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ORIGINAL PAPER

When dynamism is the baseline: long-term ecology of a Mediterranean seasonal wetland in the Doñana National Park (Southwestern Europe)

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Abstract

Mediterranean seasonal wetlands are amongst the world's most endangered ecosystems. Although seasonal wetlands' conservation is a European continental-scale priority, their long-term ecological dynamics are not well known, hampering the detection of baseline conditions. However, a long-term ecological viewpoint could aid in the detection of spatiotemporal factors controlling wetland development. We have applied a multi-proxy palaeoecological approach (palynological, microcharcoal, magnetic susceptibility, loss on ignition and diversity estimates analyses) on a 360-cm core retrieved from the El Sopetón (ElSo), a temporary wetland nested between dunes in the paradigmatic Doñana coastal area. The palaeoecological analyses reveal ~ 300–500-year-long wetland phases linked to dune immobilisation during humid periods. During the first wetland phase (AD ~ 40–315), upland and wetland vegetation diversity dynamics follow opposite trends owing to the different effect that dune proliferation had on them. Fixed dune landscapes provided upland spatial diversification, while they promoted a longer hydro-period in ElSo, simplifying wetland vegetation. During the second wetland phase (AD ~ 1550–2012), land-use change drove environmental dynamics. The mid-eighteenth-century pine afforestation to fix moving dunes marked an environmental tipping point, with the ElSo wetland transitioning from seasonal to permanent. This translated into a rising trend in upland diversity and a decreasing trend in the wetland one. Despite the recent pine afforestation, the palaeoecological findings evidence the autochthonous character of *Pinus pinea*, as well as the naturalness of the wetland species *Hydrocharis morsus-ranae* and *Ricciocarpos natans*. The geomorphological dynamism of the diverse Doñana coastal setting is the baseline for the area, modulating wetland-upland water connectivity and, ultimately, controlling biodiversity trends. The preservation of Doñana natural dynamism and landscape heterogeneity should be considered for the management, conservation and restoration of its seasonal wetlands.

Keywords 3170* habitat · Baseline · Holocene · Iberian Peninsula · Land-use change · Palaeoecology · Palynology · Priority habitat · Wetland conservation

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Introduction

Above 80% of the European wetlands are under threat (Custodio 2001). Seasonal wetlands, particularly, are extremely sensitive to perturbations and amongst the most receding type of wetlands (Blaustein and Schwartz 2001; Keeley and Zedler 1998). Seasonal wetlands are small, shallow, oligotrophic water bodies, waterlogged during the rainy season only, and exceptionally during all seasons in extremely rainy years (Camacho et al. 2009). Owing to their singularity, they are key habitats that provide many ecosystem services, such as water provisioning and purification (Camacho et al. 2009; Kumar et al. 2017).

These ephemeral habitats lie often on Mediterranean climate areas, withstanding strong human pressures. Not surprisingly, Mediterranean wetlands have demised at an alarming rate during the last century, and large conservation efforts are taking place in order to restore them and prevent their extinction (Silva et al. 2007), including their consideration as priority conservation habitat by the European Union (Habitat 3170*, 92/43/EEC). In addition to the already lost wetlands, the increasing aridity trend projected for the Mediterranean areas under the current global change scenario (Barredo et al. 2016) will surely trigger new waves of wetland demise, hence conservation efforts become even more critical (Blaustein and Schwartz 2001). It is in this context where the need for a wide temporal approach has been identified (Sousa and García-Murillo 2005). Wetlands store landscape- and local-scale information allowing a long-term environmental monitoring key for the evaluation of ecological dynamics under different climate scenarios (e.g. Valero-Garcés et al. 2000; Vegas-Vilarrúbia et al. 2011), as well as the identification of baseline conditions useful for their management (e.g. Daoud-Boattour et al. 2011; López-Merino et al. 2011; Willis et al. 2010).

Here we present the palaeoecological study of the Laguna del Sopetón (ElSo), a wetland located in the Doñana National Park (DNP, Southwestern Spain). The DNP is a hallmark site for conservation declared UNESCO Biosphere Reserve, UNESCO World Heritage Site, and Ramsar Wetland Site. This paradigmatic setting provides an excellent natural laboratory for environmental research. First, because its geomorphological dynamism of mobile and sub-mobile dunes promotes the appearance and disappearance of vernal wetlands (López Albacete 2009; Rodríguez Ramírez 1997). Second, because the DNP is a biodiversity hotspot due to its complex palaeogeographic history in the southwesternmost corner of Europe (García-Murillo et al. 2014; Médail and Quézel 1999). Lastly, because of the cultural significance of the area, with historical records documenting changes in land use and the landscape (García García 2016; Gómez-Bagghetun et al. 2012; Granados 1987).

With the overarching aim of recovering palaeoecological data useful for the conservation and management of vernal wetlands in the DNP, the objectives of this work are threefold. First, to assess the dynamism and lifespan of dune-supported water bodies. Second, to reconstruct long-term upland and wetland vegetation dynamics and their response to environmental change. Finally, to shed light on the autochthonous character of key and critically endangered taxa.

Materials and methods

Regional and local environmental settings

The DNP is located on the right bank of the mouth of the Guadalquivir River, in the Southwestern part of the Iberian Peninsula (Fig. 1a). Under a typically Mediterranean climate, the annual average temperature is 16.7 °C. Precipitation occurs mostly in autumn and winter, averaging ~ 543 mm annually (1978–2007 period). SW winds are dominant with a prevalence of 22.5% of the days in this direction (Jiménez Moreno et al. 2015).

The eastern sector of the DNP is covered by an extensive seasonal marshland of 140,000 ha, isolated from the Atlantic Ocean by a mobile dune complex and a spit barrier. To the west, it contacts with an extensive aeolian complex (Rodríguez Ramírez 1997; Fig. 1b). The marshlands and the aeolian complex are separated by a transitional fringe of graminoid pastures locally known as *vera* (Fig. 1c and d). The aeolian complex and the spit barrier are of littoral origin. They comprise fixed, sub-mobile and mobile dune systems. The mobile dune system consists of parallel dune trains slowly advancing north and westwards into the marshland. The dune crests are vegetated by *Ammophila arenaria, Artemisia crithmifolia, Armeria pungens* and *Juniperus phoenicea* ssp. *turbinata*, while the interdunal depressions are covered by *Pinus pinea* (Fig. 1c and d). The advancing dunes bury the pines in the leeward front, while regeneration occurs on the windward side of the precedent dune (López Albacete 2009; Fig. 1d). Recruitment of *P. pinea* is related to groundwater levels, occupying intermediary sandy ridges at the dune slacks. This position provides flood and drought protection for the seedlings (Muñor-Reinoso and de Castro 2005; Fig. 1d).

The stabilised systems are the remains of ancient dunes that span inland in E-NE direction (Fig. 1c and d). Their vegetation is locally known as *cotos*. *Cotos* are extensive savannoid formations spread over the stable sands and where vegetation segregates along a groundwater level gradient. On the one hand, *monte blanco*, a sparse scrubland with *Halimium halimifolium* and *Stauracanthus genistoides*, and usually accompanied by *Juniperus phoenicea* ssp. *turbinata,* dominates the more xeric enclaves. On the other hand, *monte negro*, an intricate nanophanerophytic Ericaceae and gorse scrub, together with *Quercus suber*, vegetate lower, moister areas (Fig. 1c and d; López Albacete 2009; Rivas Martínez et al. 1980).

More than 3000 water bodies are found in the dune depressions of Doñana (Díaz-Paniagua et al. 2010; Florencio et al. 2014). Most of them emerge during the wet season only, except for a series of eight permanent and semi-permanent ponds that appear in the hinge between the sub-mobile and stabilised dune systems (Fig. 1b, aeolian systems IV and V). These are the largest upland water bodies, spanning 1.4–45 ha and with maximum water depths of 0.7–3.4 m (Díaz Paniagua and Aragonés 2015). Wetland vegetation consists of concentric bands. Deeper, central areas are vegetated by submersed macrophytes, such as *Chara connivens, Chara galioides*, *Myriophyllum alterniflorum*, *Potamogeton pectinatus*, *Zannichellia obtusifolia* and species belonging to the *Ranunculus peltatus* complex. Marginal areas undergoing immersion-emersion cycles are vegetated by grasses, such as *Panicum repens, Agrostis stolonifera* and *Cynodon dactylon*, when desiccated. The outer rim of the wetlands is covered by helophytes, mainly Juncaceae and Cyperaceae (*Juncus acutus, J. maritimus, J. effusus, Scirpoides holoschoenus*), which contact with the upland *monte negro* or *monte blanco* communities (Sousa and García-Murillo 2005).

