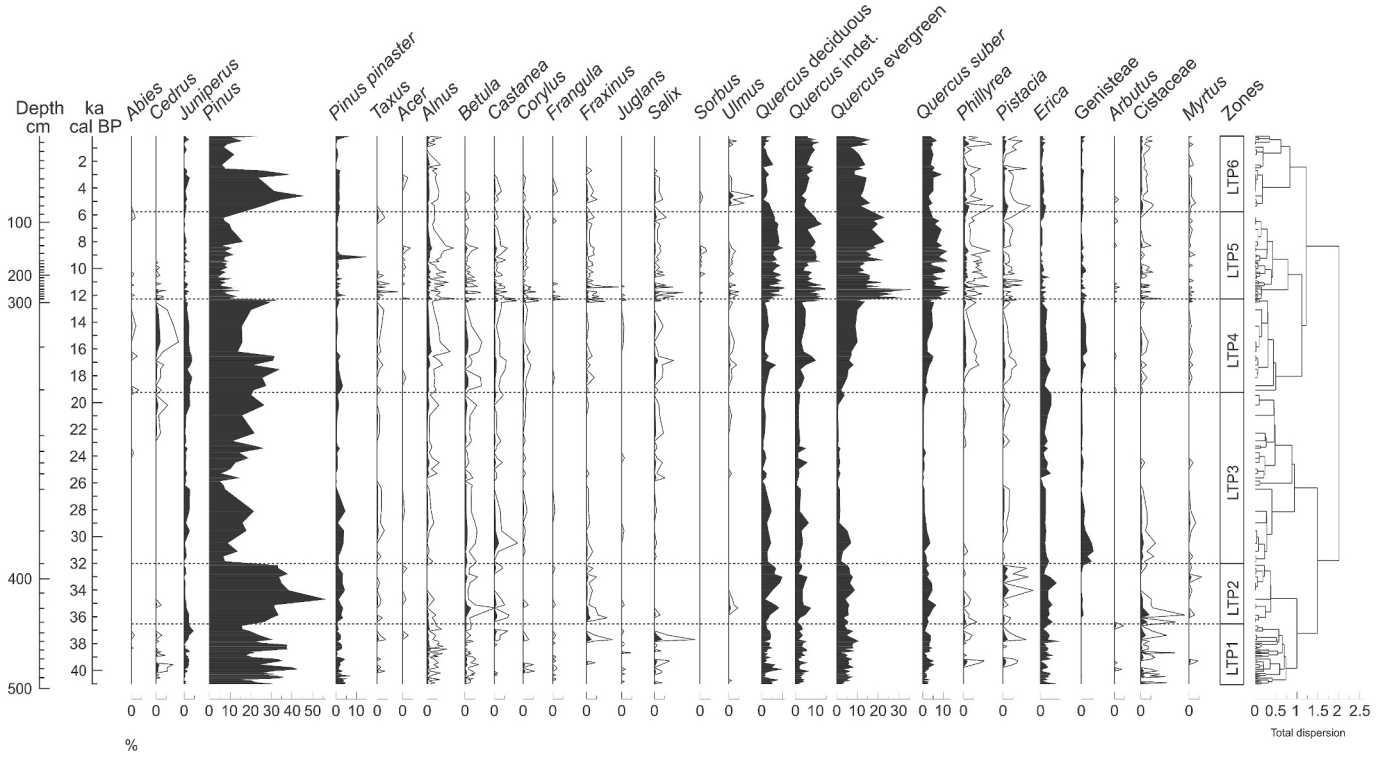


Fig. 7. LT pollen diagram (i). Trees and shrubs.

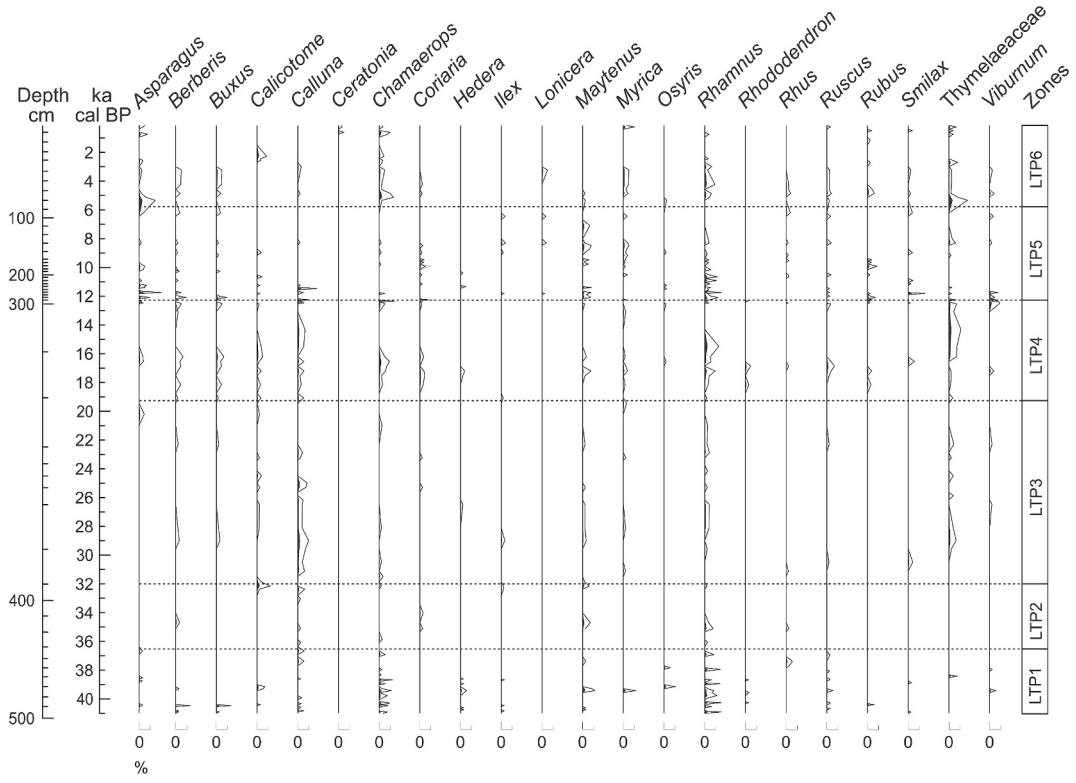


Fig. 8. LT pollen diagram (ii). Additional shrubs).

of *Pinus pinaster* (1–5%). Pine pollen oscillates inversely to the sum of xerophytes. *Quercus* frequencies are between 6 and 22%, with evergreen *Quercus* between 2 and 11%, deciduous *Quercus* exceeding 10%, and *Quercus suber* reaching 6%. Indeterminate *Quercus* pollen grains range between 1 and 7%. Total *Quercus* show maxima at c. 41, 40, and 37.2–38.3 cal kyr BP. *Erica* (1–9%) and *Juniperus* (below 5%) show continuous curves. The occurrence of *Cedrus*, *Alnus*, *Betula*, *Fraxinus*, *Salix*, *Phillyrea*, *Pistacia*, Cistaceae, *Rhamnus*, *Olea*, *Ephedra distachya-*

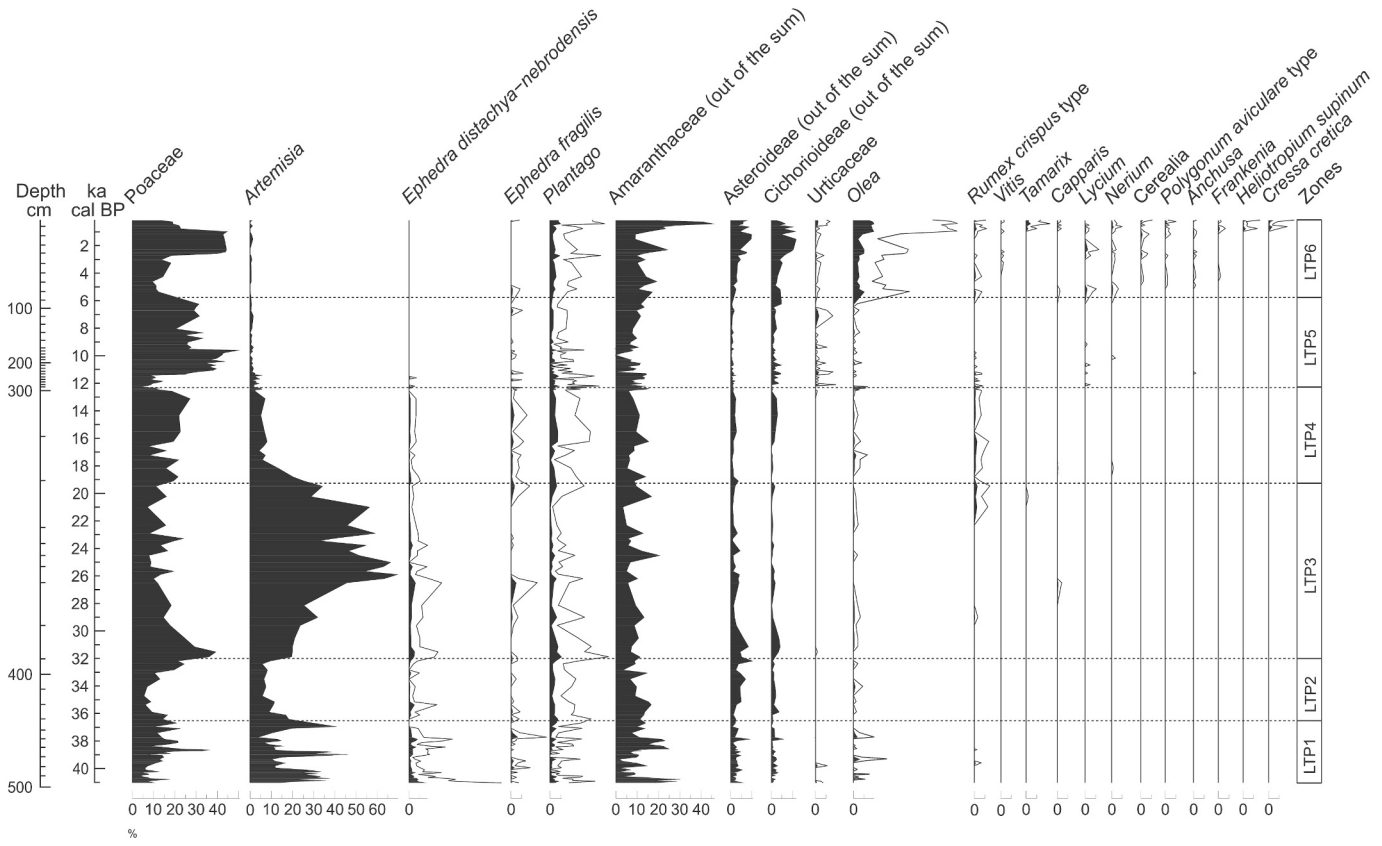


Fig. 9. LT pollen diagram (iii). Mainly herbaceous taxa, and indicators of human activities).

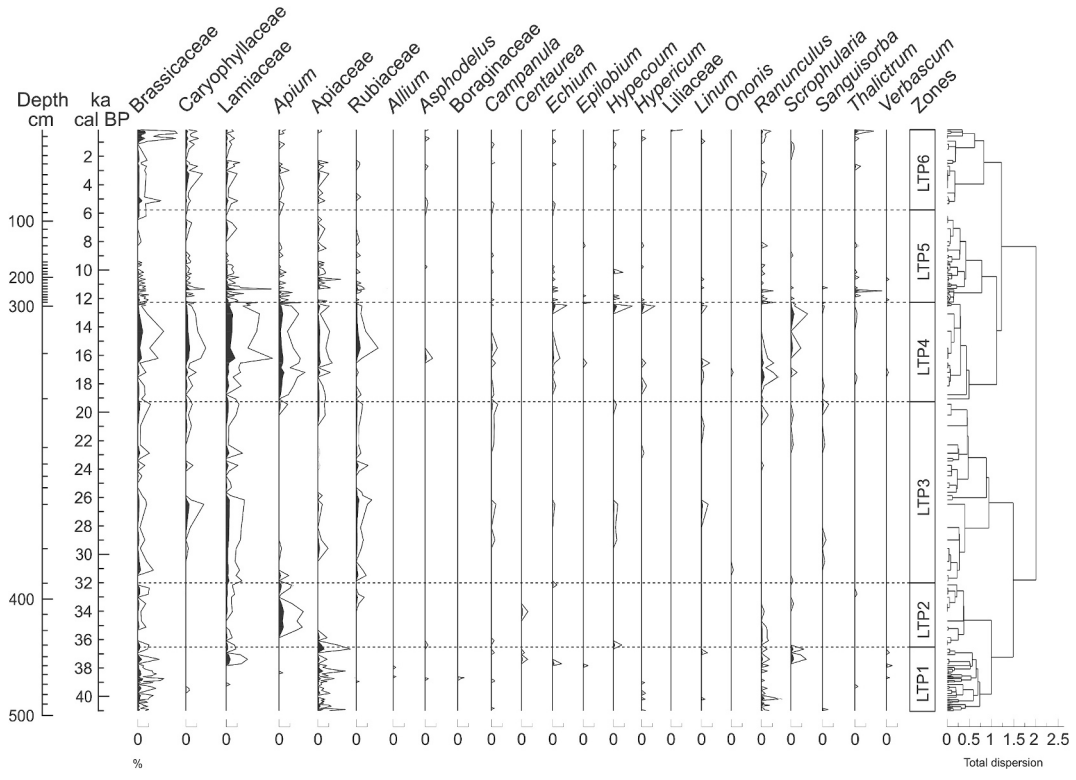


Fig. 10. LT pollen diagram (iv). Additional herbs).

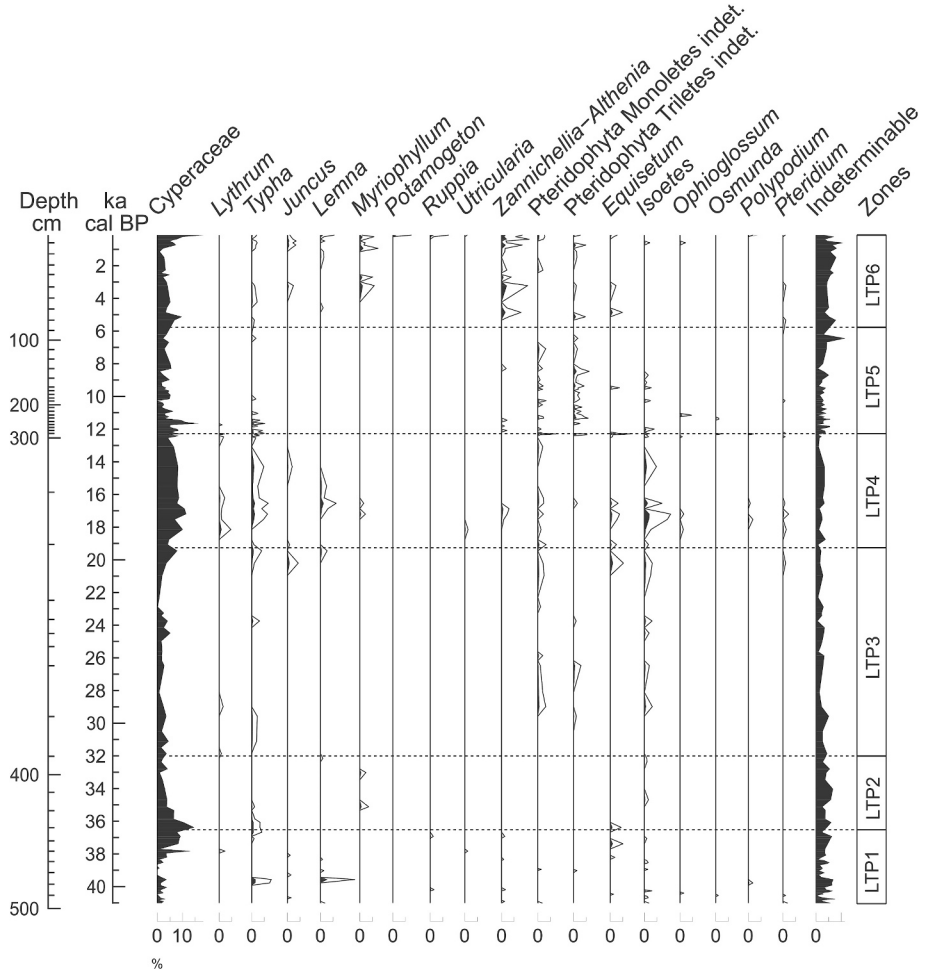


Fig. 11. LT pollen diagram (v). Hygrophytes and hydrophytes, and pteridophytes).

nebrodensis, Ephedra fragilis, Taxus, *Castanea*, *Corylus*, *Frangula*, *Arbutus*, *Myrtus, Ruscus*, *Calluna*, *Chamaerops* and *Maytenus* is noticeable. Other ecologically meaningful taxa with minor frequencies include *Abies, Acer, Juglans, Ulmus, Berberis, Buxus, Calicotome, Hedera, Ilex, Myrica, Osyris, Rhododendron, Rhus, Rubus, Smilax, Viburnum*, and Thymelaeaceae (Figs. 7, 8). Concerning non-arboreal pollen (NAP), it is worth mentioning the abundance of *Artemisia* (4–46%), Poaceae (4–37%), Amaranthaceae (2–30%) and Cyperaceae (1–13%) (Figs. 9, 10). *Artemisia* sharply fluctuates throughout this zone with three maxima at c. 40.6, 38.9, and 36.9 cal kyr BP, which coincide with oak declines. Two *Artemisia* minima at c. 39.2 and 38.2–37.7 cal kyr BP parallel increases in *Pistacia*, *Phillyrea,* total Mediterranean taxa, and sum of thermophytes (Fig. 15). Asteroideae, Cichorioideae, *Plantago*, Brassicaceae, Lamiaceae, Apiaceae, *Ranunculus*, *Typha* and *Lemna* are also frequent. Non-pollen microfossils are represented by a large number of fungal palynomorphs, reaching out-of-total frequencies close to 82% (Fig. 12). Other fungi sum up to 68%. Type 128 values fluctuate between 2% and 33%, and Type 122 occurs in one sample. The presence of *Spirogyra* (3–56%) is significant. *Glomus*, *Botryococcus*, Sordariaceae and *Zygnema* are also relatively high. The algal spectrum is also characterized by the presence of *Chara* gyrogonite fragments, *Debarya, Gloeotrichia,* and *Rivularia* (Fig. 12). Charcoal concentration is low except for the uppermost samples, which date to c. 38 cal kyr BP (Fig. 13).