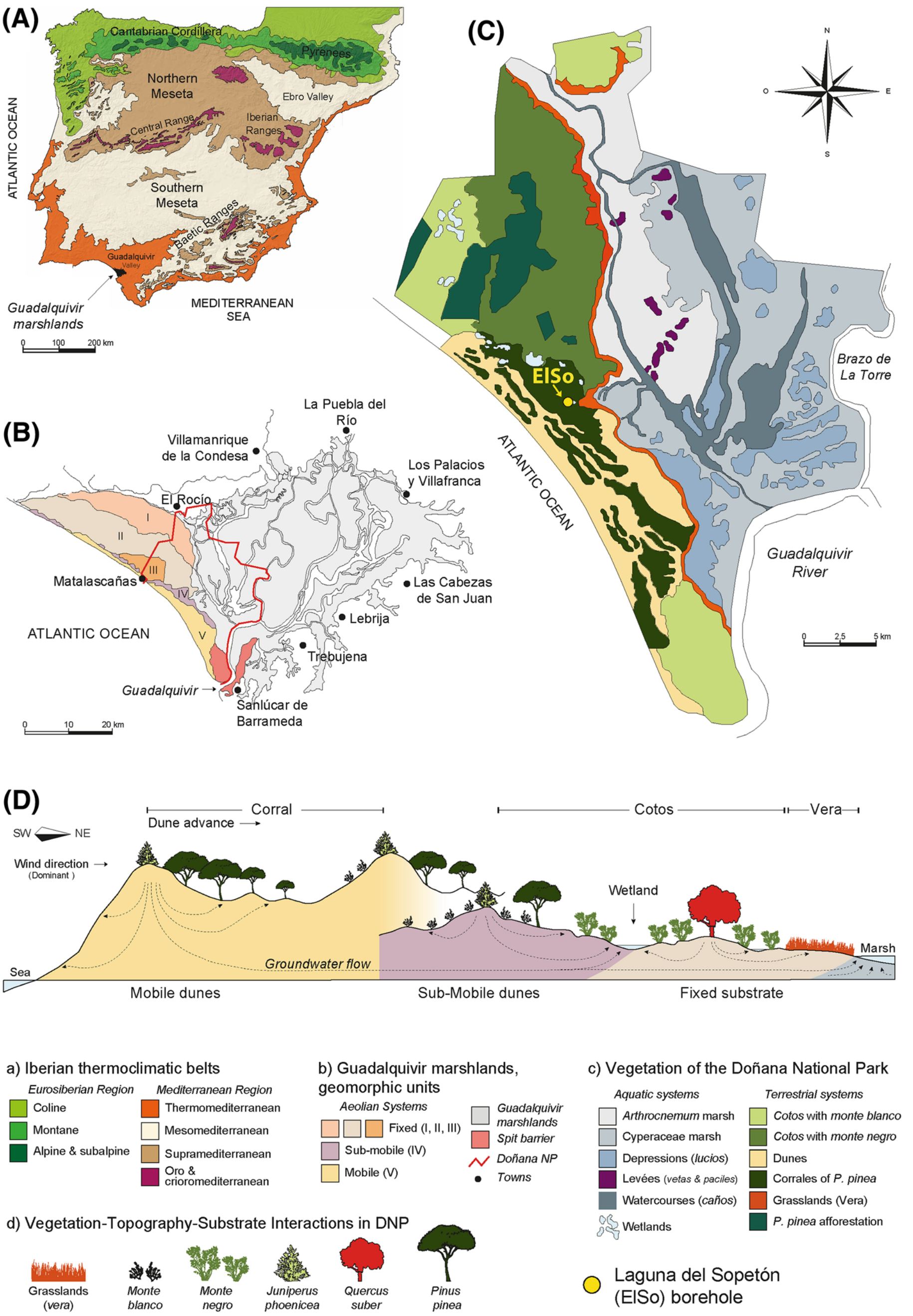


Fig. 1 Regional and local environmental settings of the study area. **a** Iberian thermoclimatic belts (modified from Manzano et al. 2017). The studied region is marked in black. **b** Guadalquivir marshlands and geomorphic units in the Doñana National Park (DNP, demarcated in red) and surroundings (after López Albacete 2009; and Rodríguez Ramírez 1997). **c** Main aquatic and terrestrial systems in the DNP and associated vegetation (from Zunzunegui 1997a and own data). The location of the ElSo core is marked with a yellow dot. **d** SW-NE transect of the DNP showing vegetation-topography-substrate interactions (modified from López Albacete 2009; Manzano et al. 2013; Rivas Martínez et al. 1980; and own data). (Color figure online)

The Laguna del Sopetón (ElSo) is a small semi-permanent pond (37% of the years undergoing summer desiccation) located near the western margin of the marshlands (Fig. 2), between the *vera* and the dune fields (Fig. 1b and c; 36°57′32.14″N, 6°27′03.69″W, Datum WGS84, 3 m asl). Maximum waterlogging covers 2.3 ha and reaches 70 cm depth (Díaz Paniagua and Aragonés 2015). Water is supplied mainly through groundwater discharges, and secondarily by surface runoff. In extremely rainy years, the pond connects with the Guadalquivir marshlands through a small temporary channel locally known as *caño*. Vegetation in ElSo follows the banded pattern described above. In addition, it also incorporated *Hydrocharis morsus-ranae* and *Ricciocarpos natans* until a few decades ago (Rivas Martínez et al. 1980), two species with a critical conservation status included in the Spanish Red List (Garilleti and Albertos 2012; Moreno 2008).

Coring, sedimentological analysis and radiocarbon dating

ElSo was cored in September 2012, when the pond was dry. A 360-cm-long core was retrieved by mechanical percussion and stored in plastic casings at 4 °C prior to visual description and subsampling for further analyses. In order to get the chronological framework of the recovered ElSo core, nine samples were sent for AMS radiocarbon dating to two laboratories, the ETH Laboratory of Ion Beam Physics (Switzerland) and the Poznan Radiocarbon Laboratory (Poland; Table 1). The analyses were performed on bulk sediment total organic carbon. The obtained radiocarbon dates were calibrated using the

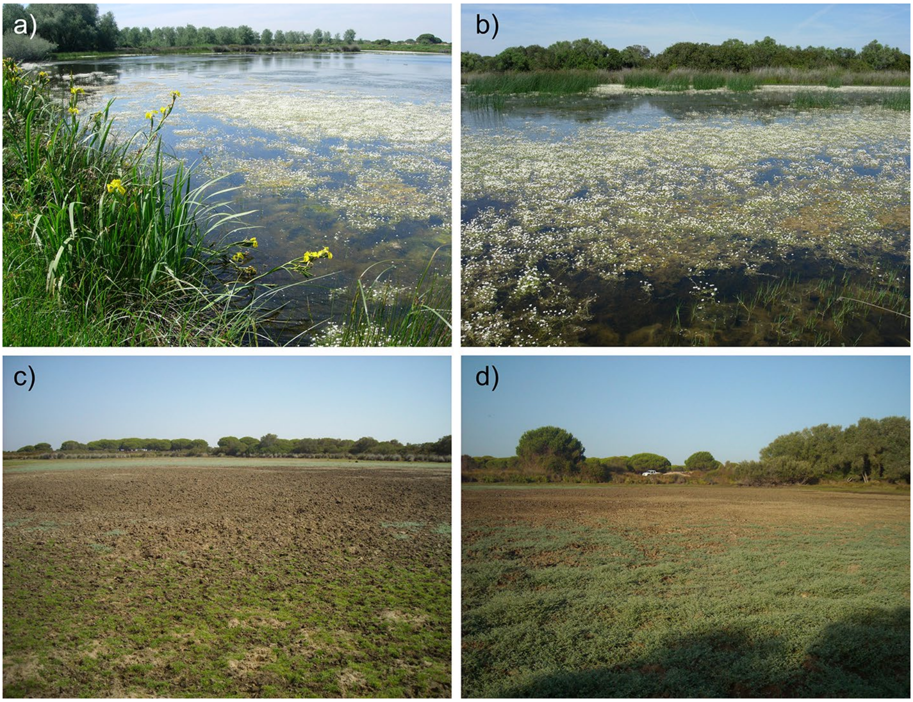


Fig. 2 Pictures showing the Laguna del Sopetón wetland, inundated during the spring 2009 (**a**, **b**), and dry during the summer 2012 (**c**, **d**), when cored. Photos by S. Manzano and P. García Murillo