5.2. Pollen zone LTP2 (36.5–32 cal kyr BP)

More continuously than in the preceding zone, AP dominates the assemblage, with total values higher than 80% (Figs. 7, 8, 13). The most remarkable feature of this zone is the increase of *Pinus* with percentages around 27–56%. *Pinus* sequence's maximum is reached at c. 34.7 cal kyr BP. *Pinus pinaster* ranges between 1 and 4%. Deciduous (2–10%) and evergreen *Quercus* (3–9%) remain frequent. Indeterminate *Quercus* reaches 7% and *Quercus suber* exceeds 6%. Total *Quercus* (11–27%) is slightly higher than in zone LTP1, with two-zone peaks at c. 35.3 and 33–34 ky BP. Total *Pinus* and *Quercus* show antagonistic fluctuations within this predominantly arboreal stage (Fig. 13). *Juniperus* consistently exceeds 2% and the occurrence of *Erica* (2–8%) is significant. Accompanying AP types include *Taxus*, *Alnus*, *Betula*, *Castanea*, *Fraxinus*, *Phillyrea*, *Pistacia*, Genisteae, Cistaceae, *Myrtus,* and *Olea*. The presence of *Cedrus*, *Acer*, *Corylus*, *Juglans*, *Salix*, *Ulmus*, *Calluna*, *Maytenus*, *Rhamnus*, *Ephedra distachya-nebrodensis* and *Ephedra fragilis* is also noteworthy (Figs. 7–9). Several woody taxa occurring in the former zone are absent in LTP2 such as *Abies, Arbutus, Asparagus, Calicotome, Buxus, Hedera, Myrica, Osyris, Rhododendron, Ruscus, Rubus, Smilax,* Thymelaeaceae, and *Viburnum*. In NAP, the abundance of Poaceae (6–25%), *Artemisia* (6–18%), Amaranthaceae (4–17%), Cyperaceae (1–15%) and *Plantago* (1–4%) are worth mentioning, although in the cases of *Artemisia*, Poaceae, and *Ephedra*, there are sharped declines respecting LTP1 (Figs. 9–11). *Artemisia* is particularly decreasing between c. 34.8 and 32.4 cal kyr BP, again correlating *Pistacia* increases. Indeed, the total xerophytic component is visibly depleted in this interval (Fig. 13). Asteroideae, Cichorioideae, Brassicaceae, Lamiaceae, *Apium*, Apiaceae, Rubiaceae, *Ranunculus*, *Typha* and *Myriophyllum*, are also noticeable, although Apiaceae, Brassicaceae, and Ranunculaceae show lower incidences (Figs. 9–11). There is a lower number of pteridophyte, aquatic and marginal angiosperm types, with *Epilobium, Lythrum, Juncus,*

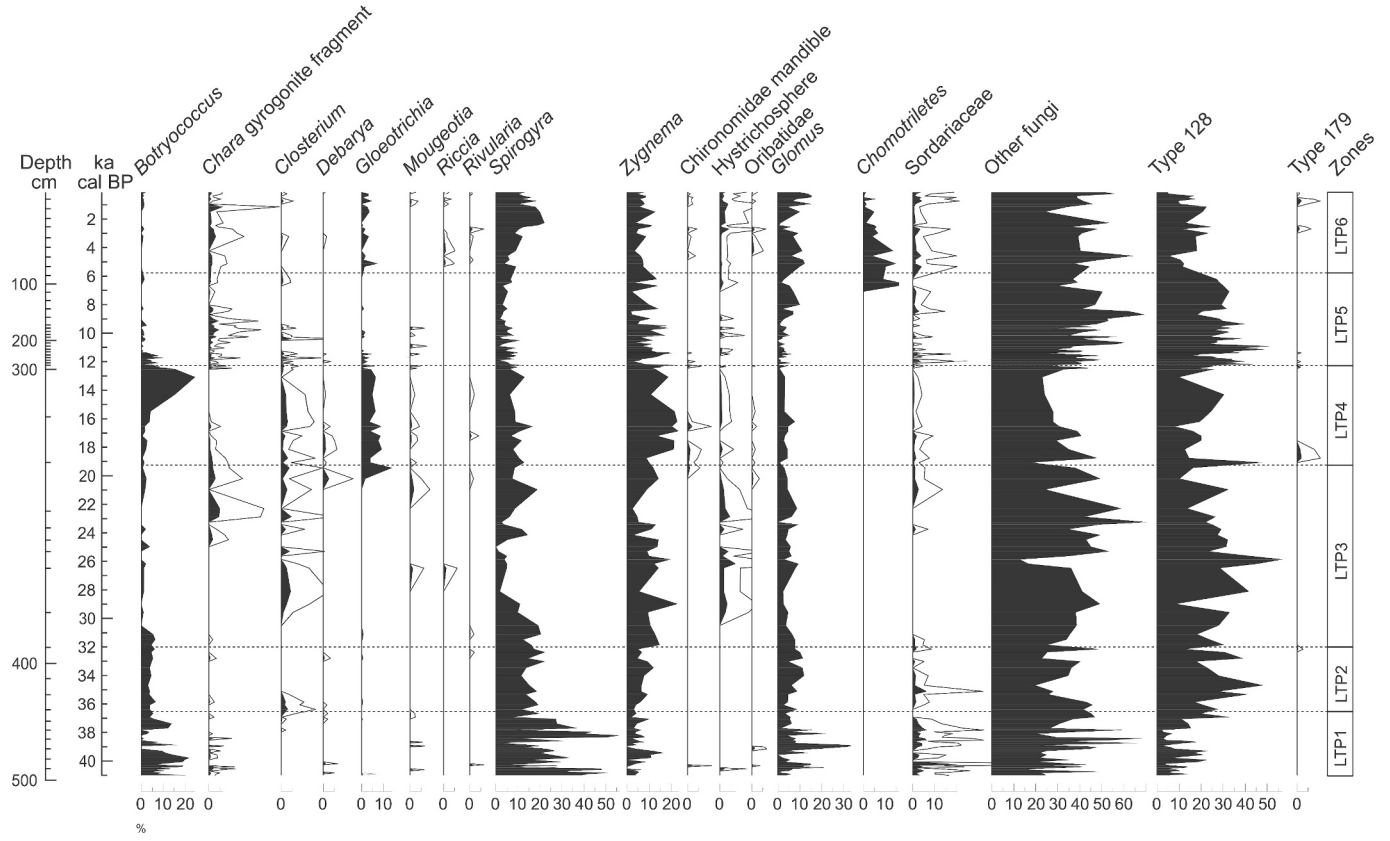


Fig. 12. LT pollen diagram (vi). Algal and fungal spores, and other NPPs).

Potamogeton, Ruppia, Utricularia, Zannichellia-Althenia, Pteridophyta, *Equisetum, Ophioglossum, Osmunda, Polypodium*, and *Pteridium* being absent in this zone (Figs. 10, 11). Fungal spores remain abundant, with percentages (out of the pollen sum) between 27 and 58% (Fig. 12). Type 128 increases noticeably to a peak of 48%. *Spirogyra* (12–22%) and *Botryococcus* (3–7%) decrease, while *Mougeotia* is absent from the zygospore record. *Zygnema* is slightly more frequent (3–12%), and *Glomus* decreases (3–12%). *Chara*, *Closterium*, *Debarya* and Sordariaceae frequencies are generally similar to the LTP1 zone (Fig. 12). Charcoal particles, although fluctuating in concentration, increase with respect to the LTP1 zone (Fig. 13).

5.3. Pollen zone LTP3 (32–19.2 cal kyr BP)

The AP shows average values close to 50% (Figs. 7, 13), but with a marked reduction (c. 10%) around 26 ka, coinciding with the lowest sequence pollen percentages of *Pinus* (5–27%) and *Quercus* (2–19%). The oak declines involve deciduous (1–7%), evergreen oaks (1–5%), cork oak (c. 3%), and indeterminate *Quercus* (6%). Total oak minima are recorded at between c. 28 and 19 cal kyr BP, with maximum depletion at c. 26 cal kyr BP. *Juniperus* ranges between 1 and 3%. Despite the lowering of trees, the diversity of woody types is still relatively high in this zone, including continuous occurrences of *Taxus, Acer*, *Alnus*, *Betula*, *Castanea, Corylus, Frangula*, *Fraxinus*, *Salix, Juglans, Ulmus, Phillyrea*, *Pistacia*, Cistaceae, *Myrtus, Buxus, Calicotome, Calluna, Chamaerops, Coriaria, Maytenus, Myrica, Rhamnus, Ruscus, Viburnum*, *Olea*, *Ephedra distachya-nebrodensis* and *Ephedra fragilis*. Several mesothermophilous tree taxa are however less frequent than formerly such as *Pinus pinaster, Fraxinus, Phillyrea, Pistacia*, Cistaceae, and *Myrtus*. The absences of *Arbutus, Berberis, Osyris, Rhododendron, Rhus,* and *Rubus*, are also worth mentioning. The highest sequence levels of *Artemisia* (20–70%) are recorded in this zone, with maxima between c. 27 and 20 cal kyr BP, and sharp peaks at c. 25.8, 24.9, 22.8, and 20.9 cal kyr BP (Fig. 9). This spread of *Artemisia* coincides with xerophyte maxima and minimum values in the thermophytic, Mediterranean and marginal vegetation pollen groups (Fig. 13). The minima for *Phillyrea, Myrtus, Arbutus*, and Cistaceae between c. 26 and 19 cal kyr BP are particularly relevant. The zone LTP3 starts with a peak of Poaceae (39%), which subsequently decreases as *Artemisia* increases. Amaranthaceae, *Ephedra, Plantago*, Asteroideae, Cichorioideae, Brassicaceae, Lamiaceae, and Cyperaceae do not experience significant variation compared to LTP2. The xerophytes *Tamarix* and *Capparis* show their first occurrences in this pollen zone (Fig. 9). Similarly to the LTP2 zone, several local/basinal herbaceous angiosperms and ferns are largely absent such as *Allium, Asphodelus, Campanula, Epilobium, Thalictrum, Juncus, Lemna, Myriophyllum, Potamogeton, Ruppia, Utricularia, Zannichellia-Althenia, Equisetum, Ophioglossum, Osmunda, Polypodium*, and *Pteridium* (Figs. 9–11). Charcoal concentration also shows its lowest values (Fig. 13). It is noteworthy the abundance of fungal spores, with percentages higher than 70% (Fig. 12). Among NPPs, an outstanding *Botryococcus* decrease is worth mentioning, together with the general absence of *Gloeotrichia* which increases rapidly in the uppermost part of the zone. Similar trends are observed in *Debarya*, Chironomidae, and Sordariaceae. Other fungi (13–70%), Type 128 (8–57%), *Glomus* (1–9%), *Zygnema* (1–23%) and *Spirogyra* (1–20%) abound, although this last is less abundant than in the LTP2 zone, while *Closterium* reaches its maxima between c. 30 and 27 cal kyr BP (Fig. 12). This zone is also characterized by the continuous occurrence of hystrichospheres, which could suggest a change in palaeolacustrine conditions ever since c. 30 cal kyr BP (Fig. 12).

5.4. Pollen zone LTP4 (19.2–12.2 cal yr BP)

The zone LTP4 is again predominantly arboreal, with AP reaching percentages close to 77%, increased *Pinus* (14–34%) and evergreen *Quercus* (2–14%) (Figs. 7, 13). The xerophytic component clearly decreases, accompanied by a general increase in marginal vegetation.

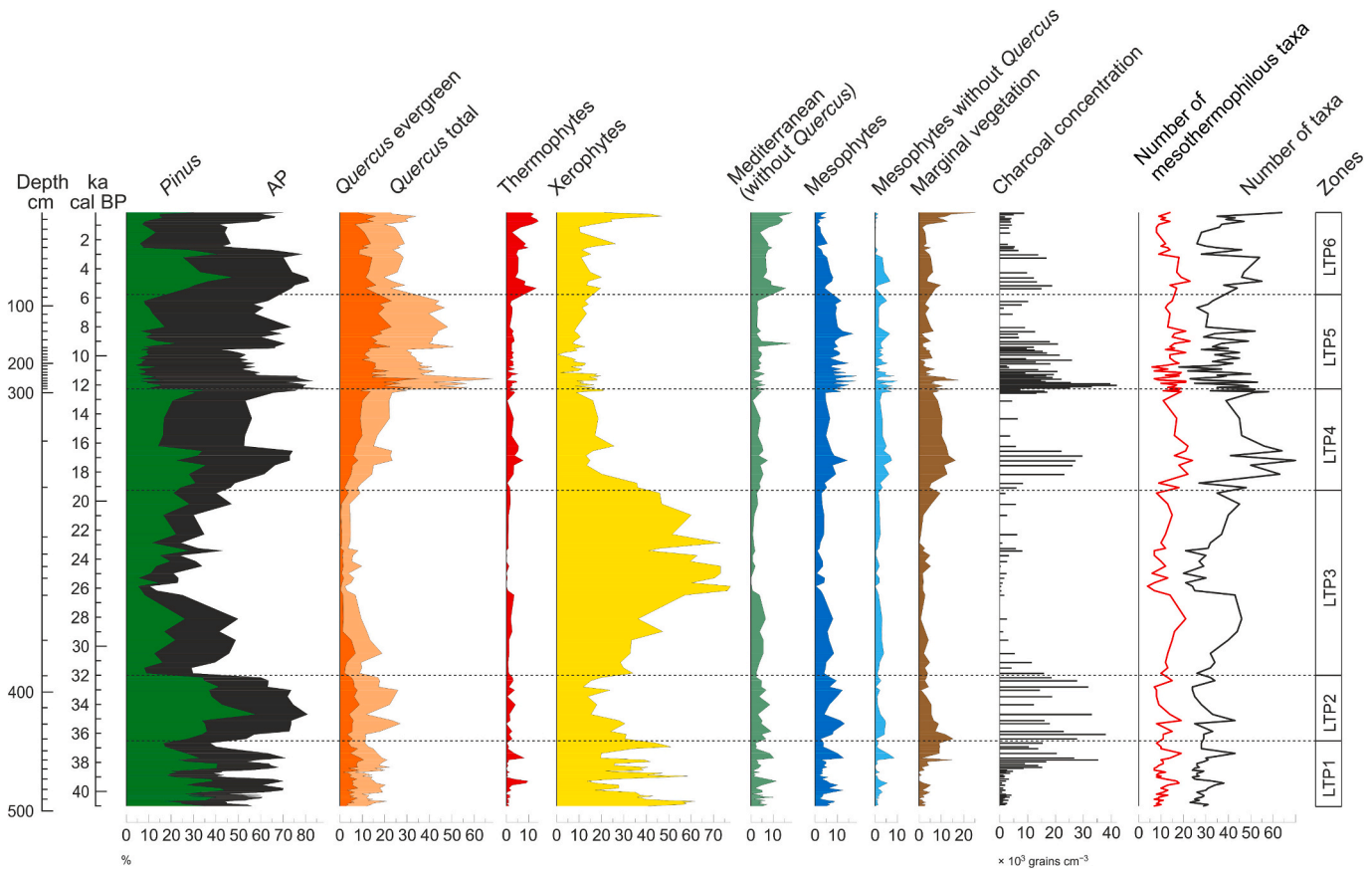


Fig. 13. Synthetic LT pollen diagram. "Thermophytes" include *Phillyrea, Olea, Pistacia, Myrtus, Chamaerops, Ruscus, Maytenus, Osyris, Calicotome, Smilax, Lycium, Tamarix*, and *Ephedra fragilis*. "Mediterranean component" includes evergreen *Quercus, Pinus pinaster, Arbutus, Phillyrea, Olea, Pistacia, Myrtus,* Cistaceae, *Lycium, Ephedra fragilis*, and *Ceratonia*. "Xerophytes" include *Artemisia*, Amaranthaceae, *Ephedra distachya-nebrodensis, Ephedra fragilis, Tamarix, Lycium, Nerium, Capparis*, and *Frankenia.* "Marginal vegetation" include *Cressa*, Cyperaceae, *Typha, Juncus, Apium, Epilobium, Lythrum, Ranunculus, Tamarix, Frankenia*, and *Heliotropium.* "Mesophytes" include *Acer, Alnus, Betula, Castanea, Corylus, Frangula, Fraxinus, Juglans, Salix, Sorbus, Ulmus, Coriaria, Hedera,* and *Ilex.*