Table 1 Radiocarbon dates from the ElSo palaeoecological record

Laboratory code	Depth (cm)	Thickness (cm)	Radiocarbon age (year BP)	Calibrated age ranges (cal. year BP)*
Surface	0			− 62 (AD 2012)
Poz-53794	48	2	135 ± 25	59–151
Poz-53795	70	2	215 ± 25	147–188
ETH-75301	90	2	353 ± 27	316–407
ETH-75302	92	2	435 ± 35	439–533
ETH-75304	151	2	1707 ± 28	1552–1637
Poz-53800	192	4	4925 ± 35	5597–5721
ETH-75308	228	10	4505 ± 30	5047–5021
Poz-53802	318	7	7790 ± 40	8506–8636

*Ages calibrated with the IntCal13 calibration curve (Reimer et al. 2013); *95% confidence intervals

IntCal13.14C terrestrial calibration curve (Reimer et al. 2013) and incorporated into the building of an age-depth model using linear interpolation and considering the top of the core as the coring date (AD 2012). The model was done using the Clam package for R (Blaauw 2010).

Organic matter (OM) and carbonate ($CaCO_3$) contents, together with the magnetic susceptibility (MS), were measured on 40 samples at Brunel University London (UK). Loss-on-ignition at 550 °C and 950 °C was used to measure OM and $CaCO_3$ contents respectively (Heiri et al. 2001). MS analysis was performed with the MS2B sensor of a Bartington MS2 susceptibility meter. The dried bulk samples were packaged in 10 cm^3 plastic pots and low-frequency measurements were taken twice at room temperature. Blank readings were obtained before and after each sample measurement to correct possible drifts. The average value of the two corrected measurements was taken as the final value (k). k values were normalised to sample mass (χ in $m^3\ kg^{-1}$).

Palynological analysis

The palynological analysis was carried out at the University of Murcia (Spain) in 100 2 cm-thick samples using a sample weight of ~ 5–15 g. The chemical treatment involved HF for silicate elimination, HCl for carbonate dissolution and NaOH for organic matter removal (Moore et al. 1991). Density separation was also incorporated (Erdtman 1969). The concentration of palynomorphs was estimated through the addition of known-concentration *Lycopodium* spore tablets (Stockmarr 1971). Palynomorph counting was completed under a light microscope at × 400 magnifications, and at × 1000 magnifications with immersion oil when required. Pollen and spore identification was aided with the University of Murcia reference collection, pollen atlases, and regional and general pollen identification keys (Díez et al. 1987; Faegri and Iversen 1989; Moore et al. 1991; Reille 1992, 1995; Saenz Laín 1982). Non-pollen palynomorphs (NPP) nomenclature largely follows van Geel (2001).

The upland pollen sum included a minimum of 200 pollen grains of upland taxa (trees, shrubs and herbs), and excluded aquatic taxa and Chenopodiaceae, whose main habitat in Doñana is the marshland (Rivas Martínez et al. 1980). Percentages of fern, bryophyte and fungal spores, as well as of other non-algal NPP, were calculated in relation to the upland sum. However, percentages of macrophytes, helophytes (including Chenopodiaceae), and algal micro-remains were calculated in relation to an independent wetland sum. Palynological diagrams were plotted with Tilia 1.7.16 (Grimm 2011). Palynological rarefaction and Pielou's evenness index were estimated independently for the wetland and upland data series using the Past software (Hammer et al. 2001). The sample at 188–190 cm depth was excluded from the wetland diversity estimates for taphonomic reasons (see "Discussion").

Microcharcoal particles larger than 10 µm were counted on the palynological slides and separated into two categories: smaller than 100 µm and larger than 100 µm. A minimum of 200 items (microcharcoal particles and *Lycopodium* spores) was counted per sample in order to calculate microcharcoal concentrations (Finsinger et al. 2004; Mooney and Tinner 2011).

Results

Sedimentological record and age-depth model

The ElSo core presents three dark layers with higher contents of organic matter at 300–297, 190–143 and 90–0 cm, alternating abruptly with sand packages (Fig. 3). Accumulation rates oscillate between 0.01 and 0.05 cm $year^{-1}$ in the sand packages and 0.11–0.26 cm $year^{-1}$ in the organic layers (Fig. 3). $CaCO_3$ and OM contents are low in the sand packages, while their values increase in the organic layers (Fig. 3). MS values are consistent with this trend. The ElSo core spans from ~ 8.4 cal. kyr BP until the present, with the three organic layers

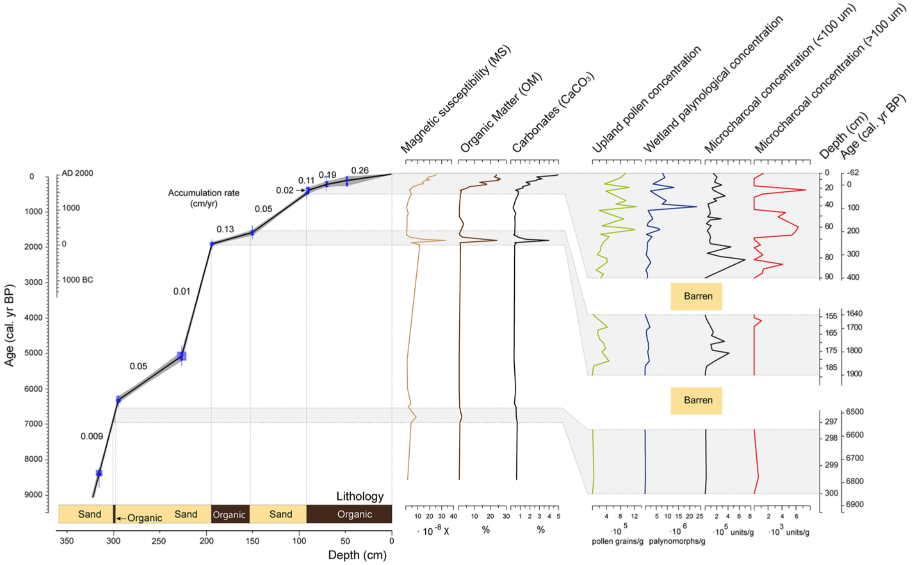


Fig. 3 Age-depth model of the ElSo sequence including lithology (bottom) and, from left to right: magnetic susceptibility, organic matter and carbonate content, upland and wetland palynomorph concentration, and microcharcoal concentrations (< 100 µm and > 100 µm). Grey shading marks the polleniferous sections. (Color figure online)

spanning at ~ 6840–6540 cal. year BP, ~ 1910–1635 cal. year BP, and < ~ 400 cal. year BP (Fig. 3). The ages of the sand packages have been linearly interpolated between available dates, derived from the contact samples between the sandy organic layers, and further constrained with three datations made within them. They span between ~ 8400–6840 cal. year BP, ~ 6540–1910 cal. year BP, and ~ 1635–400 cal. year BP (Fig. 3).

Palynological records

Although 100 samples of the ElSo core were palynologically studied, only 39 samples, distributed in three polleniferous packages, contained palynomorphs. The three polleniferous packages (ElSo-1 to ElSo-3) correspond with the organic layers, while the sand packages were barren (Figs. 3 and 4, supplementary material). The polleniferous packages presented a large number of different taxa and all palynomorphs had good preservation states, so there is no indication of a bias in differential preservation.

In **Zone ElSo-1** (two samples, 300–297 cm, ~ 6840–6540 cal. year BP, ~ 4890–4590 BC), the upland and wetland palynological concentrations are the lowest of the three organic layers, averaging ~ 20,900 and ~ 79,900 palynomorphs g^{-1} respectively (Fig. 3). Open landscapes dominate the upland vegetation (Fig. 4). Poaceae is the taxa dominating the upland assemblage with percentages of ~ 35%. Cichorioideae is also an important herbaceous element, with percentages of ~ 10%. The *monte blanco* taxa prevail over the *monte negro* taxa, with *Halimium/Helianthemum* type as the dominating shrub (~ 10–15%). Evergreen *Quercus* is the prevalent tree taxon (~ 5–10%), with the secondary presence of *Pinus pinea/halepensis* type and *Quercus suber.* The NPP HdV-200 shows high values (60–250%), especially at the bottom sample. Macrophytes are the main assemblage of the wetland vegetation (Fig. 4), with *Myriophyllum alterniflorum* type (~ 30–35%) and *Potamogeton* (~ 7–10%) as the best-represented ones, while *Gloeotrichia* is the most abundant algal taxon (~ 10–15%). Microcharcoal values are consistently low (Fig. 3).

In **Zone ElSo-2** (11 samples, 190–143 cm, ~ 1910–1635 cal. year BP, AD ~ 40–315), the upland and wetland palynological concentrations are an order of magnitude larger than in ElSo.1, averaging ~ 219,300 and ~ 976,600 palynomorphs g^{-1} respectively (Fig. 3). *Halimium/Helianthemum* type dominates the upland vegetation (~ 90%) in the bottom sample of ElSo-2. However, the herbaceous component, with Poaceae (~ 35–70%), Cichorioideae (~ 10%) and *Aster* type (~ 5%), dominates the rest of ElSo-2 (Fig. 4). The tree stratum is represented by *Pinus pinea/halepensis* type (~ 5–10%), evergreen *Quercus* (~ 5%) and *Quercus suber* (~ 5%), becoming more important in the middle part of ElSo-2 (AD ~ 100–250; Fig. 4). The *monte negro* scrub (*Erica* type, *Phillyrea, Olea, Pistacia;* ~ 5–10%), and some wetland taxa (*Myriophyllum alterniflorum* type, ~ 24–42%; Ranunculaceae, ~ 5–11%; *Gloeotrichia*, 12–18%), are also more abundant in the middle part of ElSo-2 (Fig. 4), as well as the microcharcoal particles < 100 µm (Fig. 3). On the contrary, the *monte blanco* elements (*Halimium*/*Helianthemum* type, *Cistus* type) and *Juniperus*, together with Zannichelliaceae, Chrysophyceae, Zygnemataceae and *Botryococcus* are better represented at the bottom and top parts of ElSo-2 (Fig. 4). Indeterminate fungal spores, fungal hyphae and *Glomus* display a similar pattern (Fig. 4). Upland diversity estimates show a peak reaching highest values in the middle part of ElSo-2 (AD ~ 100–250), while wetland diversity estimates show two peaks with high values at the bottom and top parts of ElSo-2 (before AD ~ 100 and after AD ~ 250; Fig. 5).

In **Zone ElSo-3** (26 samples, 90–0 cm, < ~ 400 cal. year BP, AD ~ 1550–2012), the upland and wetland palynological concentrations are high, averaging ~ 5,454,000

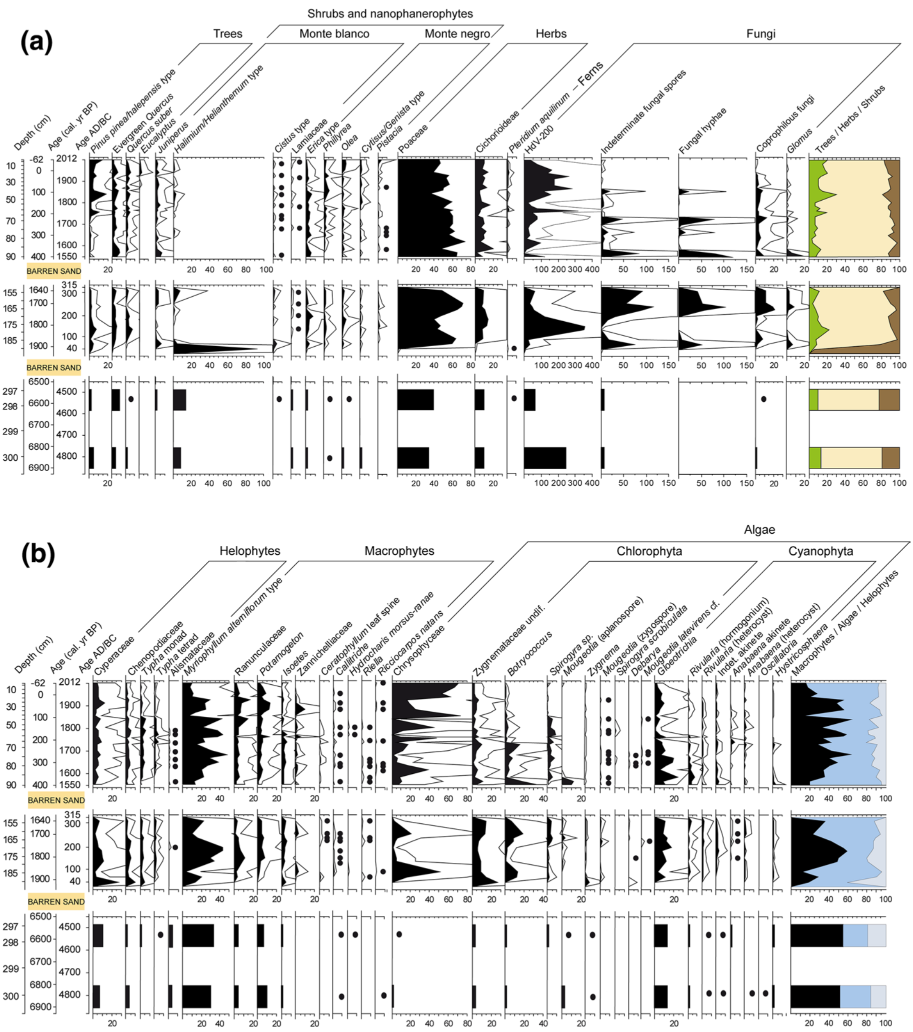


Fig. 4 Synthetic palynological diagram of the ElSo core plotted against age. **a** Upland taxa and fungi. **b** Wetland taxa. Exaggeration curves (×5) are plotted in white. Refer to supplementary material for the complete palynological diagram

and ~ 4,366,000 palynomorphs g^{-1} respectively (Fig. 3). Although Poaceae is again the main component of the upland vegetation (~ 40–70%), a rising trend in tree and shrub pollen is observed (Fig. 4). Evergreen *Quercus* and *Pinus pinea/halepensis* type are the best-represented trees (Fig. 4). *Juniperus* and the *monte blanco* elements are more prevalent from AD ~ 1750 onwards. In the same fashion, *Phillyrea*, *Pistacia*, *Cytisus/Genista* type and *Pteridium aquilinum* are better represented towards the top of ElSo-3. *Eucalyptus* appears at AD ~ 1920. The wetland vegetation is dominated by *Myriophyllum alterniflorum* type and Chrysophyceae, both displaying opposite see-saw patterns. The former shows a decreasing trend from AD ~ 1750 onwards, while the latter shows an increasing trend and peaks every 50–100 years (Fig. 4). *Gloeotrichia*, *Botryococcus* and *Spirogyra* are more important at the ElSo-3 onset, decreasing their values after AD ~ 1750 (Fig. 4).