Total *Quercus* is also higher and increasing upwards (8–34%). *Juniperus* continues to be around 3–4%. *Quercus suber* overcomes 6% and *Erica* reaches 5%. Accompanying AP include *Cedrus*, *Pinus pinaster*, *Alnus*, *Betula*, *Castanea*, *Corylus*, *Salix*, *Phillyrea*, *Pistacia*, Genisteae, *Ephedra fragilis*, *Olea* and to a lesser extent, *Abies*, *Taxus*, *Fraxinus*, *Ulmus*, Cistaceae, *Myrtus*, *Buxus*, *Calicotome*, *Calluna*, *Chamaerops, Coriaria, Hedera, Ilex, Maytenus, Osyris, Rhododendron, Rhus, Ruscus, Rubus, Smilax*, *Myrica, Viburnum*, *Rhamnus*, Thymelaeaceae and *Ephedra distachya-nebrodensis*. In NAP, it should be emphasized the abundance of Poaceae (8–27%), the decreasing trend of *Artemisia* (26–2%), as well as the continuous curves of Amaranthaceae, Asteraceae, Cyperaceae, *Plantago* and *Rumex crispus*. Other frequent herbaceous taxa include Brassicaceae, Caryophyllaceae, Lamiaceae, *Apium*, Apiaceae, Rubiaceae, *Campanula, Echium, Ranunculus*, *Scrophularia, Lythrum*, *Typha* and *Lemna* (Figs. 9–11). Several hygro-hydrophytes reappear such as *Juncus, Utricularia, Zannichellia-Althenia, Equisetum, Isoetes,* and *Ophioglossum* (Fig. 11). The Type 128 (8–48%) continues to be very abundant, together with other fungi (18–48%), *Zygnema* (9–23%) and *Spirogyra* (6–17%) (Fig. 12). *Gloeotrichia* shows maximum values. *Botryococcus* is again increasing with maxima (24%) at the end of this zone. Other relatively abundant NPPs are *Closterium, Debarya, Mougeotia, Rivularia*, Hystrichosphere, and Sordariaceae. The Type 179 is characteristic of this zone (Fig. 12). Charcoal shows a peak between c. 18 and 16 cal kyr BP (Fig. 13).

5.5. Pollen zone LTP5 (12,276–5770 cal yr BP)

The AP is predominant, reaching levels higher than 88% (Figs. 7–13). It is most remarkable the abundance of oak pollen, with maximum values at the onset of this zone (c. 12.5–11.4 cal kyr BP, and later on c. 9.3 cal kyr BP) in coincidence with the sequence's maximum of microcharcoal (Fig. 13). Evergreen *Quercus* (10–36%), *Quercus* indeterminate (4–15%), *Quercus suber* (4–14%) and deciduous *Quercus* (4–11%) are all abundant. Conversely, *Pinus* (4–16%) decreases. The amount of *Pinus pinaster* (1–15%) is however noteworthy, reaching its maximum of the sequence in this zone. Several woody taxa show slight increases: *Taxus*, *Alnus, Acer, Betula*, *Castanea*, *Corylus, Frangula*, *Fraxinus*, *Salix, Sorbus*, *Ulmus*, *Phillyrea*, *Pistacia, Arbutus*, *Myrtus, Asparagus, Berberis, Coriaria, Maytenus, Myrica, Rhamnus*, *Olea, Rubus,* and *Smilax*. *Lycium* occurs for the first time (Figs. 7 and 8). Poaceae increases (4–50%), *Artemisia* declines substantially, *Ephedra fragilis* is now discontinuous and *Ephedra distachya-nebrodensis* disappears from the pollen record. Amaranthaceae does not show relevant variation. *Plantago*, Asteroideae, Cichorioideae, Urticaceae, Brassicaceae, Caryophyllaceae, Lamiaceae, *Apium*, *Thalictrum* and *Typha* show frequent appearances (Figs. 9–11). Urticaceae pollen and fern spores occur continuously. Fungal spores are abundant in this zone (Other fungi maximum 69%). Type 128 ranges from 16 to 51%. Although decreasing, *Zygnema* (2–22%) and *Spirogyra* (1–11%) are still noticeable. *Botryococcus* and *Gloeotrichia* decline and become occasional, while charophyte gyrogonite remains increase, and *Rivularia* disappear. *Chomotriletes* (formerly *Pseudoschizaea*, but see: van de Schootbrugge et al., 2024) appears and abruptly increases from c. 7 cal kyr BP (Fig. 12).

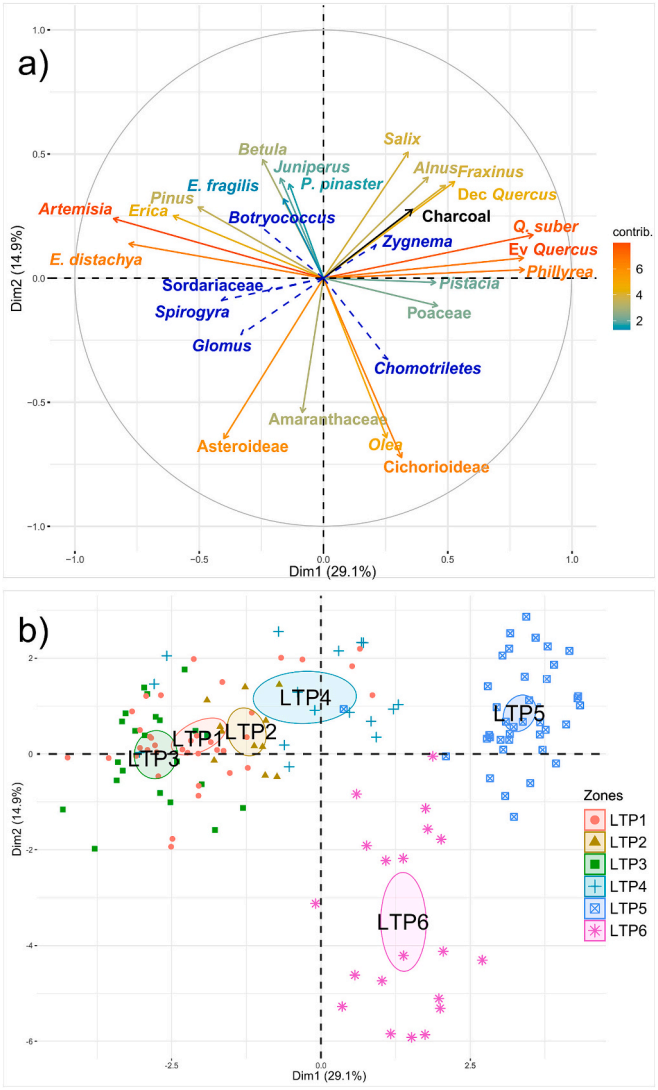


Fig. 14. Principal Component Analysis (PCA) of pollen data from Los Tollos. (a) Correlation plot of pollen taxa. (b) Scatterplot of observations and relative pollen zones.

5.6. Pollen zone LTP6 (5770–124 cal yr BP)

AP dominates the pollen assemblages, with total values higher than 81% (Figs. 7, 8 and 13). The most remarkable feature of this zone is the abundance of *Pinus*, with percentages up to 46%, while *Pinus pinaster* type ranges between 1 and 7%. Evergreen *Quercus* (7–16%) is also abundant with other oak pollen types: *Quercus suber* reaches 9%, and deciduous *Quercus* exceeds 5%. *Juniperus* does not exceed 3%, and *Olea* (2–10%) occurrence is particularly significant. Other woody pollen types include *Alnus*, *Ulmus*, *Phillyrea*, *Pistacia*, *Erica*, Genisteae, Cistaceae, *Myrtus*, *Asparagus*, *Chamaerops*, *Rhamnus* and Thymelaeaceae (Figs. 7 and 8). The presence of *Acer*, *Betula*, *Castanea*, *Fraxinus*, *Salix*, *Ulmus*, *Buxus* and *Myrica* is noteworthy. Several tree taxa disappear from the pollen record at the end of this zone, generally after 5–4 ka, such as *Abies, Acer, Betula, Castanea, Sorbus, Arbutus, Buxus, Rhus* and *Ruscus*. Other taxa are thoroughly absent in LTP6 such as *Juglans, Taxus, Berberis, Hedera, Ilex,* and *Rhododendron*. Among NAP, Poaceae (10–45%), Amaranthaceae (9–46%), and Cyperaceae (1–18%) are outstanding (Figs. 9, 10). *Plantago* (1–5%) is continuously present. Asteroideae, Cichorioideae, Urticaceae, *Rumex crispus*, *Tamarix*, *Lycium*, *Nerium, Vitis,* Cerealia, *Polygonum aviculare, Capparis, Anchusa, Frankenia, Heliotropium supinum, Cressa cretica,* Brassicaceae, Caryophyllaceae, Lamiaceae, *Apium*, Apiaceae, *Myriophyllum* and *Zannichellia-Althenia* are also worth mentioning (Fig. 11). As in former pollen zones, fungal spores, Type 128, *Glomus, Spirogyra* (4–22%), and *Zygnema* (3–13%), are abundant NPPs. The euglenophyte *Chomotriletes* (upto 15%) continues to be frequent although showing a decreasing tendency (Fig. 12). The frequencies of *Botryoccocus, Closterium, Debarya,* and *Mougeotia* are comparatively low. The occurrences of *Riccia,* and *Type 179* are noticeable (Fig. 12). Charcoal concentration decreases after c. 3 cal kyr BP (Fig. 13).

6. Ordination analysis and paleotrends

The two axes of the PCA biplot account for 44% of the data variability (Fig. 14a). The first axis displays a clear climatic gradient, with low scores reflecting boreal steppe and cold taxa like *Artemisia*, *Ephedra*, *Pinus*, *Juniperus*, and *Betula*, and high scores reflecting temperate and mesothermophilous taxa like *Fraxinus*, *Pistacia, Olea, Phillyrea,* and *Quercus.* In the second axis, low scores correspond to herbaceous and anthropic taxa such as Amaranthaceae, Cichorioideae, Asteroideae, and Poaceae, together with *Olea,* which represents the unique arboreal taxon in the lower half of the factorial plan. Apart from this exception, all the rest of the arboreal taxa correspond to high axis 2 scores, while *Artemisia* is the only herbaceous taxon in the upper half of the diagram.

The distribution of pollen zones in the corresponding PCA biplot reveals distinct assemblages, with a clear divergence from zones LTP1 to LTP4, located in the left sector of the factorial space, to zones LTP5 and LTP6, located in the right sector of the plan (Fig. 14b). This pattern reflects the transition from Pleistocene to Holocene, coinciding with the maximum development of a mesothermophilous forest vegetation in zone LTP4 culminating in zone LTP5. The following zone, LTP6, shifts to the bottom-right sector of the diagram, which is mainly characterized by *Olea* and anthropogenic indicators, suggesting a change in the natural vegetation during the last 6000 years, when also the human impact increased. Passive plotting of the supplementary variables in the ordination plot allowed us to visually assess an overall positive correlation between the microcharcoal concentration and the arboreal component in the pollen data, especially with temperate and Mediterranean forest taxa. This suggests a regional fire regime that is mainly driven by biomass availability, as also highlighted by the good correspondence of AP % and microcharcoal concentration profiles in the pollen diagram (Fig. 13). In the ordination plot, *Glomus* and *Chomotriletes* (ss. van de Schootbrugge et al., 2024) show a bottomward orientation, reflecting a negative correlation between runoff intensity and forest cover. In particular, *Chomotriletes* shows a similar orientation to *Olea* and Cichorioideae, suggesting enhanced runoff activity during the last few millennia, possibly in relation to increasing human activity in the region. As far as *Spirogyra* and *Botryococcus* are concerned, there is a left-oriented distribution in the biplot, perhaps suggesting mesotrophic conditions of the waterbody during the glacial stage. On the contrary, *Zygnema* is right-oriented in the diagram, which could be connected with eutrophication associated with increased forest colonization of the lake basin. However, since we do not know the species of Zygnemataceae involved, this observation must be regarded as purely speculative. The lack of a clear and compelling pattern for Sordariaceae in the biplot suggests that these fungi are more or less ubiquitous throughout the sequence. In the biplot, these largely coprophilous fungal spores seem to be more closely related to Pleistocene abundant taxa rather than Holocene emerging taxa, suggesting that their concentration is somewhat related to natural dynamics of faunal frequentation at the site (herbivory). Nonetheless, it is worth mentioning that although many Sordariaceae species are certainly coprophilous (van Geel et al., 1981), others are growing on decaying wood (Lundqvist, 1972).

A second PCA was carried out to highlight the relations between NPPs, aquatics, and some selected helophytic taxa (Fig. 15). The cumulative percentage of explained variance by the two principal components is relatively low (36.7%). In the biplot, the upper sector of the

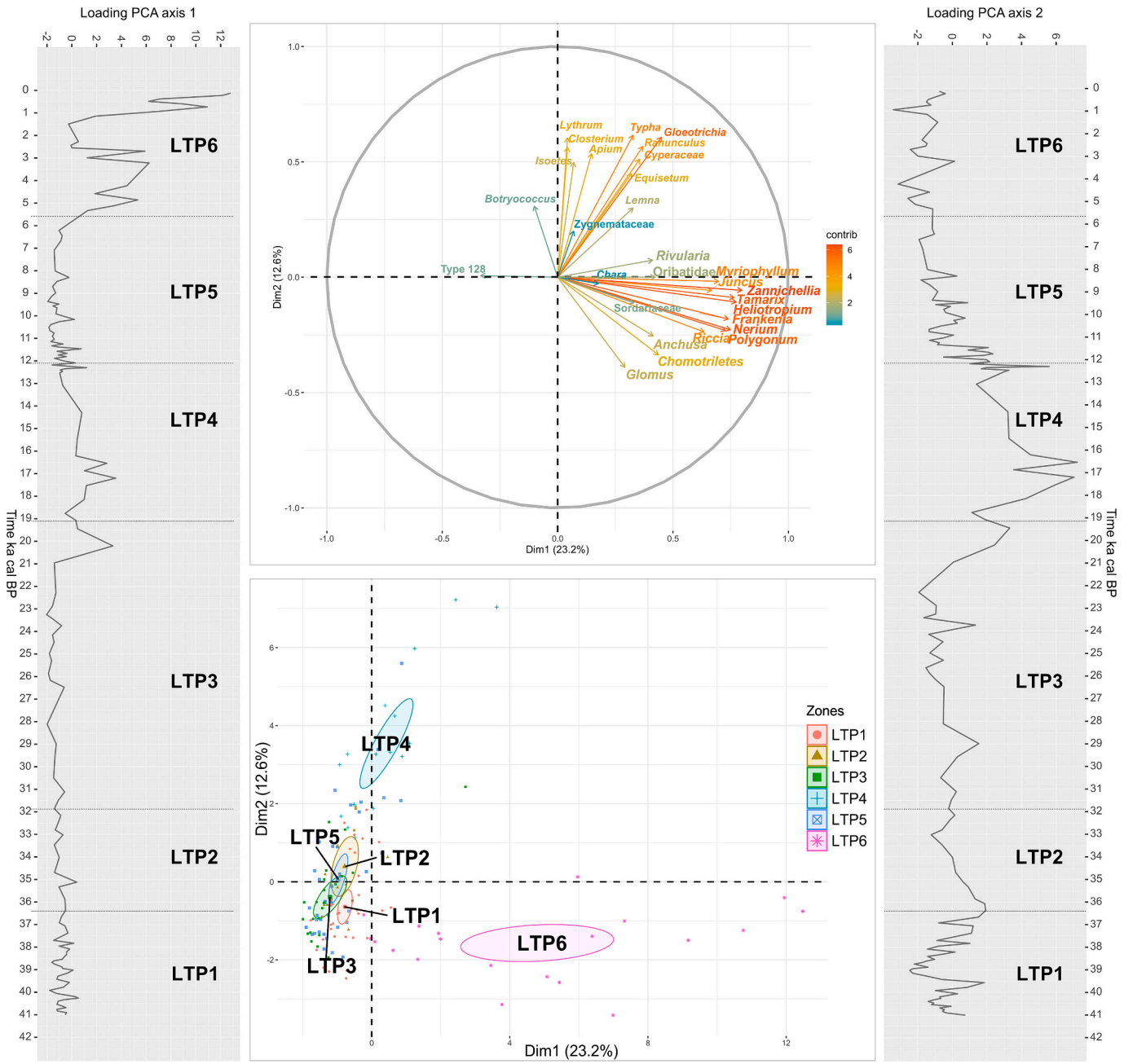


Fig. 15. Principal Components Analysis (PCA) of NPPs, aquatics, and helophytic taxa; (a) Correlation plot of selected taxa. (b) Scatterplot of observations and relative pollen zones. Loadings of Axis 1 and 2 are reported in left and right gray panels in relation to time.