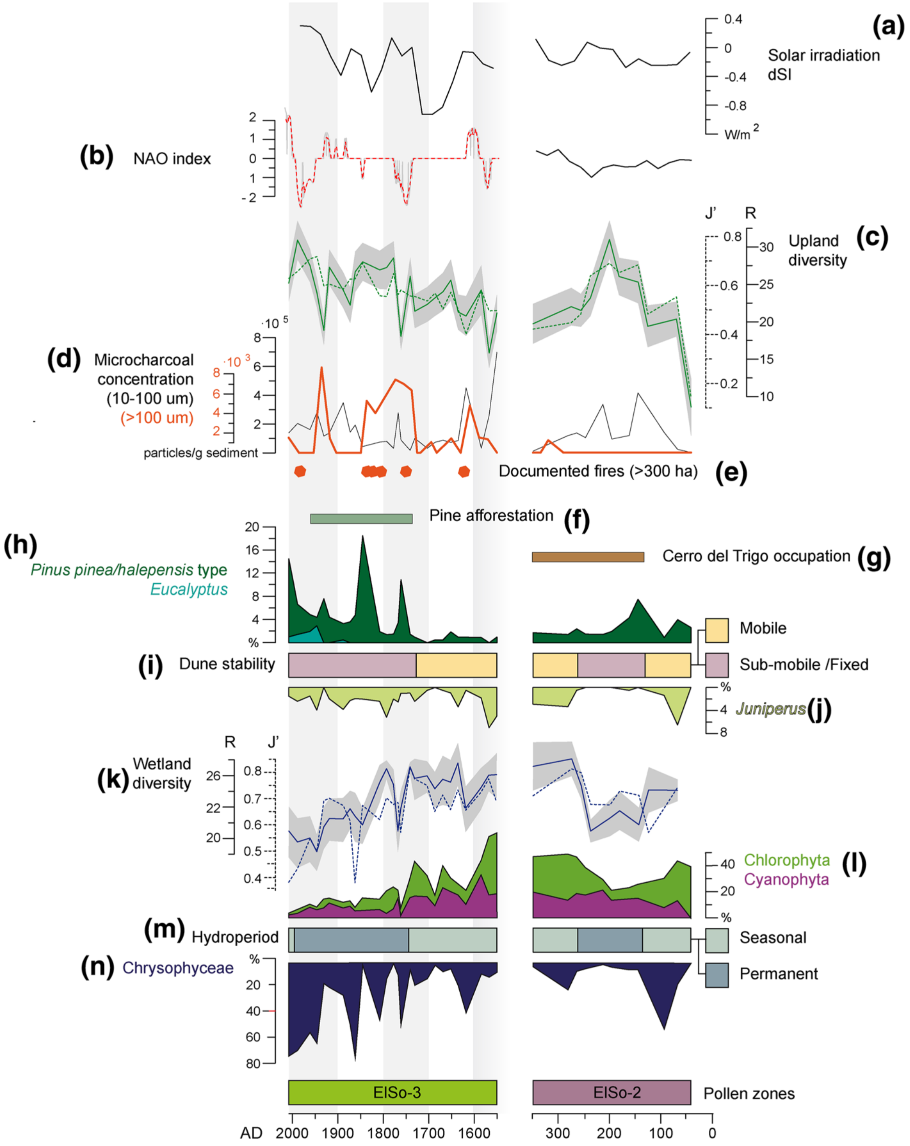


Fig. 5 Chronology of palaeoecological and palaeoclimate changes during the ElSo-2 and ElSo-3 wetland phases. **a** Solar irradiation (Solanki et al. 2004). **b** NAO index (red dashed line from Trouet et al. 2009; solid line from Olsen et al. 2012). **c** Upland palynological rarefaction (R) and Pielou's evenness index (J'). **d** Microcharcoal concentrations (< 100 µm and > 100 µm). **e** Documented fires of more than 300 ha (Sousa and García-Murillo 2005). **f** Documented *Pinus pinea* afforestation (Díaz-Paniagua et al. 2015). **g** Occupation of the Cerro del Trigo Roman fishing and salting factory (Campos et al. 2002). **h** Pollen percentage records of *Pinus pinea/halepensis* type and *Eucalyptus*. **i** Inferred dune mobility at a landscape scale. **j** Pollen percentage record of *Juniperus*. **k** Wetland palynological rarefaction (R) and Pielou's evenness index (J'). **l** Percentage records of Chlorophyta and Cyanophyta. **m** Inferred hydroperiod for the ElSo wetland. **n** Percentage record of Chrysophyceae. (Color figure online)

Microcharcoal particles < 100 µm show higher concentrations at AD ~ 1550–1750. Microcharcoal particles > 100 µm show more abrupt dynamics, with maxima at AD ~ 1630, ~ 1780–1860 and ~ 1940. Wetland and upland diversity estimates display opposite trends, with an upland increasing trend and a wetland decreasing trend (Fig. 5).

Discussion

The palaeoecological record of a Doñana seasonal wetland

Origin of the organic layers in the ElSo palaeoecological record

The recovered ElSo core cuts across three organic layers and three sand packages (Fig. 3). The oldest organic layer ElSo-1 is 3 cm thick only, spanning about ~ 300 years (~ 6840–6540 cal. year BP). It is most likely that ElSo-1 belongs to a hydromorphic soil that developed when an excess of moisture prevented total decomposition of the organic matter and allowed soil formation. This could have happened after the deflation of a previously existing dune nearing the phreatic layer to the soil surface. Although total decomposition did not happen, as the organic matter content is higher than in the previous and following sand packages and samples were not barren, the ElSo-1 phase is characterised by the lowest upland and wetland palynomorph concentrations of the three organic layers (Fig. 3). This is probably related to the poor pollen preservation in soils compared to wetland deposits (Dimbleby 1961). The wetland vegetation represents either periodic stagnant waters or the occasional development of ephemeral pools in an edapho-hygrophilous environment, such as an interdune depression (López Albacete 2009). The reconstructed upland vegetation provides further evidence in this direction (Fig. 6), as it features a very open landscape dominated by grasses and rockroses (*Halimium/Helianthemum* type). Locally, rockroses include psammophilous (*Halimium commutatum, H. halimifolium*) and pioneer (*H. halimifolium*) species on the windward side of mobile dunes (Zunzunegui et al. 1997b).

The development of the hydromorphic soil depicted by the ElSo-1 organic layer at ~ 6840–6540 cal. year BP, is coeval with the Holocene sea-level maximum, occurring locally at ~ 6900–6500 cal. year BP (Zazo et al. 1994). Higher sea levels translate into higher aquifer discharge levels, triggering a rise in the phreatic layer (Werner and Simmons 2009). The end of the Holocene marine transgression at ~ 6500 cal. year BP would have contributed to a decrease in the phreatic layer and prompted the mobilisation of sand (Fig. 6). Local dune expansion episodes have been attributed to the regional development of an aridity trend from ~ 5000 cal. year BP (Fletcher et al. 2007; Jiménez-Moreno et al. 2015). Indeed, the ElSo-1 organic layer is topped by a 107-cm thick sand package, depositing at rates of 0.05–0.01 cm year^{-1} for a period of ~ 4600 years, until the development of a new organic layer ElSo-2 (Figs. 4, 6).

The subsequent ElSo-2 and ElSo-3 organic layers have a thickness of 47 and 90 cm respectively. Their larger thickness, organic matter levels, accumulation rates, and palynological concentration (Fig. 3), evidence the development of two wetland environments at AD ~ 40 and AD ~ 1550, spanning ~ 275 and ~ 460 years respectively (Figs. 4 and 5). These wetland episodes are also separated by a sandy horizon derived from a new episode of aeolian reactivation burying the ElSo-2 wetland sediments (Fig. 6).

Fig. 6 Landscape dynamism and heterogeneity of the are inferred after the palaeoecological study of the ElSo record. The long-term fluctuation in the phreatic level affects the vegetation dynamics, impacting on dune mobility. Humid periods promote the development of denser vegetation, fixing the substrate and allowing the formation of hygrophilous soils (**b**) or wetlands (**d**, **f**). During drier periods, low phreatic levels hamper the development of vegetation, allowing dune mobility (**a**, **c**, **e**). The subsequent development of mobile aeolian systems buries the organic edaphic or wetland deposits (**c**, **d**). Colour code of the developing dune systems follows the aeolian geomorphic units of Fig. 1b ▶

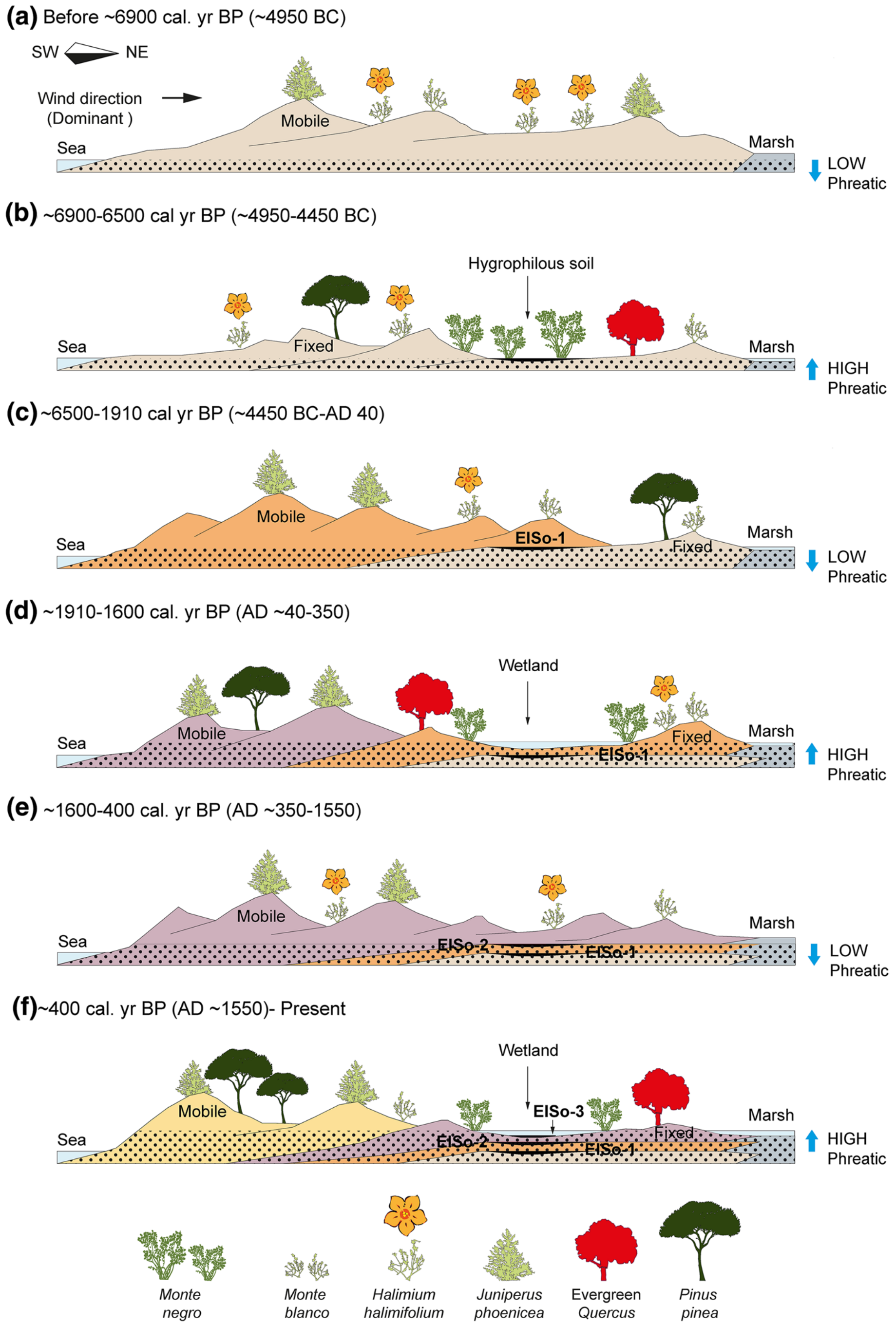
Although these sand accumulation phases are recurrent, their palynological barrenness hampers the reconstruction of the past vegetation history. Nonetheless, mobile sandy environments represent a major constrain for the development of vegetation, with very few specialists adapted to them. Therefore, it is probable that their past vegetation was analogous to the present vegetation.

The first wetland phase (ElSo-2; AD ~ 40–315)

The onset of the ElSo-2 organic layer is framed within the last centuries of the Ibero-Roman Humid Period (IRHP, 5th century BC—5th century AD). The IRHP is coincident with the most negative phases of the North Atlantic Oscillation (NAO), which result in intensified autumn and winter precipitation regimes in the South of the Iberian Peninsula (Ramos-Román et al. 2016). Under moister circumstances with enhanced groundwater discharges and a higher phreatic layer, the expansion of a denser *Pinus*, *Quercus* and scrubby upland vegetation traps dunes, stabilising the geomorphological profile and allowing the development of hydromorphic soils and wetlands (Dabrio et al. 1996; Fig. 5).

The basal sample of the ElSo-2 organic layer shows very high percentages of *Halimium/Helianthemum* type (Fig. 4), pointing to the development of a rockrose formation on the windward side of a deflated dune. In this basal sample, upland and wetland palynomorph concentrations are comparable to those found in the ElSo-1 organic layer (Fig. 3), suggesting that the ElSo-2 wetland phase occurred after the development of a hydromorphic soil in a dune depression (Fig. 6). High percentages of *monte blanco* and *Juniperus,* likely the inland dune-crest species *Juniperus phoenicea* ssp. *turbinata,* indicate an undulating landscape. Sinuous dune landscapes in Doñana enhance water supply to the lower lying environments (Manzano et al. 2002; Muñoz Reinoso and de Castro 2005), promoting the emergence of water bodies (Fig. 1d).

Three wetland sub-phases are identified in ElSo-2, after the development of the previous hydromorphic soil, at AD ~ 50–100, AD ~ 100–250 and AD ~ 250–315. They are likely climatically-induced by changes in solar irradiation—locally controlling wind direction and intensity (Zazo et al. 1994)—, and NAO modes—determining autumn–winter precipitation (Ramos-Román et al. 2016) (Fig. 5). The first wetland sub-phase (AD ~ 50–100) pictures a surrounding mobile substrate, as evidenced by the notable presence of indeterminate fungal spores, fungal hyphae and the soil erosion indicator *Glomus* (Anderson et al. 1984; Fig. 4). This first wetland sub-phase shows the co-occurrence of ecologically divergent algal taxa (Fig. 6) such as Chlorophyta-Cyanophyta (eutrophic habitats) and Chrysophyceae (oligotrophic, weakly buffered habitats), indicating a marked seasonal character. Eutrophic phases would correspond to the waterlogged season, whereas oligotrophic conditions would dominate during the desiccation process. The seasonal, temporary character of the first ElSo-2 wetland sub-phase is also supported by the presence of *Riella* (Cirujano et al. 1988).



The second ElSo-2 wetland sub-phase (AD ~ 100–250) is synchronous with a more negative NAO phase (Fig. 5). In this sub-phase, a decrease in the *monte blanco* is detected, while a development of the *monte negro* hygrophilous scrub (*Erica* type, *Olea*, *Phillyrea*, *Pistacia*) together with the higher presence of evergreen *Quercus* and *Quercus* suber (Fig. 4), evidences a rise in the groundwater levels (Dabrio et al. 1996). This change in the upland vegetation mirrors in the wetland environment. The proliferation of macrophytes commanded by *Myriophyllum alterniflorum* type, Ranunculaceae and *Potamogeton* together with the sharp decrease in Chrysophyceae and Chlorophyta point to the development of a permanent water table (Fig. 5).

During the last ElSo-2 wetland sub-phase (AD ~ 250–315), a reactivation of the dune systems is identified, likely linked to the drier conditions of a more positive NAO mode (Fig. 5). The reactivation of the dune systems and the less humid conditions are evidenced by the larger importance of *Juniperus* and the *monte blanco* together with the decrease in the *monte negro* elements (Figs. 4 and 5). In addition, these changes in the upland vegetation are, again, reflected in the wetland environment. The previous permanent water body returns to a seasonally contrasting stage. This is manifested by the co-concurrence of Chrysophyceae, Chlorophyta and *Riella* (Figs. 4 and 5).