factorial space is characterized by aquatics plants (*Lythrum, Ranunculus*, *Typha*, Cyperaceae, *Lemna*) and algae indicators of oligo- mesotrophic conditions (*Gloeotrichia*, *Closterium,* Zygnemataceae, *Botryococcus*), while the lower sector of the factorial space is characterized mainly by ruderal taxa (*Polygonum*, *Heliotropium*, *Anchusa*, *Frankenia*, *Tamarix*, *Nerium*), runoff indicators (*Glomus*, *Chomotriletes*), coprophilous fungi spores (Sordariaceae) and *Zannichellia.*

Despite the total amount of explained variance being relatively low, the analysis revealed some explicative patterns in the distribution of pollen zones in the scatter diagrams (Figs. 14 and 15). The observations of the zones LTP2, LTP3, and LTP5 show a more or less homogeneous characterization, resulting in a group on the left sector of the factorial space. This is likely due to the absence, or the low occurrence, of several taxa in these pollen zones. Zone LTP1 is predominantly represented by *Glomus* and *Spirogyra,* which indicate runoff, shallower water, and more eutrophic conditions. In contrast, the zone LTP4 zone is characterized by the presence of Zygnemataceae (*Mougeotia*, *Debarya*, *Zygnema*), suggesting more mesotrophic conditions, and *Gloeotrichia*, a nitrogen-fixing organism. This pioneer cyanobacteria could change the trophic status of the water providing suitable conditions for later hydroseral succession and development of aquatic plants (Cyperaceae, *Typha, Lythrum, Ranunculus, Lemna)*. The increase in *Gloeotrichia* is often recognized during the Late Glacial phase from multiple European sites (Van Geel et al., 1989; Van Geel, 2002; Carrión and Dupre, 1996; Carrión and Van Geel, 1999; Pini et al., 2010; Innes et al., 2021; Revelles, 2022; Muñoz Sobrino et al., 2013). In the LT record, this signal is evident in the higher PCA axis2 scores of the zone LTP4 and could represent a response of the aquatic ecosystem to a deglaciation pulse. Conversely, the LTP6 pollen zone shows increasing axis-1 and decreasing axis-2 scores (Fig. 14b). This trend reflects a greater influence of both *Glomus* and *Chomotriletes*,

suggesting enhanced runoff and soil erosion. The increasing importance of Sordariaceae, both with the concomitant shift towards ruderal taxa, reflects the rising influence of human activities during the Mid and Late Holocene. At the same time, the larger contribution of *Zannichellia* and *Spirogyra* to the LTP6 pollen zone points to shallower water with higher salinity and less oligotrophic conditions.

These palaeolimnological trends inferred from the ordination analysis agree with former studies. Overall, the picture inferred from pollen, spores and NPPs in LT corresponds to a lacustrine environment, fluctuating from more pelagic to shallow, and probably experiencing seasonal desiccation phases (Fig. 15). The abundance of Type 128, the continuity of *Isoetes, Closterium* and *Botryococcus* (especially during the Pleistocene) suggests oxygen-rich fresh water (Pals et al., 1980). In the Navarrés basin of eastern Spain (Carrión and van Geel, 1999), the Type 128 was associated with *Closterium* during dry, cold stages of the Upper Pleistocene. Its presence throughout the sequence suggests a higher ecological versatility for this aquatic microfossil. The continuous abundance of Zygnemataceae (*Zygnema* and *Spirogyra*, and to a lesser extent *Mougeotia*) spores suggests zones of meso- to eutrophic stagnant shallow open water. Increases in *Botryococcus* could indicate rises of the water table to more limnic conditions (Mateus, 1992; Carrión et al., 2001b; Carrión, 2002b) during glacial and late-glacial stages. *Chomotriletes*, occurring exclusively after c. 7 cal kyr BP, maybe, as suggested above, an indicator of seasonal desiccation and/or increased runoff. Cyperaceae generally suggests hygrophilous, temporary stagnant soils in lake margins. Its increases may, therefore, indicate advances in marginal vegetation, which are also supported by minor increases in *Typha*. Decomposing fungal activity is noticeable across the sequence, and there must have been probably higher in the marginal vegetation belts (van Geel et al., 1981, 1983, 1989; Carrión and van Geel, 1999; Carrión et al., 2001b).

After a comparison of the basinal modern vegetation with the palaeoecological record, it is clear that, ever since the Pleistocene to present-day, Cyperaceae (*Scirpus maritimus, S. lacustris*) and Amaranthaceae (*Salicornia ramosissima, Microcnemum coralloides, Suaeda splendens, S. albescens, S. spicata, S. vera, Halopeplis amplexicaulis, Sarcocornia perennis*) species must have been colonizing the basin and marginal areas when drought and salinity increased, while *Chara* thrived in the submerged zones. Likely, a large part of the Poaceae and Asteraceae curves (Fig. 9) correspond to in-situ grasses (*Phragmites australis, Hordeum marinum, Polypogon maritimus*) and composites (*Crypsis aculeata*). Concerning the present-day communities with *Cressa cretica, Heliotropium supinum, Frankenia laevis*, and *Tamarix* species, they are the result of a recent millennia assemblage (LTP6). *Ruppia drepanensis* has also expanded recently, while *Althenia orientalis* has done so over the past few thousand years.

7. Modern pollen rain

A palynological study on grass swards was carried out to shed light into the relationships between modern pollen rain and vegetation in the Alcornocales Natural Park of Cádiz (Gutiérrez, 2008) (Fig. 2). The transects under scrutiny, embracing the full spectrum of plant communities of the Natural Park and beyond within the Strait of Gibraltar, were located between c. 40 and 80 km southeastwards LT. In general, oak pollen spectra properly reflected the vegetation cover of the populations involved of *Q. canariensis, Q. suber, Q. ilex, Q. faginea, Q. lusitanica,* and *Q. coccifera*. Other taxa well balanced in their pollen rain-vegetation relationships included *Olea europaea, Salix pedicellata*, and *Corylus avellana* (Gutiérrez et al., 1997; Gutiérrez, 2008). Pines were well represented, largely over-represented with the distance. The most pertinent information from Gutiérrez (2008) in our study is that several ecologically significant fossil pollen taxa were remarkably under-represented in the modern pollen rain. Thus, their occurrences in LT must be taken as suggestive of higher abundances in the local past vegetation. The most striking cases affect *Rhododendron ponticum, Frangula alnus, Pistacia lentiscus, P. terebinthus, Myrtus communis, Chamaerops humilis, Ceratonia siliqua, Nerium oleander, Ruscus aculeatus, Smilax aspera, Tamus communis*, and to a lesser extent, *Arbutus unedo, Phillyrea angustifolia, P. latifolia, Daphne laureola, Ilex aquifolium, Rubus ulmifolius, Hedera helix*, and several species of *Genista, Halimium* and *Cistus* (Gutiérrez, 2008). Delving into this matter, it can not be discarded that some species absent from LT (e.g., *Laurus nobilis, Tamus communis*) were present in the region during the Quaternary since they also do not appear in the modern pollen rain, or if they do, only a few pollen grains are recorded, even when sampling occurs near their growth area. In general, the frequency of insect-pollinated scrub and tree pollen types decreases with distance to respective plant species populations (Carrión, 2002b; Gutiérrez, 2008). However the case of *Rhododendron* is worth stressing, because, even with high local cover, most of its pollen is missing in modern pollen rain samples. *Alnus glutinosa* pollen is also under-represented and only counted in proximity samples.

Modern pollen samples collected across a variety of habitats in SW Iberia were selected by Val-Peón et al. (2023a) to explore pollen-vegetation relationships by multivariate analysis. The lake surface samples from areas near mountain systems exhibit relatively high percentages of arboreal pollen (AP) compared to the rest of the studied samples, which show an underrepresentation of AP. In the case of LT, a representation indicative of various vegetation zones, including high-mountain pine forests, is observed (Val-Peón et al., 2023a).

8. Insights into paleobiogeography

Cedrus pollen in LT (Fig. 7) should be mostly a pollen contributor from cedar populations in northern Morocco, although the existence of *Cedrus atlantica* in southern Spain during the study period cannot be categorically discarded (see confronting views in Magri and Parra, 2002, and Jiménez-Moreno et al., 2020). González-Hernández et al. (2022) modeled the potential habitat of *Cedrus atlantica* and propose that it would have covered a significant portion of the high Iberian mountains during the Last Glacial Maximum (LGM). According to these researchers, the Holocene Thermal Optimum would have led to an upward shift in the species' altitude, resulting in isolated populations that eventually became extinct during the late Holocene. The interaction with *Pinus nigra* might have contributed to the loss of connectivity, leading to the exclusion of cedar populations from shared habitats in the Iberian territories. While this hypothesis is intriguing, it requires support from paleobotanical data, with macrorremains playing a crucial role.

Notwithstanding its low counts, the presence of *Abies* in LT (Fig. 7) is noteworthy because this taxon exhibits low dispersal capacity (Arista and Talavera, 1994). Today, several populations of the endemic *Abies pinsapo* are found eastwards of the core site in Sierra de Grazalema, Cádiz; Sierra de las Nieves and Sierra Bermeja, Málaga (Alba-Sánchez et al., 2010, 2018, 2020) (Fig. 2), constituting one of the most unique forest formations in the Iberian Peninsula. Pollen rain within oak-fir forests from these localities below 800 m is clearly dominated by oak pollen, while *Abies* shows extremely low percentages (Val-Peón et al., 2023a). It appears that the range of *Abies pinsapo* was more extensive in the Andalusian Pleistocene, as evidenced in Bajondillo (López-Sáez et al., 2007), Abrigo del Humo (Ochando et al., 2020a), and Boquete de Zafarraya (Lebreton et al., 2003); in all cases, these are territories where this species is absent today. A recent palynological study by Alba-Sánchez et al. (2023) in Cañada de Enmedio (Sierra de las Nieves, Málaga) shows the continuous presence of an *Abies pinsapo* forest (relatively high pollen frequencies) over the last eight centuries. However, this forest has progressively lost coverage due to shipbuilding, mining, charcoal production, extensive agriculture, tree crops, livestock farming, grazing, and reforestation processes with pines (Alba-Sánchez et al., 2023). *Abies* records in LT add to suggest a distribution of the Spanish fir westwards its current range. Another possibility is that the *Abies* populations were located in lower areas of the countryside north of LT, for example, in the southern sierras of the province of Seville, and

that *Abies* pollen was transported by the muds of the Guadalquivir River.

Here we also provide evidence supporting the native status of certain species, such as *Pinus pinaster* (Carrión et al., 2000b; López-Sáez et al., 2010) and *Juglans regia* (Carrión and Sánchez-Gómez, 1992), previously defended as indigenous to the Iberian Peninsula. The native status of *Pinus pinea* in the southwest of the Iberian Peninsula has been a subject of debate (Pérez Latorre et al., 1999) but the fossil record indicates its presence in Doñana and other southwestern Iberian sites since at least the Late Pleistocene (Stevenson and Harrison, 1992; Carrión et al., 2018b; Manzano et al., 2019). Cones, bracts, and seeds suggest this pine species' survival during the Upper Pleistocene's cold stages (Martínez and Montero, 2004; Badal et al., 2012). Similar findings indicate that *Pinus pinea* thrived around Cueva de los Murciélagos (Peña-Chocarro, 2007) and in Puerto de Santa María (López-Sáez et al., 2002a) during the Holocene. Charcoal evidence, including strobili and charred wood, confirms the local presence of *Pinus pinea* in Gorham's Cave (Carrión et al., 2008).

Another worth-mentioning ocurrence is *Maytenus senegalensis*, a Tertiary relict and threatened species common today in xerothermic coastal areas of Málaga, Almería and Murcia supposedly as a degradation stage of *Quercus rotundifolia* forests (Pérez Latorre et al., 2006). Despite its very low dispersal capacity (Carrión, 2002b), *Maytenus* pollen has been found relatively frequently during the late Quaternary in what is today semi-arid Spain (Carrión et al., 1995, 2003a, 2003b, 2018a; Ochando et al., 2020a). However, the presence of *Maytenus senegalensis* in LT adds to previous findings in Pleistocene Gibraltar (Carrión et al., 2008, 2018b) and mid-Holocene mesophytic optimum of Gádor (Carrión et al., 2003a). This allows us to suggest a different paleoecological affinity for the species, possibly as an understorey species of mixed oak forests.

9. The need for fresh continental pollen data

Few pollen records from the Iberian Peninsula span the late Pleistocene and the entire Holocene (e.g. Pons and Reille, 1988; Montserrat-Martí, 1992; Allen et al., 1996; Peñalba et al., 1997; Muñoz-Sobrino et al., 2004; González-Sampériz et al., 2006, 2017, 2020; Burjachs et al., 2007; López-Merino et al., 2012; Aranbarri et al., 2014; Camuera et al., 2019; Magri et al., 2017; Carrión et al., 2024b, 2004). In addition, many are fragmentary and/or obtained from archaeological records, exhibiting gaps and taphonomic biases (e.g. Lebreton et al., 2003; López-Sáez et al., 2007; Carrión et al., 2007b, 2008, 2018b; Ochando et al., 2020a). Records obtained from the continental shelf and the deep ocean off the Iberian Peninsula's coast (e.g. Sánchez-Goñi et al., 1999; Coussin et al., 2022) are not exempt from problems regarding the origin of pollen spectra. This is particularly the case given the difficulty in distinguishing between pollen originating from the African continent and that from southern Europe (Carrión et al., 2004). Other lagoonal and estuarine pollen records (López-Sáez et al., 2002a; Fernández et al., 2021; Val-Peón et al., 2021, 2023b; Mediavilla et al., 2023; Fletcher et al., 2007; Manzano et al., 2018, 2019), are not endorheic, sometimes adjacent to the Guadalquivir and Guadiana rivers, and therefore highly influenced by marine transgressions and river floods, which also imposes difficulties for discriminating the paleoecological signal from inland mountainous areas where presumably the tree populations refuged during the Pleistocene (climate change) and Holocene (human impact). Pedoanthracological studies on paleosols provide insights into the vegetation changes of relatively short periods, mostly recent periods (Gómez-Zotano et al., 2023; Pardo Martínez et al., 2023). An outstanding pollen record from fluvial terrace in the Portuguese Algarve, 10 km from Cadiz gulf, cover most of the Holocene (Fletcher et al., 2007). When considered collectively, all the aforementioned data is highly informative, but a long continental pollen sequence in the region, as presented here, was much needed.

10. The Great Pleistocene hotspot

The LT vegetation sequence replicates some general patterns observed hitherto in Mediterranean Iberia, including a fluctuating dominance of pines and heliophytes during the Pleistocene and late Holocene, and the continuous occurrence of angiosperm trees during the Pleistocene (Carrión et al., 2024a, 2024b, 2024c: https://www.paleofloraiberica.org/). However, LT represents an increase in the spectrum of reported disparities in vegetation dynamics of the Mediterranean Region. The first singularity is depicted by the magnitude of the pollen percentages to validate the existence of a glacial refugium of forests and mesothermophilous taxa in the south of the European continent. These comparatively high percentages and continuous occurrences of different groups of oaks, and other angiosperm trees are noticeable during full-glacial stages at LTP1-LTP4 (41–12.3 cal kyr BP), especially during LTP1 (c. 41–36 cal kyr BP) and LTP3 (c. 32–19 cal kyr BP), and probably reflect strongholds in adjacent mountains, although perhaps also on rivercourses, valleys, and coastal shelves. Total *Quercus* is mostly above 4%, reaching up to 18% during LTP3. Furthermore, LT pollen percentages suggest thermic refugia for *Olea, Pistacia, Chamaerops, Maytenus, Myrtus, Osyris, Ruscus* and *Myrica*. Other taxa (*Alnus, Corylus, Castanea, Juglans, Salix, Taxus, Fraxinus*) point to high groundwater levels or even relatively attenuated summer drought characteristic of Atlantic influence on the terrestrial ecosystems of the SW mountains and littoral (Sumner et al., 2001; Yanes and Moral, 2022). Several genera, such as *Pistacia*, reach striking pollen percentages at phases during full glacial LTP1 and LTP3.

Andalusian pollen sequences such as Padul, in a more continental territory near Sierra Nevada (Fig. 2a), show similar trends of oak variation during MIS 3 and MIS 2 between c. 60 and 14 cal kyr BP. Still, percentages of Mediterranean forest do not reach values above 2% (Camuera et al., 2018). The Siles pollen record, in the mid altitudes of the Segura Mountains, to the northeast of LT (Fig. 2a), shows total maximum oak percentages of about 5% during the zone SP1 (c. 20–12 cal kyr BP; Carrión, 2002a). In comparison, total *Quercus* amounts up to 35% in LT during LTP4 (Fig. 15). Regarding *Quercus suber*, the data presented here undoubtedly indicate that we are dealing with the primary glacial refuge in the Iberian Peninsula, as suggested by previous phylogeographical studies on this species (López de Heredia et al., 2007) and other woody taxa (e.g. *Laurus*) (Rodríguez-Sánchez and Arroyo, 2008).

In El Asperillo Cliff of Doñana, 69 km west of LT along the thermomediterranean Atlantic coast (Fig. 2b), pollen records from exposed sandy, peaty layers dated between c. 22 and 31 cal kyr BP showed oak values up to 10% (Fernández et al., 2021). Oaks included cork oak, and other evergreen and deciduous species. Pines were dominant and accompanied by other ecological indicators of mesothermic forests such as *Taxus, Salix, Populus, Alnus, Betula, Corylus, Ulmus, Castanea, Juglans, Myrica, Olea, Phillyrea,* and *Arbutus*. Macro-remains from the same stratigraphical units include *Alnus, Betula* and *Quercus* (Morales-Molino et al., 2011). In addition to *Pinus nigra* (Desprat et al., 2015), macrofossils of the Mediterranean pines *P. pinaster, P. halepensis, and P. pinea* are part of the Pleistocene macrofossil record of the SW (Carrión et al., 2008; Postigo-Mijarra et al., 2010b; Morales-Molino et al., 2011), together with *Juniperus phoenicea, Olea europaea, Quercus faginea, Q. ilex, Fraxinus, Ulmus, Salix, Populus, Sorbus domestica, Acer monspessulanum, Crataegus, Pistacia lentiscus, P terebinthus, Arbutus unedo, Prunus mahaleb, P avium, P spinosa, Rhamnus*, and *Sambucus nigra* (Ramos-Muñoz and Weniger, 2023). Still in Doñana, the organic layers from Mari López lagoon dated between approximately 50 and 30 cal kyr BP show relatively high values of *Quercus* and *Olea* pollen (Yll et al., 2003; Yáñez et al., 2006). Charcoal analysis in the Paleolithic of the Nerja Cave at Málaga, eastward from LT (Fig. 2a), showed evidence of *Pinus nigra* and *P. pinea* from 29.3 cal kyr BP onwards (Badal, 2001; Aura et al., 2002; Jordá Pardo and Aura Tortosa, 2008).

These data reinforce the inferences derived from other pollen and

charcoal analyses in archaeological sites and marine pollen sequences. Relevant terrestrial paleobotanical records include Abrigo 3 del Humo (Ochando et al., 2020a), Los Ardales (Ramos-Muñoz and Weniger, 2023), Bajondillo (López-Sáez et al., 2007), Gorham's (Carrión et al., 2008), Zafarraya (Lebreton et al., 2006), and Vanguard Caves (Carrión et al., 2018b). Relevant offshore records include, among others, IMAGES cores MD95–2043 (western Mediterranean Sea), MD95–2042 (off Portugal) (Sánchez-Goñi et al., 1999, 2002; Fletcher et al., 2010a, Cutmore et al., 2022), and 8057-B (Hooghiemstra et al., 1992).

In addition to the fossil plant data, the current floristic composition helps to depict long-term refugia in the Strait of Gibraltar area. Several species are of subtropical origin or Tertiary relics, such as *Rhododendron ponticum, Laurus nobilis, Myrica gale, Frangula alnus, Prunus lusitanica, Drosophyllum lusitanicum,* and *Culcita macrocarpa* (Ojeda et al., 1996; Arroyo-García et al., 2001; Mejías et al., 2007; Rodríguez-Sánchez and Arroyo, 2008; Postigo-Mijarra et al., 2009, 2010a; Verdú et al., 2020). Phylogeographic studies on some of these taxa corroborate this hypothesis and indicate that the Strait of Gibraltar may be considered a glacial refuge and a hotspot for Tertiary relicts (Arroyo-García et al., 2001; Guzmán and Vargas, 2009; Gil-López et al., 2017, 2022; Martín-Rodríguez et al., 2020). These data must also be contextualized within the framework of the extraordinary similarities between the current flora and vegetation of the study area (S Spain) and those of the northern African continent (Valdés, 1991; Galán de Mera et al., 2003; Lavergne et al., 2013). However, the phenomenology of the involved plant species is diverse, and their biogeographical interpretation is complex, which is probably related with their biological traits (Lavergne et al., 2013; Molina-Venegas et al., 2015), with a similar situation occurring in animal species (Mas-Peinado et al., 2022).

The concept of glacial refugia has been a subject of discussion, largely due to the difficulty in establishing the ecological characteristics of the refugia and their latitudinal structure (Tzedakis et al., 2002; Bennett and Provan, 2008; Svenning et al., 2008; Stewart et al., 2010; Nieto Feliner, 2011; Keppel et al., 2012). The situations in northern and southern Europe are undoubtedly very disparate, both in terms of paleoecology and inferences about genetics and evolutionary complexity (Behre and van der Knaap, 2023; Tinner et al., 2023). According to Rodríguez-Sánchez et al. (2008) the territories in the east and southeast of LT comprise a nested sub-hotspot within the S Iberian-N African Mediterranean hotspot for plant biodiversity. They provided a detailed account of the important relict flora, the high level of endemism, and the dominance of vegetation types that are unique to Europe. These singular habitats would have provided optimal conditions for the development of mesic forests and shrub formations with high biological diversity. They also explored the causes of this high biodiversity and found that a significant portion of the endemism stock is associated with riparian and humid habitats (hydro-refugia), which have remained more or less stable since at least the Neogene (Carrión et al., 2024a). Rodríguez-Sánchez et al. (2008) also analyzed the role of microevolutionary processes in generating sympatric speciation and concluded that the region is prone to changes in reproductive and regeneration systems associated with biotic and abiotic conditions. In this context, what we can conclude from the present work is that the extent of phytodiversity refuges in southwestern Iberia was greater than it is today. It should be noted that the current forests of the mountains located to the east and southwest of LT represent refuges over the past millennia against the aridifying pressure of climate and the deforestation and biodiversity reduction caused by human activity.

11. Strongholds in motion

11.1. Some notes on abrupt global climate changes

Another noteworthy aspect involves the responses of LT vegetation to Pleistocene climatic changes. During the last glacial period (MIS 4–2: 73.5–14.7 cal kyr BP), rapid climatic changes occurred multiple times (González-Sampériz et al., 2006; Capron et al., 2010; Sánchez Goñi et al., 2017; Steffensen et al., 2008). Among these, the Dansgaard-Oeschger (D-O) events stand out as sudden shifts in glacial climates, initially identified through records from Greenland ice cores (Dansgaard et al., 1984). In Greenland, these events are marked by temperature variations of up to 16 °C, often occurring within centuries, and sometimes even decades (Erhardt et al., 2019). The impact of D-O events extends globally, triggering interconnected changes in atmospheric, oceanic, and hydrological cycles. According to the guidelines of the INTIMATE (Integration of Ice Core, Marine, and Terrestrial records of the North Atlantic) working group (Rasmussen et al., 2014), the warm phase of D-O events is termed the Greenland Interstadial (GI), while the cold phase is referred to as the Greenland Stadial (GS). GIs are linked to an active state of the Atlantic Meridional Overturning Circulation (AMOC) (Böhm et al., 2015), characterized by increased heat transport into high-latitude oceans. Conversely, GS phases are associated with a weakened AMOC. Some stadials (HS) include Heinrich events, characterized by layers of ice-rafted debris in North Atlantic marine sediment cores, indicating substantial iceberg discharges and representing the most arid and coldest periods at studied site latitudes (Rodrigo-Gamiz et al., 2022) (Fig. 16).

HS events may have extended to the western margin of the Iberian Peninsula (Eynaud et al., 2009). Pedro et al. (2022) used near-surface temperature reconstructions synchronized to a timescale covering 50–10 thousand years before present to elucidate the regional manifestation of D-O and HS in the North Atlantic. They concluded that the western Iberian Margin exhibits a structure reminiscent of Greenland, albeit with more noticeable surface cooling during transitions between GIs and HS compared to transitions between GIs and non-Heinrich stadials (GSs). Specifically, near-surface temperatures in the Iberian Margin stack dropped by approximately 6–9 °C below the preceding interstadials during HS, whereas the cooling was weaker, about 2–3 °C, between GI and GS. Additionally, the LGM (c. 24–18 cal kyr BP) was warmer than MIS3 in the Iberian Margin stack. This observation is consistent with proxy data (Böhm et al., 2015) and model-based evidence (Brady et al., 2013) indicating an active AMOC during the LGM. This would be particularly evident in the southern end of the Iberian Margin, as we will discuss later.

The palynological types whose variation could best reflect the influence of climatic changes on the vegetation in the LT catchment are *Artemisia* (GS, HS) and *Quercus* (GI), and, to a lesser extent, AP (Fig. 16). While AP may parallel *Quercus*, it does not do so throughout the entire sequence, primarily due to the influence of *Pinus*. However, AP exhibits a Pleistocene variation pattern that show some similarities with the organic matter-bound bromine (Br norm) and Ln (Zr/Al) ratio from contourite Site U1387 in the Cádiz Gulf (Bahr et al., 2014), which is influenced by the upper core of the MOW (Mediterranean Outflow Water dynamics) (Fig. 16d). The bromine record, serving as a proxy for organic content, preserves the pristine climate signal regardless of lithological fluctuations, thus enabling its use for chronostratigraphy in addition to stable isotope stratigraphy. During the Holocene sea-level high stand, we observed a marked opposite trend between the Zr/Al ratio (a proxy for MOW strength) and AP in LT (Fig. 16d). This connection can be explained by the fact that MOW strength is primarily influenced by changes in rainfall in and around the Mediterranean (Nichols et al., 2020). *Quercus* at LT also shows an interesting correlation with the last sapropel deposit S1 in the Eastern Mediterranean (Fig. 16f), providing additional evidence of the role of rainfall in Mediterranean flora and thermohaline circulation (Sierro et al., 2020).

11.2. Responses of vegetation between 40 and 19 cal kyr BP

During LTP1, between c. 40.8 and 36.5 cal kyr BP, the three initial peaks of *Artemisia* occurred around 40.6, 38.9, and 36.9 cal kyr BP, coinciding with decreases in *Quercus*. This could be indicative of steppification in the catchment area in response to the abrupt cooling events

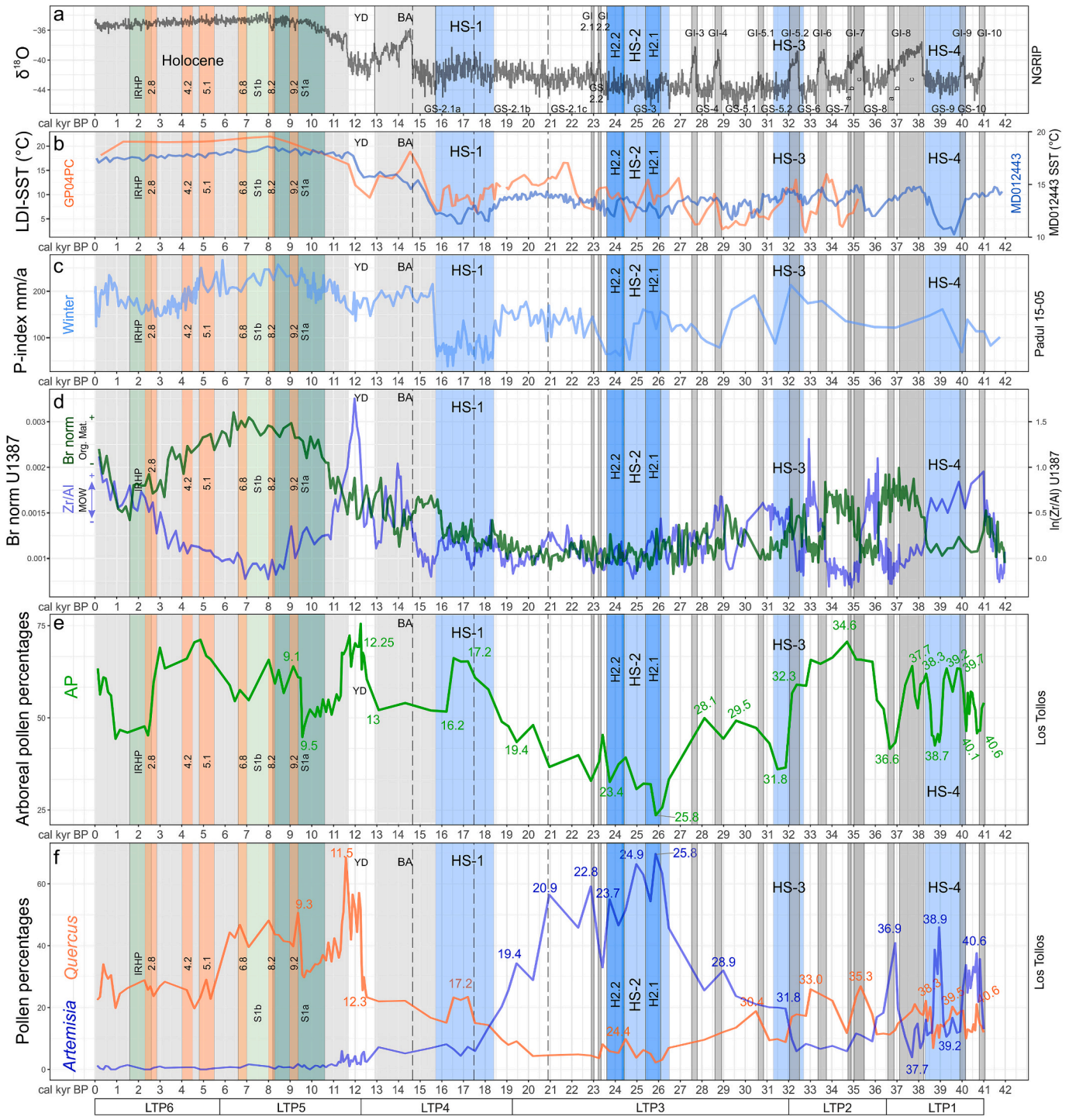


Fig. 16. Comparison of selected pollen profiles from Los Tollos and (a) 20-year average values of $\delta^{18}O$ from NGRIP on the GICC05modelext time scale (Rasmussen et al., 2014). Gray shading illustrates Greenland Stadials (GS) and Greenland Interstadials (GI) numbered following the INTIMATE events stratigraphy (Rasmussen et al., 2014). (b) The blue line shows Sea Surface Temperature SST °C from the MD012443 record (Martrat et al., 2007), the orange line shows long-chain diol index LDI SST °C from the GP04PC record (Morcillo-Montalbá et al., 2021). (c) Precipitation reconstruction through fossil pollen data from the Padul-15-05 lake sediment record (Ramos-Román et al., 2018; Camuera et al., 2019, 2021, 2022). The quantitative precipitation reconstructions were performed using the performance statistics of the Weighted Averaging-Partial Least Squares (WA-PLS)-based transfer function model under cross-validation (Camuera et al., 2022). (d) Variation of organic matter-bound bromine (Br norm) and Zr/Al in the contourite deposits from the Site U1387 in the Cádiz Gulf (Bahr et al., 2014). (e) Arboreal Pollen (AP) from Los Tollos. (f) *Quercus* and *Artemisia* pollen profiles. Age in major peaks in pollen trends are labeled. Orange vertical bands represent arid periods during the 2.8, 4.2, 5.5–4.8, 7–6.6, 8.2, and 9.2 kyr events (Bernal-Wormull et al., 2023). Green vertical bands represent the Iberian Roman Humid Period (Martín-Puertas et al., 2008) and Sapropel Units S1b and S1a (Filippidi and De Lange, 2019). Heinrich stadials are reported in pale blue according to Camuera et al., 2021 (HS1) and Sánchez-Goñi and Harrison, 2010 (H2, H3, and H4). Heinrich events H1.1 and H1.2 (Hodell et al., 2017) and H2.1 and H2.2 (Cui et al., 2024) are reported with dark blue bands. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

of GS10, GS9 (HS4) and GS8. However, in the latter case, there is a chronological discrepancy since GS8 is centred at 36 cal kyr BP. This discrepancy, along with other ones that will be discussed subsequently, may be attributed to inaccuracies in our age model, but also to a lack of synchronization in the vegetation responses. Nevertheless, these are significant increases in *Artemisia*, and their coincidence with cold events is still notable. Similarly, the increases in *Quercus* around 41, 40, and 37.2–38.3 cal kyr BP parallel GI10, GI9, and GI8. The latter (GI8: 38.17 cal kyr BP) resulted in a considerable warming in Greenland and is frequently observed in long marine sequences, with an interstadial period of about 2000 years (Wolff et al., 2010). In LT, this warm event led to forest expansion and an increase in the diversity of woody plants, as well as an increase in fire incidence (higher concentrations of charcoal; Fig. 13), which could be part of a global trend according to Sánchez Goñi et al. (2017). These authors also noted that during GI-8, the Mediterranean forest and climate were linked to the African and Asian monsoon through the Rodwell and Hoskins zonal mechanism (Marzin and Braconnot, 2009), or through shifts in the mean latitudinal position of the Intertropical Convergence Zone (Tzedakis et al., 2009).