Diversity estimates (palynological rarefaction and evenness) of both the upland and wetland palynological assemblages present similar curves. However, upland and wetland diversity dynamics display inverse trends (Fig. 5). Wetland palynological diversity presents higher values during the reconstructed seasonal wetland sub-phases (AD ~ 50–100 and AD ~ 250–315), while it shows lower values during the reconstructed permanent wetland sub-phase (AD ~ 100–250). Upland palynological diversity, on the contrary, peaks during the most humid period when the wetland was permanent (Fig. 5). On the one hand, wetland diversity responds favourably to seasonal inundation-desiccation cycles, as species of different ecological affinities could coexist in space and in time; while the more stable conditions of a permanent waterbody host taxa with similar ecological affinities. On the other hand, the diversity of the upland landscape is fostered under moister conditions, when the *monte negro* scrub is prominent and the substrate is stabilised (Fig. 4). In sum, both upland and wetland diversity trends are controlled by changes in groundwater supply linked to precipitation, and ultimately by the geomorphological configuration of the surrounding landscape, which defines the aquifer volume and recharge surface (Manzano et al. 2002).

It is noteworthy that for most of the ElSo-2 timespan, the fishing-and-salting Roman factory of Cerro del Trigo (second–sixth centuries AD) was active (Fig. 5). This settlement was situated 10 km S of the ElSo wetland, near the Guadalquivir palaeoestuary (Campos et al. 2002; Rodríguez-Ramírez et al. 2016). The maximum values of coprophilous fungi and a small rise in microcharcoal particles (> 100 µm) detected during the last century of the zone ElSo-2 could indicate the intensification of the human pressure (Fig. 5). However, the lack of further evidence impedes a conclusion, as fire and grazing indicators could be influenced by both natural (e.g. higher fuel load triggering wildfires, and wild fauna) and anthropogenic causes.

The second wetland phase (ElSo-3; AD ~ 1550-present)

The onset of the second wetland phase indicated by the ElSo-3 organic layer is also associated with a wet period (AD 1580–1650, Rodrigo et al. 1999). In a similar fashion to the development of the ElSo-2 wetland, the ElSo-3 wetland phase undergoes changes in its hydroperiod throughout its time span. From the onset of the wetland phase (AD ~ 1550) to the mid-eighteenth-century the aquatic environment shows a seasonal character, as indicated by the coexistence of the oligotrophic and eutrophic algal taxa *Ceratophyllum* and *Riella* (Figs. 4 and 5). Diversity estimates remain stable during this first sub-phase. From

AD ~ 1750 onwards, permanent, weakly-buffered conditions are inferred from the large increase in the representation of the remains of the oligotrophic Chrysophyceae, and from the disappearance of meso-eutrophic algal taxa (Zygnemataceae, *Gloeotrichia*) and *Riella* (Fig. 4). The wetland permanent conditions meant a simplification of the aquatic environment that translated into a decrease in the aquatic diversity due to the extinction of the palynological signal of some helophytes (e.g. Alismataceae), macrophytes (e.g. *Riella, Ceratophyllum*) and algae (e.g. *Spirogyra scrobiculata, Mougeotia latevirens* cf.) associated with fluctuating, rather than permanent, environments (Fig. 4).

In the case of ElSo-3, and in contrast with ElSo-2, this seasonal-to-permanent transition is not only linked to climate (i.e. more humid conditions) but also to land-use change (Fig. 5). The early ElSo-3 landscape, framing the development of the seasonal wetland, displayed an open character with sparse evergreen *Quercus* and *Quercus suber*, as well as *Pinus*. High percentages of *Juniperus*, *Glomus* and fungal hyphae evidence the existence of an undulating, mobile substrate at the onset of ElSo-3. This landscape had been managed as a hunting reserve since the fourteenth century AD (Granados 1987; Sousa and García-Murillo 2005). However, after AD 1682, the intensification of animal husbandry and timber production for the Dukes of Medina Sidonia—the local landowners—marked a historical land-use change in the area (Díaz-Paniagua et al. 2015; Granados 1987; Sousa and García-Murillo 2005). Increased lumbering and harvesting of psammophilous species for thatching diminished forest cover and restricted the presence of *Pinus pinea,* a major soil fixation species, to the southern tip of the Doñana spit barrier (García García 2016; García-Murillo, unpublished data). Under such management, a regional-scale landscape smoothing is recorded in ElSo-3 with a demise in *Juniperus* (Fig. 5), a dune crest coloniser. This explains the early ElSo-3 seasonal hydroperiod: landscape smoothing reduces the volume of the dune aquifer, hence the summer drought groundwater compensation (Fig. 5).

As consequence of the increasing exposition of sandy substrates (Díaz-Paniagua et al. 2015; García García 2016), a pulse of enhanced westerlies under the arid and colder conditions of the first decades of the eighteenth century provoked the aeolian reactivation in Doñana (Costas et al. 2012; Granados et al. 1988; Rodrigo et al. 1999). To the west of the DNP the undulating dune landscape was deflated (geomorphic units I–III; Fig. 1b), whereas to the east, on the Doñana spit barrier, an active dune system developed (Fig. 1b). The development of a sinuous dune landscape, hence greater groundwater storage capacity, mirrors in the switch to a permanent hydroperiod from this moment onwards (Fig. 5).

Nonetheless a general concern arising from nearby populations in relation to the advancing dunes marked another tipping point in the management of Doñana (Granados et al. 1988). An extensive afforestation with *Pinus pinea* was commissioned to trap the advancing dunes at AD 1737. A rising trend in the percentages of *Pinus pinea/halepensis* type in the topmost part of the ElSo-3 evidences the local importance of *P. pinea* in since the eighteenth century. The higher background values of *Juniperus* provide palaeoecological support for the effectiveness of pine afforestation in dune fixation, a effectiveness also recorded in documentary archives.

However, superimposed to the impact of human management on landscape dynamics, fluctuations in *Pinus* and *Juniperus* curves spanning to the present indicate local substrate dynamism linked to changes in solar insolation and in the NAO modes (Fig. 5). Solar-controlled dune movements and reshaping force continuous but spatially uneven physiographical rejuvenation, which in turn diversifies upland Doñana landscapes (Muñoz-Reinoso and García Novo 2005). This translates in an increasing trend in the estimates of upland palynological diversity in ElSo-3 (Fig. 5). Indeed, the secular coexistence of stabilised substrates to the west and of parallel trends of advancing dunes in the surroundings of the larger, permanent ponds is recorded in contemporary maps (complied by Sousa and García-Murillo 2005). The maps show modifications in shape and extension of the ponds as a consequence of dune advance (Sousa and García-Murillo 2005). These maps do not depict the ElSo pond until the nineteenth century (Sousa and García-Murillo 2005), which is striking given it is currently one of the larger wetlands in the area. Its absence in the early maps, hence, has to be related to the hydro-period of the wetland. Plausibly, cartographers, interested in rangeland management and animal husbandry would have overlooked a wetland desiccating during the summer.

The amelioration of the climate after the Little Ice Age, in the late 1800s, could have influenced the land-use change detected in the ElSo palaeoecological record with the decrease in silvicultural practices and the plantation of *Eucalyptus* (Díaz-Paniagua et al. 2015; Figs. 4 and 5). In addition, lower values in the record of coprophilous fungi are noticeable in the most recent stages of the ElSo-3 wetland. The lower values in coprophilous fungi are synchronous with the declaration of the DNP in 1969 (Fig. 4), when the presence of humans and animal husbandry was strongly restricted (Díaz-Paniagua et al. 2015).