The phase between c. 36.5 and 32 cal yr BP (LTP2) is generally more forested than the previous one. Interestingly, there are other sites within the same region that show forested conditions, particularly with oaks, during the GI-7 and GI-6 interstadials. These sites include ODP 976, and MD95–2043 (see Fletcher et al., 2010b for synthesis). This forested context, even more marked than during GI-8, is also visible at Padul (Camuera et al., 2019). At this LT phase, the response of forest ecosystems to climate change could be to be mediated to a greater extent by competitive dynamic relationships, perhaps partially in feedback with fire (Figs. 13, 16). As previously, the peaks of *Quercus* coincide with interstadials, in this case, GI7 and GI6, but there are no peaks of *Artemisia* for the interval GS8, GS7, and GS6, during which pine forests reached considerable coverage.

During the period between 32 and 19.2 cal yr BP (LTP3), which encompasses the LGM, the vegetation is responsive to last glacial climates, yet its response is clearly distinctive. The peaks of *Artemisia* and xerophytes represent the driest and coldest stage of the entire sequence, including HS3, GS5-GS3, HS2, and GS2.1b-c (Figs. 9, 13, 16). Here, the correlation between abrupt climatic events and palynological fluctuations is not thoroughly synchronous, and what is observed instead is a multimillennial trend of vegetation towards the heliophytism characteristic of a full glacial phase in southern Europe. Nevertheless, the minimum of AP and the peak of *Artemisia* around 25.8 ka fits into HS2. We must not forget that even in these steppification phases, there is a continuous high diversity of woody plants, probably in the adjacent mountains. Lobo et al. (2001) analyzed the biological history of vascular plant richness in the Iberian Peninsula and concluded that the mountains have been the main biodiversity reservoirs, especially those with rugged orography and that reach a considerable height with several vegetation belts. Arpe et al. (2011) compared climate model simulations for the LGM and created maps with locations of potential summer-green tree refugia in Europe. They concluded that warm-loving summer-green trees could have survived mainly in Spain due to a less cold and more humid climate than that traditionally inferred from pollen data.

Some pollen sequences from southern Spain are in line with the patterns described above. The record from Carihuela Cave, inland in eastern Andalusia, showed peaks for *Artemisia* around 45–40 cal kyr BP and subsequently more sustained high values around 28–19 cal kyr BP (Carrión et al., 2019). The dynamics of oaks also show similarities between Carihuela and LT, with a significant increase in pine around 34–30 cal kyr BP alongside a notable increase in oak just before the LGM. Similar trends are found in the nearby Padul site (Camuera et al., 2019, 2021). Recently, for this period, Vidal-Cordasco et al. (2022) observed how the Net Primary Productivity differed between the four main biogeographical regions of Iberia: the Eurosiberian region in the temperate areas of the North; the Supramediterranean in the Northern Plateau and Iberian System; and the two bioclimatic belts that make up the Mediterranean region (the Mesomediterranean and the Thermomediterranean regions) affecting, therefore, the herbivore guild composition between GI and GS phases. The different ecosystem productivity among regions has been proposed to explain the spatio-temporal disappearance of Neanderthals in Iberia.

11.3. Full-glacial steppes in the warm south

The expansion of steppes during the cold stages of the Quaternary could be a result of low pCO2 concentrations affecting the photosynthetic rate and water use efficiency of vegetation (Polley et al., 1993; Prentice et al., 2017). Regarding the LGM, the situation remains uncertain. Some studies suggest that the maximum ice volume extent of the LGM shifted the polar front southwards, intensifying the westerlies over southern Europe (Eynaud et al., 2009), potentially leading to increased precipitation over the Iberian Peninsula. However, other simulations indicate a drying trend (Braconnot et al., 2007). Simulated cold-dry conditions align with the dominance of steppe vegetation in the records including LT. In our case, it is essential to view the complex topography of the Strait region (Fig. 2). We suggest that a general aridification that might affect exposed areas could coexist with increased precipitation at mid- and high altitudes, providing refuge for woodlands. Additionally insolation values remains high in South Iberia even during the LGM (Maier et al., 2022) and vigorous warm currents appear to reach the Gulf of Cadiz during the glacial period (Rogerson et al., 2004; Duarte et al., 2024) likely favoring warmer conditions in continental areas. In any case, lower LGM temperatures and reduced winter precipitation may have favored the expansion of steppe taxa, but the reduced seasonality caused by the summer insolation minimum may have decreased summer evaporative conditions, allowing for moderate levels of effective moisture that could sustain mesophytes (Cutmore et al., 2022). In fact lake high level stands despite arid conditions is a common feature in South Iberian during the glacial/stadial conditions associated with a low evapotranspiration (Camuera et al., 2019).

A vexing question for palynology concerns the glacial location of *Artemisia*, given that it is a genus with a wide ecological amplitude. Although some species are found in subalpine and alpine meadows, and others are weeds, species in the genus are most commonly present on lower to middle stony slopes of mountains, sometimes on salty soils of plains, metal soils, deserts, gypsic substrates, and sandy desert soils (Kapustina et al., 2001; Lu et al., 2022). Other *Artemisia* species are often found together with chenopods in arid and semi-arid grasslands of the Northern Hemisphere. It is thus worth stressing that there are different habitat ranges, and *Artemisia* is not only restricted to arid and semi-arid environments. In our case, *Artemisia herba-alba*, a cold-tolerant species (Lyons, 1973), may have been a major contributor to the last glacial *Artemisia* pollen. Bougoutaia et al. (2021) used genetic, cytogenetic, and niche modeling tools to investigate the natural history of this species. Their findings revealed a complex phylogeographical structure in harmony with the species stable distribution on both sides of the Strait of Gibraltar. If we look at other records from the southern Iberian Peninsula where the peaks of *Artemisia* coincide with those of LT (Carrión et al., 2024b), it seems coherent to sustain that the majority of the *Artemisia* area must have been in low coastal zones, perhaps also abundant upwards in the Guadalquivir Basin in more inland areas.

11.4. MIS2 forest developments

Given the reactivity of forest vegetation to the abrupt cold spells of MIS3 (60–29 cal kyr BP), it is worth questioning why, as early as c. 21 ka, *Artemisia* definitively declines in the LT sequence, while AP, *Pinus*, *Quercus*, and the thermophilic and sclerophyllous Mediterranean component begin an upward trend (Figs. 7–9, 13, 16). There is substantial evidence that the most recent part of GS2, including HS1 (c. 18.4–15.7 cal kyr BP), was characterized by extremely cold conditions (He et al., 2021) (Fig. 16) that had a profound impact on European

vegetation. This resulted in the loss of forest cover and the expansion of steppes (Pini et al., 2022). Nevertheless, it seems that the LT region was experiencing woodland encroachment at the end of the LGM, while the incidence of fire increases with the available fuel (Fig. 13). One hypothesis is that the thermal collapse was not as severe regionally as previous ones, which is supported by the Padul pollen record (Camuera et al., 2019). In fact, HS1 shows a complex pattern that includes an intra-warming episode at Iberian latitudes (Hodell et al., 2017). Another possibility is that it was accompanied by greater water availability for the vegetation in the pollen catchment basin. Not incompatible with the two latter is the possibility that before HS1, woodland ecosystems had gained resilience through an increase in species diversity after millennia of isolation and population fragmentation (Fig. 15). We postulate that the presence of stationary populations of broadleaf trees and conifers in the southern Baetic mountains might have cushioned the effect of the penultimate major cold pulse of the Pleistocene, HS1.

Leaving aside the possibility of inconsistencies with the age model, the difficulties in aligning rapid palynological variations with global climatostratigraphy in this region persist throughout the interval c. 19.2–12.3 cal kyr BP (LPT4), even extending into the early Holocene until approximately 10 cal kyr BP. It is evident that vegetation underwent a series of reactions to the multimillennial deglaciation phase, which involved the expansion of woodlands and forests and the sustained regression of *Artemisia* and xerophytes. However, it is more challenging to explain the peaks of *Quercus* around 17.2 (within HS1) or between 12.3 and 11.5 cal kyr BP (within the Younger Dryas), both cases accompanied by high values of *Pinus* (Figs. 7, 13, 16). In other words, if we use the chronology of Camuera et al. (2021) corrected for the Mediterranean, the expected vegetation response to temperature fluctuations during HS1, the Bølling–Allerød Interstadial (BA), and the Younger Dryas cold spell (YD) (12.8–11.8 cal kyr BP) would not occur. The same would apply if we used other scales (e.g., Cutmore et al., 2022: 15.4–13.2 cal ka BP for BA, and 13.2–12 cal ka BP for YD). In contrast, further westwards the Atlantic coast, the palynological signals of the BA and YD are evident in the record from the Beliche river (CM5 borehole), at the Guadiana Estuary in the Algarve, south Portugal (Fletcher et al., 2007), as well as in various sequences of the Iberian Peninsula (González-Sampériz et al., 2010).

As previously hypothesized, an altitudinal variation in precipitation could explain these observations. Camuera et al. (2022) approach this paradox by combining the Padul pollen data with the newly developed Scale-normalized Significant Zero crossing (SnSiZer) method to detect statistically significant precipitation changes in the western Mediterranean during the past 200 kyr. Six principal West Mediterranean Humid Periods (WMHP) were identified which parallelled, not only other west and central Mediterranean paleohydrological records, but also, although less accurately, African Humid Periods, suggesting similar drivers in North Atlantic Ocean-atmospheric dynamics and orbital forcing. Camuera et al. (2022) hypothesized that the reduction in mean annual precipitation during glacial periods does not necessarily imply a reduction in summer precipitation. Thus, the lower summer temperature and evapotranspiration may have facilitated the eventual spread of pine forests, and in the case of LT, the development of mixed oak-pine forests. Interestingly, the most recent WMHP1 is dated between 15.5 and 5 kyr BP, a period during which high values of oaks and other broadleaf trees are recorded in LT (Fig. 13). Other studies of paleohydrological dynamics using hydrogen isotopes from sedimentary leaf waxes plus a pollen proxy for precipitation from the Padul 15–05 record also suggested enhanced precipitation during 15.5–5 cal kyr BP, and a clear decreasing trend in rainfall thereafter (García-Alix et al., 2021). Cutmore et al. (2022) integrated detailed pollen records with paleoceanographic indicators from deep-sea cores SHAK06-5 K and MD01–2444 in the southwestern Iberian Margin. Their study elucidated regional vegetation dynamics in response to orbital and millennial-scale climate fluctuations spanning the last 28 thousand years. The most significant expansion of thermophilous woodland was documented between 10.1 and 8.4 cal ka BP. Several pollen sequences reflect similar responses. As observed in Padul (Camuera et al., 2019, 2021), the Carihuela sequence shows the first significant expansion of oaks as early as around 15 cal kyr BP (Carrión et al., 2019). Pre-Holocene oak colonization in LT would have occurred at an earlier date, around 20–19 cal kyr BP, which would indicate a closer proximity to full glacial refugia populations.

11.5. *Do not expect linear responses: biocomplexity in the Strait of Gibraltar Region*

Without detracting from the previous argumentation, which was necessarily imprecise due to the lack of regional and local climatic resolution, we must also point out that, in an ecological system that could have gained in biotic interactions and forest complexity since the LGM, the influence of species interactions and disturbances by fire and herbivory could superimpose on climatic influence, especially on a multicentennial scale (Williams et al., 2021). Palynological data from the Iberian Peninsula show precisely that the climatic factors, such as rainfall heterogeneity, and biological factors, such as phytodiversity, combine to produce a broad picture of "unexpected responses" to Pleistocene, Late Glacial and Holocene climate changes, especially in the Mediterranean Region (Carrión, 2001; Carrión et al., 2010; González-Sampériz et al., 2020). The dates of *Quercus* colonizations would be proportional to the distance from forest stands located in mountainous hydro-refuges. For example, at 1320 m in Siles, Sierra de Segura, in the northeastern sector of the Baetic mountains, the development of arboreal angiosperm formations would be around 12 cal kyr BP, with evidence of glacial refugium during the interval around 20–12 cal kyr BP (Carrión, 2002b). In other instances, the inertia of local pine forests impedes the colonization of *Quercus* (Carrión and van Geel, 1999). Reflecting on this matter, Rull (2022) posits that the inductive prediction power diminishes with the increasing complexity of biological responses that significantly distort astronomical periodicity. The response of long-lived tree species to climate changes can be synchronous in specially vulnerable areas (i.e., González-Sampériz et al., 2006; Pérez-Sanz et al., 2013), but also can take centuries to manifest because is influenced by a multitude factors, including their own traits such as phenotypic plasticity, competitive abilities, migratory capacity over long distances, tolerance to abiotic disruption, reproductive characteristics, life cycle duration, and others. These factors collectively would affect the community level in unpredictable manner (Rull, 2022).

12. Postglacial vegetation history

12.1. *Summary of the postglacial record*

From around 12 cal kyr BP (LPT5-LPT6), the highest values of AP are recorded, influenced primarily by the abundance of deciduous and evergreen *Quercus*, plus *Quercus suber*. It is also noteworthy a more continuous presence of *Fraxinus, Salix, Ulmus, Phillyrea, Pistacia, Olea, Arbutus, Frangula, Myrtus, Asparagus, Berberis, Chamaerops, Myrica, Rhus, Ruscus, Rubus, Coriaria, Maytenus, Smilax, Viburnum,* Thymealeaceae, Poaceae, and Urticaceae. Several taxa that were nonexistent in the Pleistocene strata are present here, such as *Sorbus* and *Lycium*. Conversely, *Juglans* disappears from the pollen record. Along with *Betula*, there is a certain regression of gymnosperms such as *Juniperus, Pinus* (only until around 5 cal kyr BP), *Pinus pinaster, Taxus*, and *Cedrus*, with some species like *Ephedra distachya* disappearing from the pollen catchment. Some groups of heliophilous woody plants have lower postglacial incidence in LT, such as *Erica*, Genisteae, Cistaceae, and *Ephedra fragilis*. Undoubtedly, the Holocene is also defined by residual values of *Artemisia*, one of the most characteristic taxa of the Pleistocene strata (Figs. 7–13).

12.2. Pristine Iberian oak woodlands

Another distinctive feature of the LT vegetation history is the prevalence of oaks throughout most of the Holocene. In several records within the Iberian Peninsula, pines were dominant or co-dominant in the first part or during long episodes of the Holocene, from Levante to the semi-arid southeast, and especially in the mountains of the interior (Peñalba, 1994; Dupré et al., 1996; Stevenson, 2000; Yll et al., 2003; Carrión and van Geel, 1999; Carrión, 2002a; Carrión et al., 2001a, 2001b, 2004, 2010; Franco-Múgica et al., 2005; González-Sampériz et al., 2010, 2020; Aranbarri et al., 2014; Manzano et al., 2019; Sánchez-García et al., 2024). It seems that early to mid-Holocene landscapes were more often dominated by oaks in territories with marked Atlantic influence, from Galicia and Portugal to SW Spain (van den Brink and Janssen, 1985; Pèrez-Obiol and Julià, 1994; van der Knaap and van Leeuwen, 1995; Muñoz-Sobrino et al., 1997; López-Merino, 2009; González-Sampériz et al., 2006; Carrión et al., 2010, 2024c). Pine forests prevail in pre-anthropic vegetation, which raises concerns about the concept of single-species dominant potential vegetation (Carrión and Fernández, 2009; Carrión, 2010; Chiarucci et al., 2010; Somodi et al., 2012; De Keersmaeker et al., 2012; Rull et al., 2017; Morellón et al., 2018). In contrast, LT pre-anthropic vegetation was dominated by *Quercus*, which, in southern Spain, adds to the cases of Mazarrón (Carrión et al., 2018a), Carihuela (Fernández et al., 2007; Carrión et al., 2019), Padul (Ramos-Román et al., 2018; Camuera et al., 2019), San Rafael (Pantaleón-Cano et al., 2003), and Medina Lake (Schröder et al., 2020), among others (Fig. 2). This finding has the potential to inform future research in the fields of forest management policies, rewilding, restoration ecology, and fire prevention (Luelmo-Lautenschlaeger et al., 2019; Manzano et al., 2020; Morales-Molino et al., 2019; Connor et al., 2021; Schwörer et al., 2024).

12.3. Holocene climate–vegetation relationships

The relationships between long- and short-term climatic changes during the Holocene and vegetation changes in LT are not straightforward to decipher. However, some patterns do align with previous records and/or fit into published models. It is uncommon in the Iberian Peninsula to find abrupt changes in vegetation during the Holocene. One example of such a change can be observed in the treeline of the northern Baetic mountains (Carrión et al., 2001b). Ilvonen et al. (2022) constructed a regional pollen-climate calibration model to estimate Holocene precipitation in the Iberian Peninsula. In the southern Iberian Peninsula, the Early Holocene (11.7–11 cal kyr BP) was marked by elevated precipitation values, gradually decreasing until approximately 9 cal kyr BP. Between 8 and 5 cal kyr BP, the reconstructed precipitation values reached their peak in most records. A subsequent decline in precipitation occurred during the late Holocene, with the model facing complexity due to the diverse impact of human activities. This trend is reflected the overall pattern of AP and *Quercus* found in LT in this study (Figs. 13, 16). It also finds parallels in the neighboring La Janda Lake (Val-Peón et al., 2021), where a significant development of *Quercus* was observed between 11.7 and 6 cal kyr BP. However, this record contains a greater number of basinal heliophytic elements, including ericaceous plants and, especially, chenopods. In a similar line of deduction, García-Alix et al. (2022) examined an 11.9 kyr paleohydrological record from the evaporitic lake Laguna de la Ballestera (inland northeastern LT), which has been primarily influenced by changes in insolation. The greatest wetland extension and highest lake levels were observed during the early Holocene, with climate transitioning towards more arid conditions during the Middle Holocene, and becoming more dramatically arid during the Late Holocene.

The pollen record from Laguna de Medina (Schroeder et al., 2018) was part of multi-proxy study covering the period from 9.5 cal kyr BP to the present. An abrupt arid climate event was described at 8.2 cal kyr BP, while the climatic optimum was placed between 7.8 and 5.5 cal kyr BP. Oaks were abundant between 9.6 and 6.4 cal kyr BP in Doñana, specifically in the record from Lucio de la Cancela de la Aulaga (Manzano et al., 2018), with a continuous presence of *Quercus suber*. Given the lagoonal nature of the sequence, it is noteworthy that during this phase, species such as *Corylus, Betula, Laurus, Ceratonia, Frangula, Celtis, Juglans, Ulmus, Acer, Castanea, Ilex*, and *Taxus* were present. This represents a significant mesophytic assemblage in a coastal biotope.

Ramos-Román et al. (2018) reported a high-resolution multiproxy record of the Holocene from Padul, integrating pollen, inorganic and organic geochemical, and sedimentological analyses. These authors observed the highest occurrence of deciduous forest formations from 9.5 to 7.6 cal kyr BP. It is proposed that this Holocene humidity optimum may have been caused by an increase in winter precipitation during a period of elevated summer insolation. Superimposed on this general pattern are rapid climate change events reflected in the paleoenvironmental record of the peat bog, particularly cold-arid events at 9.6, 8.5, 7.5, 6.5, 5.4, 4.7, 2.7, and 1.3 cal kyr BP. On the southern coast of Portugal, Fletcher et al. (2007) found that the Holocene began with a dry and warm climate, but soon a maximum of oak forest was established, persisting between 9000 and 5000 cal kyr BP. They also identified abrupt pulses of aridity dated to 10.2, 7.8, 4.8, 3.1, and 1.7 cal kyr BP, correlated with Bond events (abrupt North Atlantic cooling events).

In the case of LT, increases in xerophytes occur at approximately 11.3, 5.3, 4.5, 2.2, and 0.3 cal kyr BP. Although the records of *Quercus* and AP, previously used as a paleoclimatic sensor in LT, exhibit some concurrence with several abrupt climatic changes previously documented for the Holocene, there is also a lack of synchronization in other instances. As has been documented in the literature, there is no general agreement on the chronologies in which these warm or arid events are situated. It is evident that in many areas of Andalusia, a foreseeable challenge for paleoclimatic interpretation is the overlapping influences of the Atlantic and the Mediterranean. However, one does not need to conjecture much to understand that if we were to review all the literature mentioning abrupt cold and/or arid events during the Holocene and attempt to place these events within a geochronological framework, we would likely find that the entire Holocene period was characterized by cold and/or arid conditions.

Among the models revised here, one that shows some synchronous changes with AP declines in LT is the arid-pulses model by Bernal-Wormull et al. (2023), based on Holocene isotopic records ($\delta^{13}C$ and $\delta^{18}O$) of stalagmites from the western Pyrenees. This study highlights centennial changes that correlate with North Atlantic events, with the signal for the 8.2 cal kyr BP cooling event being particularly visible. Other significantly arid events are dated to 9.2, 7–6.6, 5.5–4.8, 4.2, and 2.8 cal kyr BP (Fig. 16). Most of these events have indeed impacted in vegetation composition from regional sequences (González-Sampériz et al., 2006, 2010, 2017, 2020; Pérez-Sanz et al., 2013). These responses are the result of paleoclimatic significance, but in other regions, where they are not so evident, they could also be coincidental within the context of Holocene fluctuations, where consistently high pollen frequencies for *Quercus* and AP could be attributed to methodological/taphonomic issues (Carrión and Dupre, 1996).

Furthermore, the situation concerning the second half of the Holocene is further complicated by human interference, which could also be affecting patterns of fire and herbivory by livestock. For instance, the Iberian-Roman Humid Period (IRHP: 2.6–1.6 cal kyr BP), characterized inland Andalucía in Zoñar Lake (Martín-Puertas et al., 2008), coincides in LT with a decline in AP (Fig. 16). To summarize, what this IRHP event observed in Zoñar indicates is the influence of a warming of the Mediterranean Sea water (Margaritelli et al., 2020). Nevertheless, the Atlantic influence in LT is unquestionable (Fig. 16), although any correlation between the LT Holocene pollen record and abrupt climate shifts must remain within a framework of speculation.

13. The cultural landscape

13.1. Anthropogenic pollen indicators

The history of human settlement in this southern region of Andalusia is very ancient and shaped by the influence of the coast, climate and soils. Acheulian, Mousterian and Upper Paleolithic evidence has been found along the coastal shelves (Bailey et al., 2008) and in the inland sierras (Arcila and Fernández-Enríquez, 2015). The LT palynological sequence contains anthropogenic indicators over the last 6000 years. This contrasts with what has been observed in records from mountain sites in the interior of Andalusia such as the Segura-Cazorla Mountains (Carrión, 2002a; Carrión et al., 2001a, 2001b, 2003a, 2007a) or Sierra Nevada (Jimenez-Moreno and Anderson, 2012; Ramos-Román et al., 2018; Manzano et al., 2019) (Fig. 2) where the main anthropogenic pollen indicators are confined to the last three millennia, often the last millennium, even the last few centuries. In LT some of the increasing elements such as Asteraceae, *Lycium, Nerium, Polygonum aviculare, Rumex crispus, Anchusa* and *Frankenia* could be linked to the ruderalisation of the agricultural environment in the vicinity of the lake (Fig. 9). However, the unquestionable indicators of agriculture are *Vitis* (c. 5–4 cal kyr BP) and Cerealia (c. 4 cal kyr BP). *Vitis* has been found in Doñana since c. 5 cal kyr BP (Stevenson and Moore, 1988; Stevenson and Harrison, 1992), often in parallel with the occurrence of taxa such as *Urtica, Plantago, Malva, Heliotropium,* and several Asteraceae types (López-Sáez et al., 2018). During the last millennium, LT underwent the processes of limnological modification by human activity mentioned above. A marker of these processes could be the invasion of taxa such as *Tamarix, Heliotropium supinum* and *Cressa cretica* (Fig. 11).

13.2. Olive tree selection and cultivation

Olea pollen is present throughout the entire LT sequence in small proportions, which supports Carrión-Marco et al.'s (2010) hypothesis of the existence of refugia in the southernmost parts of the Mediterranean peninsulas and the retraction of the species' distribution area during the LGM. However, the increase of *Olea* from around 5.5 cal kyr BP can be interpreted as the result of the selection and/or cultivation of the olive tree in the area. Our findings align with the circumstances defined by Langgut et al. (2019), who employed a fossil pollen dataset comprising high-resolution pollen records to investigate the historical patterns of olive cultivation across the Mediterranean Basin. The presence of human activity is identified when *Olea* pollen percentages experience a sudden increase, not accompanied by a rise in other Mediterranean sclerophyllous trees, and when this increase coincides with consistent archaeological and archaeobotanical evidence. Langgut et al. (2019) concluded that approximately 6500 years BP marked the advent of two distinct origins for olive cultivation: the southern Levant and the Aegean. They further proposed that the earliest known olive tree management practices in the Iberian Peninsula can be dated to around the mid/late third millennium BP. In this region of Andalusia, olive trees probably started to be selected and planted earlier. Archaeobotanical evidence indicates that the olive tree has been a primary resource since at least the Chalcolithic period (Ramos-Muñoz and Weniger, 2023). The presence of pollen and charcoal of wild olive tree (*Olea europaea* var. *sylvestris*) at numerous sites provides compelling evidence of human selection and cultivation. This thermophilic, long-lived species can reach up to 10 m in height, although it adopts a bushy form due to being browsed by livestock (Aparicio et al., 2001b). It displays optimal fuel properties, especially for maintaining domestic fires burning in open-air sites (Ramos-Muñoz, 2008). The Lake Zóñar pollen records, from Córdoba (inland Andalusia), mark the beginning of the continuous *Olea* curve around 2.7 cal kyr BP (Valero-Garcés et al., 2006; Martín-Puertas et al., 2008).

13.3. Human activities, changing landscapes and biodiversity loss

During Prehistory, the vegetation landscape in the study region underwent major modifications in some areas and remained unaltered in others (Fyfe et al., 2019). It is evident that some of the plant communities have experienced a considerable range retraction, accompanied by local population extinctions of species, especially woody and even more so deciduous ones. This phenomenon has also been observed in other regions of Andalusia (Carrión et al., 2003b; Anderson et al., 2011; Alba-Sánchez et al., 2018; Gómez-Zotano et al., 2023; Pardo Martínez et al., 2023) and in the eastern Segura Mountains in Murcia, southeastern Iberian Peninsula (Carrión et al., 2004). Some pollen signals from LT point to this phenomenon, as evidenced by the absence of *Juglans, Taxus*, and *Ilex* during LTP6, or the disappearance of *Abies, Acer, Betula, Castanea, Sorbus, Buxus, Arbutus, Rhus,* and *Ruscus* (Figs. 7, 8). The recent partial substitution of *Quercus* by *Pinus* and then Poaceae also suggests the process of deforestation as a result of human activity.

Undoubtedly, the vegetation landscape became increasingly fragmented, with more and more anthropogenic structures. For example, the dehesa (a type of anthropogenic *Quercus* savanna) has been identified through palaeoecological studies in the southwest since the Late Neolithic and more reliably from the Chalcolithic to the present (Stevenson and Harrison, 1992; López-Sáez et al., 2018; Carrión et al., 2024c). In fact, the Chalcolithic occupation is very numerous from about 5.2 cal kyr BP (García-Rivero, 2004; Lillios et al., 2016). However, historical texts mention that until a few centuries ago, there was a significant amount of holm oak groves in the countryside, cork oak groves on acidic sandy soils, gall oak groves in more humid enclaves, and wild olive groves on the more clayey soils (Arcila and Fernández-Enríquez, 2015).

Southwestern Iberia plays a central role in unraveling the process of Neolithization in the Iberian Peninsula (Martín-Socas et al., 2018). Evidence of Neolithic settlements dates back to at least 7.5 cal kyr BP, marking a rapid transition from the coastal economies of Mesolithic populations (López Sáez et al., 2011; Val-Peón et al., 2021, 2023b). Uzquiano et al. (2021) provided a comprehensive review of the palynological and palaeoanthracological information from archaeological sites on the Cádiz coast and inland between 8 and 3 cal kyr BP, spanning from the Late Mesolithic to the Late Bronze Age. The main sites studied were Palmones (Late Mesolithic), El Retamar (Early Neolithic), Campo de Hockey (Neolithic to Bronze Age), La Esparragosa (Neolithic), Parralejos (Late Neolithic), Loma del Puerco (Early Bronze Age), and Asteroides (Late Bronze Age). Some of the general patterns they found include a greater presence of deciduous oaks towards the west, less tree cover, and less presence of mesophytes as time progresses and we move eastwards. The decline and even anthropogenic degradation of forest cover and the loss of deciduous, broadleaf trees in the Middle and Late Holocene are well documented. In the Bay of Algeciras, the starting point could be situated between 8 and 7.5 cal kyr BP with a great diversity of environments, including extensive woodlands associated with high water availability coexisting with dry conditions. The human population was already dense, with hunter-gatherer occupations based on coastal resources (shellfish) and game hunting (e.g. horse, red deer). It is also worth noting the importance of agriculture and livestock herding acquired from the Neolithic onwards, although it has been shown that between 6.4 and 5.3 cal kyr BP, scrublands were still dominant near the coast. In addition, cereal activities were present, as suggested by the accumulation of production surpluses stored in pits within La Esparragosa site (Ramos Muñoz and Pérez Rodríguez, 2003). The archaeological confirmation of agriculture could be dated to 6 cal kyr BP, although it could have started a millennium earlier or even around 7.5 cal kyr BP (García-Rivero et al., 2022).

The Middle Neolithic, spaning 6.5–6.0 cal kyr BP, marks a significant shift in the agricultural economy of the region, characterized by the establishment of a monoculture of naked wheat, with a limited presence of naked barley. This shift represents a transition from intensive to

extensive agriculture, which has been associated with a loss of forest cover (Rodríguez-Ariza, 1996; Peña-Chocarro et al., 2018). Consequently, it is pertinent to explore how much of the observed change in LT between LTP5 and LTP6 can be attributed to human impact.

During the Bronze Age in the region (c. 4.0–3.2 cal kyr BP), archaeobotanical research indicates that open landscapes were dominated by xeric and steppic taxa, in addition to junipers, Cistaceae, Ericaceae, and ruderal taxa. However, the presence of riparian, sclerophyllous, and mesophilous trees, including deciduous oaks plus *Quercus suber, Q. ilex, Q. coccifera* and, plausibly, *Q. canariensis*, indicates a certain recovery of woodlands in comparison to the Neolithic occupation. The coastal and pre-coastal areas (e.g., Campo de Gibraltar, La Janda lagoon) were densely populated due to the abundance of fishing resources. The countryside to the north of the Guadalete River experiences a less intense wind regime than that in the south, and the soils have an excellent agricultural capacity in an ideal context of significant endorheic conditions (Aparicio et al., 2001a). The archaeological site of Pocito Chico, in the coastal area of Cádiz, between the marshes of the Guadalquivir and the Bay of Cádiz, provides evidence of continuous human settelements from the Copper Age to at least the 15th century (López Amador et al., 2008). Archaeobotanical studies (Badal, 2002; López-Sáez et al., 2001, 2002a, 2002b; Peña-Chocarro, 2007) show a highly anthropized environment with evidence of irrigated agriculture, as well as forests comprising cork oaks, holm oaks, and kermes oaks. The sequence begins with the presence of cereal pollen, and further evidence includes carbonized pine bracts and pine nuts, as well as seeds of wheat, barley and legumes.