For the last 50 years, the urban development of Matalascañas and the establishment of intensive irrigated farming next to the DNP have controlled the ecological dynamics of Doñana (Rodríguez and De Stefano 2013). Both anthropogenic activities rely on groundwater extraction, competing with the Guadalquivir marshes and surrounding wetlands for water (Muñoz Reinoso 1996). Abusive, often illegal, groundwater extraction (Rodríguez and De Stefano 2013) superimposed to a decreasing precipitation trend (Rodrigo et al. 1999) explain the general demise of the wetlands at Doñana. The most patent evidence of this demise is the disappearance of some ponds (e.g. Laguna del Brezo), the switch from a permanent to a temporary hydroperiod in other ponds (e.g. Laguna del Taraje, Laguna Dulce, Charco del Toro), and the general reduction in their size (Díaz Paniagua and Aragonés 2015; Serrano and Serrano 1996; Sousa and García-Murillo 2005). The two latter circumstances are the case of the ElSo wetland (Fig. 2), which accordingly shows wetland diversity minima during the last 50 years (Fig. 5).

Biogeographical and conservation remarks

On baseline conditions and conservation perspectives

The ElSo palaeoecological record evidences the key role of substrate dynamism and landscape heterogeneity in the biodiversity dynamics of the area. Waterlogged environments form in the dune valleys, where hygrophilous soils or ponds develop depending on the position of the phreatic layer (Manzano 2001; Muñoz Reinoso 1996). In turn, the phreatic level is related to the groundwater stored in the dune aquifer whose volume depends on the size and shape of the dunes (Manzano et al. 2002; Fig. 6).

Wind is a major driver of the ecological dynamics of Doñana (Fig. 6). Considering the inherent uncertainty of radiocarbon-based age-depth modelling, the lifespan of the ElSo organic layers (~303, ~275 and ~462 years; Fig. 3) seems to be tuned to the 200–400-year rhythmicity found by Zazo et al. (1994) in the evolution of the beach ridges of the Doñana spit barrier. This periodicity, attributed to sunspot cycles (Zazo et al. 1994), has also been found in the Early to Mid-Holocene sequence from the Lucio de la Cancela de la Aulaga at the Doñana marshlands (Manzano et al. 2018), pointing to enhanced westerlies episodes as major drivers of substrate dynamism (Costas et al. 2012). At a landscape scale, however, the impact of wind is not even. Dune development and movement, prompting physiographical rejuvenation, responds to local, variable factors (Rodríguez-Vidal et al. 2014). The consequent landscape heterogeneity promotes an environmental mosaicism in which ecologically different wetlands at different senescence stages coexist (Florencio et al. 2014). Therefore, the Doñana substrate dynamism and geomorphological heterogeneity is the baseline.

Under the projected scenarios of global change (Barredo et al. 2016), the ongoing aridification trend forecasted for Southern European Mediterranean environments most likely will place the Doñana temporary pools in the brink of extinction. Superimposed to the consequences of global change, the massive groundwater extraction taking place in Doñana contributes to the same direction as global change, accelerating the rates of environmental degradation and wetland destruction. Proof of this degradation can already be found in the total desiccation of some of the formerly permanent ponds of the DNP (Díaz Paniagua and Aragonés 2015; Serrano and Serrano 1996; Sousa and García-Murillo 2005). The future of the highly diverse and heterogeneous environments of Doñana will then rely on the agreement between stakeholders to balance resource extraction, biodiversity conservation and an adequate ecological restoration.

On the autochthonous character of Pinus pinea: an architect species in the dynamic baseline of Doñana

The naturalness of pines in the Iberian Peninsula has been widely debated during the last decades (Carrión et al. 2000, 2004; Pérez Latorre et al. 1999). Such is the case of *Pinus pinea* in SW Iberia (e.g. López Albacete 2009; Martínez and Montero 2004; Pérez Latorre et al. 1999). Phytosociological floristic interpretations, supported on the general assumption that the present-day presence of *Pinus pinea* in SW Iberia derives from the eighteenth-century afforestation (Rivas-Martínez 1987), have dominated the twentieth-century scientific literature (López Albacete 2009). The ElSo palaeoecological record supports the occurrence of this species since the Mid-Holocene, much earlier than the eighteenth-century plantations (Fig. 5). This agrees with the palaeoecological evidence in Doñana (Jiménez-Moreno et al. 2015; Yll et al. 2003; Manzano et al. 2018) and the broader SW Iberia (e.g. Badal 1998; Carrión et al. 2008; López-Sáez et al. 2002; Menéndez-Amor and Florschütz 1964; Stevenson 1985, 1984; Stevenson and Harrison 1992; Stevenson and Moore 1988), supporting the presence of this species from, at least, the Late Pleistocene. The ascription of *Pinus pinea/halepensis* type to *Pinus pinea* is supported by the coetaneous occurrence of *Pinus pinea* pinecones, bracts and seed remains across the region (see Martínez and Montero 2004 for review).

Palaeobotanical evidence endorses, thus, the autochthonous character of *Pinus pinea* in the sandy environments of SW Iberia. *Pinus pinea* relationship with substrate stabilisation suggests its architect role locally, contributing to the baseline dynamism of the area (Fig. 6). Its presence has been related to increasing landscape diversification, and thus a positive upland diversity response. However, to date, only the ElSo palaeoecological record provides enough evidence to assess the baseline ecological role of this pine locally. According to historical documentation, the intense afforestation, carried out since the late eighteenth-century, altered the structure of the pre-existing plant communities in the area (Granados 1987; Granados et al. 1988, García Murillo 2000; Sousa Martín et al. 2010). Besides, it probably brought about some crucial changes in plant interspecific relations, in such a way that the role of *Pinus pinea*, in this type of systems, could have changed. Further palaeobotanical and historical evidence is needed to define more precisely what the current role of this pine is, as well as what the past ecological role of *Pinus pinea* formations in Doñana has been.

On the critically endangered Hydrocharis morsus-ranae and Ricciocarpos natans

The populations of the critically endangered *Hydrocharis morsus-ranae* (Hydrocharitaceae, Magnoliophyta) and *Ricciocarpos natans* (Ricciaceae, Marchantiophyta) in the DNP represent relict populations at the edge of their distribution areas (Garilleti and Albertos 2012; Moreno 2008). Both species have a wide distribution range, usually thriving in quiet waters under temperate climate. A demise in the Iberian populations during the twentieth-century has left a few isolated populations on the brink of extinction (Cirujano et al. 1998; García-Murillo et al. 2000). Their distribution is so restricted in the Iberian Peninsula that doubts on their autochthonous character in the DNP have arisen in the last decade (DNP technical office, pers. comm.). Their intermittent presence in several moments along the ElSo sequence, especially in the last wetland sub-phase, is proof of their naturalness in Doñana (Fig. 4). Furthermore, botanical collections indicate that populations have never been very abundant during the last century and that their emplacement has jumped between water bodies within the DNP (Cirujano et al. 1998; García-Murillo et al. 2000). The exploration of more wetlands in the area will help in ascertaining their present distribution. That is, whether their sparse presence responds to a general regression, or rather their occurrence have always been scant, following stepping-stone dynamics between ponds. This evidence will be able to inform the design of future conservation strategies for these locally-endangered globally-important taxa.

Conclusions

The global demise of temporary wetlands is a worldwide problem. In Europe, the highest concentration of seasonal wetlands is located in the Mediterranean area, with Doñana as a hotspot. According to palaeoecological evidence, Doñana upland and wetland vegetation dynamics seem to be controlled by solar activity modulating wind regimes, hence affecting dune development and movement and, therefore, the lifespan of interdune hygrophilous environments.

Although wetland development depends on the sinuosity of the landscape, it relies on groundwater supply. This means that the natural alternation of arid and humid periods with the resulting landscape-scale creation and destruction of water bodies is an intrinsic dynamic in the area. Therefore, the Doñana geomorphological diversity and dynamism is the baseline condition for this kind of environmental systems. This dynamism modulates water connectivity between upland and wetland environments and controls biodiversity trajectories. Therefore, the dynamism must be considered for the management, conservation and restoration of Doñana wetlands in order to harmonise nature preservation and human exploitation under the current scenario of global change.

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Author contributions JSC designed the outlay of this investigation and carried out preliminary fieldwork. JSC, PGM and SM participated in the site coring. Laboratory analyses were conducted by SM. LLM conducted numerical analyses. SM wrote the first draft of this article to which all authors, especially LLM, have revised and contributed to. The final version of the manuscript is the result of the collaboration of the four authors.

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