13.4. *The vanishing forests of the Iberian Pyrite Belt*

In order to comprehend the potential impact of human activity on the prehistoric landscape and plant diversity, it is essential to consider the role of metallurgical activity. This is particularly evident in the southwest of Sierra Morena at the northwest of LT (Fig. 2a), where the intensity of this activity is particularly noteworthy. Rodríguez-Bayona et al. (2012) have studied the Iberian Pyrite Belt, which is the most prolific metallogenic province of massive sulfides in the world and the main mining district in Western Europe. There was a prehistoric presence of intensive and specialized mining-metallurgical settlements, which were associated with already hierarchical populations. The most important sites are Cabezo Juré (Huelva) and Valencina de la Concepción (Sevilla; Fig. 2b) (Nocete et al., 2011). It has been established that the extraction and smelting activities of copper metallurgy resulted in the emission of gases into the atmosphere and the enrichment of trace metals (García-Alix et al., 2013). Pollen analyses at the site of La Junta de los Ríos, near Cabezo Juré (western end of Sierra Morena; Fig. 2a), showed that at 6–4 cal kyr BP, before mining exploitation, there was a mosaic landscape with oaks, pines, hazelnuts, birches, alders, elms, strawberry trees, mastic trees, and myrtles. However, several centuries after the start of mining activities at Cabezo Juré, the degradation of forest cover and the loss of tree species was dramatic (Fuentes et al., 2006). Later, that area of the western and southwestern Sierra Morena persisted as a major mining and metallurgical zone throughout the Bronze and early Iron Ages, particularly in relation to the extraction of copper and silver in the Iberian Pyrite Belt (Hunt Ortiz, 2003; García-Alix et al., 2013).

13.5. *Doñana before present*

In terms of vegetation and floristic change, comparisons with the Holocene of Doñana, despite its proximity (Fig. 2), are not particularly fruitful. The local geomorphological and hydrological dynamics, as well as the presence of mobile dunes and saline environments, influence the pollen record and introduce irresolvable biases related to transport and preservation. Furthermore, the marine conditions prevailing in the estuary (transgressions) and, in some cases, the consequences of tsunamis are also reflected in the records (Manzano et al., 2018). Palynological work in Las Madres (Fig. 2b; Stevenson, 1981, 1985; Stevenson and Harrison, 1992; Yll et al., 2003) provided paleoenvironmental information between c. 6.3 and 0.9 cal kyr BP, showing a coastal landscape with pines, oaks, and junipers, along with extensive shrubland, grassland, and marshland, especially chenopods, grasses, heathers, Cistaceae, *Myrtus*, and *Phillyrea*. The paleofloristic situation was similar in the El Acebrón neighboring site (Fig. 2b) (Stevenson and Moore, 1988), between c. 5.1 and 0.15 cal kyr BP. The Marismas de Doñana marshland area, in general, showed an overwhelming palynological dominance of chenopods, composites, grasses, hydrophytes, and hygrophytes (Cyperaceae, Ranunculaceae, *Typha*, Alismataceae, *Myriophyllum, Polygonum*, Apiaceae, *Lemna, Botryococcus*, Zygnemataceae) (Yáñez, 2005; Yáñez et al., 2006). Those pollen spectra surely masked possible changes in the immediate surrounding vegetation landscape, undoubtedly more forested and edaphically more stable. Similar difficulties occur in the La Janda pollen sequence, although the level of palynological discrimination in this case is higher, allowing for a more solid interpretative process (Val-Peón et al., 2021, 2023b).

Still in Doñana, Jiménez-Moreno et al. (2015) investigated the S7 and S11 sedimentary sequences, which included pollen records dating back to the Mid to Late Holocene. They were able to identify a gradual aridification trend starting at least 5000 cal yr BP, marked by a reduction in forest cover, and linked this trend to a decline in summer insolation. Methodological difficulties resulting from the hyperinfluence of the local catchment can also be observed in other sedimentary environments. A study conducted in a peat bog in Sierra del Aljibe (400 m a.s.l., 1140 cal yr BP) (Fig. 2b), within a currently highly forested area, showed a significant prevalence of heather pollen, with minor occurrences of *Quercus* and *Corylus* (Gutiérrez et al., 1996, 1997). In the Core S1 record (c. 5–2.8 cal kyr BP) in the marsh area of Hinojos (northeastern Doñana marshland area), López-Sáez et al. (2018) provided a range of evidence suggesting that prehistoric human impact on Doñana ecosystems may have been highly variable both temporally and spatially. For example, during the period c. 3.5–3.14 cal kyr BP, there were no palynological indications of anthropization: no cereal pollen or ruderalization indicators, while coprophilous fungal spores were scarce. Conversely, during the period c. 3.14–2.8 cal kyr BP, there was an increase in the presence of anthropogenic herbaceous plants, coprophilous fungi, microscopic charcoal, and cereal pollen. The study of Manzano et al. (2018) in Lucio de la Cancela de la Aulaga (western margin of Doñana marshland; Fig. 2b), with high palynostratigraphic resolution, revealed a connection with the terrestrialization of the Guadalquivir palaeoestuary. Here, the Early Holocene aquatic and upland vegetation showed resilience at the millennial scale.

14. The strait vegetation: always “on fire”

Climate must have had a powerful influence on the structure, function and floristic composition of the vegetation in the Strait of Gibraltar region. However, there are other interacting factors that are equally relevant. Among them, fire and herbivory are probably the most significant, or perhaps we should say that, unlike other processes of ecological interaction, they are palaeoecologically researchable. The involvement of fires, whether natural and climatically favored, or anthropogenic or of mixed origin, in the observed vegetation change of LT around 6 cal kyr BP (LTP5-LTP6 transition; Fig. 13) is evident. However, the variation in microcharcoal concentration indicates that fire has been a natural phenomenon in the region since the Pleistocene, at least during the last 40,000 years. There is a notable decline in the incidence of fire during the periods 31–20 and 16–13 cal kyr BP, followed by a resurgence between 38 and 32 and 19–16 cal kyr BP (Fig. 13). A visual interpretation of the ordination plot (Fig. 14) suggests that the plant communities of the region of the Gibraltar Strait have been under recurrent fire regimes since the Pleistocene, and that these fires may have been dependent on available wood fuel biomass, especially

that of *Quercus* species (*Quercus suber*, deciduous *Quercus, Q. ilex-coccifera, Q. lusitanica*) and other woody angiosperms such as *Phillyrea* and *Pistacia*.

It is important to note that the lack of correlation between the palynological variation of some highly pyrophytic taxa (e.g. *Erica* spp., *Pinus pinaster*) and the concentration of microcharcoal particles in LT (Figs. 7, 8, 13) does not necessarily imply the absence of an ecological connection. It is also likely that the measurement of fire incidence through the counting and calculation of the concentration of microcharcoal particles in microscopic preparations may have been affected by multiple taphonomic factors (Clark, 1988; Whitlock and Larsen, 2001; Finsinger and Tinner, 2005). It shall also be stressed that a fire can spread with only the presence, not necessarily dominance, of flammable plant species such as *Calluna vulgaris, Erica* spp., *Cistus* spp., *Arbutus unedo* or *Pinus pinaster*.

Other studies support this perspective. The occurrence of fire is also documented in the La Janda sequence, with a higher frequency between 11.5 and 8.2 cal kyr BP (Val-Peón et al., 2023b), as in the LTP5 zone of LT (Fig. 13). Evidence of deforestation on the Doñana coastal area during the 5th millennium cal BP (Stevenson and Moore, 1988) also coincides with the interpretation from the LTP6 zone (Fig. 13). The phenomenon of burning amplification from the Lateglacial to c. 8–9 cal kyr BP is not exclusive to the southwestern Iberian Peninsula; it is also frequent in the eastern and northeastern side (Gil-Romera et al., 2014; Leunda et al., 2014). For example, it has been observed in Villena Lake (Sánchez-García et al., 2024) and in the Navarrés peat bog (Carrión and van Geel, 1999). In the eastern and northern ends of the Baetic Mountains (Fig. 2a), anthropogenic fire seems to be a determinant feature of post-glacial plant change, as evidenced by observations in Sierra de Baza (Carrión et al., 2007a), Sierra de Gádor (Carrión et al., 2003b) or Sierra de Segura in Siles Lake (Carrión, 2002a). Sometimes, it even causes changes in the ecological structure, as in Ojos de Villaverde and Sierra de Alcaraz (Carrión et al., 2001b). In Laguna Seca of Sierra Nevada, Jiménez-Moreno et al. (2023) showed that microcharcoal maxima during the Holocene between 11 and 10.2 and 9.4–8.4 cal kyr BP were also linked to the available biomass under a mesothermal context. Some studies have proposed that, in terms of spatial extent, fire in Mediterranean Iberia may have been more significant (and occurred earlier during the Holocene) in coastal and pre-coastal ecosystems, affecting both flat areas and mountainous regions (Gil-Romera et al., 2010).

In a multi-sequence study, Connor et al. (2019) analyzed centennial- and millennial-scale changes in fire regimes to trace the consequences of fire on Mediterranean vegetation diversity during the Holocene. They found that the timing and direction of changes in fire and plant diversity in Mediterranean Iberia can be explained by long-term human-environment interactions dating back perhaps 7500 years, which aligns with those of previous studies (Carcaillet et al., 2002; Vannière et al., 2011). It can be reasonably inferred from the evidence that burning during the Neolithic period caused significant deforestation in areas subject to agricultural influence. This disturbance appears to have intensified between 5.5 and 5 cal kyr BP and has continued to do so throughout the last two millennia.

It can thus be concluded that climatic and anthropogenic factors influence the variation in fire incidence. The study indeed shows an increase in fire incidence associated with human activities, but this phenomenon has also been documented in other Mediterranean climate biomes where the fire is an inherently natural process, such as the South African Cape fynbos (Cordova et al., 2019; but see Mosher et al., 2024). The scenario in the southwestern Iberian Peninsula is reminiscent of an ever-burning vegetation type, such as the South African fynbos (Cordova et al., 2019; Mosher et al., 2024). Indeed, to the south-west of the LT study area, Mediterranean heathlands are prevalent in Los Alcornocales Natural Park (Fig. 2) (Gil-López et al., 2018). These Mediterranean heathlands are not only highly dependent on fire (Ojeda et al., 2010; Ojeda, 2020), but also exhibit strong similarities and convergence with fynbos (Ojeda et al., 2001). Although not universal to Mediterranean biomes, recurrent fires represent an intrinsic feature of the physiognomy and structure of various vegetation types in Mediterranean climate regions (Verdú and Pausas, 2007; Schwörer et al., 2024).

15. Herbivory

The identification of herbivory in pollen records is typically achieved by observing changes in the percentages or concentrations of ascopores of coprophilous fungi. However, it shall be noted that these fungi occur on both the dung of wild herbivores and domestic livestock (van Geel et al., 2003; Lee et al., 2022). In the case of LT, these spores have been observed from the beginning of the sequence, suggesting that large mammals frequented the lake margins during the Pleistocene and Holocene. A notable absence of Sordariaceae is observed between c. 31 and 24 cal kyr BP (Fig. 12). During the late Holocene, surrounding herbivory is most likely related to livestock, but there is no significant increase in Sordariaceae spores in the pollen record to suggest a greater impact of livestock compared to earlier phases.

In any case, at least during the Pleistocene, paleoecological indicators are not necessary to support the impact of large wild herbivores on ecosystem properties. After a meta-analysis of 297 studies and 5990 individual observations across six continents, Trepel et al. (2024) showed that large herbivores, especially megafauna, alter soil nutrient availability and promote open vegetation landscapes and biodiversity. By applying the REVEALS vegetation reconstruction method to 96 pollen records from the Last Interglacial in the temperate forest biome, Pearce et al. (2023) found that more than half of the interglacial forests, conventionally assumed as dense and ombrophilous, would have had less than 50% tree cover. They also found that the levels of heliophytism and forest heterogeneity were highly variable and only partially linked to climatic factors, strongly suggesting the involvement of natural disturbance regimes, especially herbivory.

It can be reasonably assumed that the situation was not markedly different in the Mediterranean basin during glacial phases and the first half of the Holocene. The Pleistocene of the southern Iberian Peninsula contains a significant record of large herbivorous and carnivorous mammals, some of which extended their regional existence compared to European temperate latitudes (Ochando et al., 2020b). The area surrounding the LT was likely grazed by a variety of species, including *Bos primigenius, Cervus elaphus, Capra pyrenaica, Capreolus capreolus, Equus caballus*, and *Stephanorhinus hemitoechus* (Vega-Toscano, 1988; Villaverde et al., 1998; Aura et al., 2002; Barroso, 2003; Finlayson et al., 2008). As previously stressed, the impact of cattle and, especially, ovicaprids in LT became increasingly significant during the Middle and Late Holocene (Wigand, 1978; Martín-Socas et al., 2004; Cortés-Sánchez et al., 2012). This is reflected in the fungal indicators (Fig. 12), although given the low level of paleomycological discrimination, their fluctuations could be taphonomically affected, making diachronic ecological interpretations speculative.

16. Final thoughts

This new paleoecological sequence from LT identifies and characterizes a major glacial refugium for the Mediterranean flora in the Strait of Gibraltar area of the Iberian Peninsula. This refugium represents a biodiversity hotspot that includes Mediterranean and Ibero-North African sclerophyllous elements, deciduous trees, conifers, thermophilous shrubs, and Tertiary relict taxa. The palynological frequencies of some mesothermic elements, especially oaks, during the full-glacial stages of the last ~40 kyr are among the highest recorded for the Mediterranean Basin.

Apart from indicating the persistence of the forest component, likely at mid-altitudes of the adjacent mountains, the pollen record from LT also shows interesting correlations with Mediterranean sea thermohaline dynamics and contains evidence of vegetation change (e.g. the spread of heliophytic herbs) in response to climate change and other

disruption factors. Some Pleistocene vegetation changes represent relatively rapid responses to abrupt global temperature changes, while others exhibit significant lags or do not occur at all. This behavior, which is episodically inertial, is a prominent feature of the forest vegetation in the southern Mediterranean Basin, documented both in short, high-resolution records (Carrión and van Geel, 1999; Carrión et al., 2001a), and in long records covering multiple glacial–interglacial cycles within the Quaternary (Tzedakis, 2007).

In addition to temperature, other factors play a significant role in the vegetation changes of LT, one of them being global atmospheric carbon dioxide, which may have influenced Mediterranean vegetation through its impact on moisture availability (Koutsodendris et al., 2023). In this scenario, rapid transitions from forest to steppe ecosystems would have occurred when precipitation thresholds were exceeded. Indeed, by the end of the Pleistocene, LT forest vegetation dynamics appear to have been strongly influenced by ecological interactions between species. However, precipitation changes may well have represented a trigger within a heterogeneous landscape with rugged orography, especially in the mountainous territories east of the study area. Once more, it appears that postglacial vegetation in LT is relatively more conditioned by the precipitation regime than temperature changes. However, competitive displacement may have also played a role. Notwithstanding, from the Neolithic period onwards, human activity undoubtedly became a fundamental factor modulating vegetation changes. Here we also report paleoecological indicators suggesting that both herbivory and fire have been present in the region throughout the entire study period.

It is provocative to note that, after several tens of millennia of showing reactivity to global temperature depletions, the southernmost part of the peninsula was reforesting at the end of the Last Glacial Maximum, while most of Europe experienced significant expansions of steppe areas, forest regressions, and biodiversity losses due to cumulative local extinctions of mesothermic species. Factors such as low evapotranspiration, changes in marine circulation, or high insolation values during the LGM could have played a role in supporting the described Mediterranean forest dynamics. Additionally, the territorial breadth and the structural, taxonomic, and interactive complexity of the woody populations and communities in the southern Baetic mountain ranges endowed these paleoecosystems with a particular biogeographical potential for the rapid expansion of species. In other words, the flora and vegetation of the Strait of Gibraltar region were resilient to climate extremes and disturbances. This resilience could be metaphorically described as “mithridatism” (Taleb, 2012: after Mithridates and his Antidotum Mithridatum method), referring to the result of exposure to small doses of a disturbance that, over time, makes the biological system “immune” to higher doses of the same disturbance.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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