



## Modern pollen representation of the vegetation of the Tagus Basin (central Iberian Peninsula)

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### ABSTRACT

The study of modern vegetation–pollen relationships has long been recognized as crucial for the proper interpretation of fossil pollen records. Despite the quickly growing number of palynological studies from central Iberia and its adjacent Atlantic margin, comprehensive studies about modern pollen representation at broad spatial scales were still lacking. In this paper, we have studied the vegetation–pollen relationships in the Tagus Basin in 62 sites located along a wide environmental gradient from Thermomediterranean evergreen mixed thermophilous woodlands by the Atlantic coast to Oromediterranean shrublands above the treeline in the Guadarrama Mountains (central Spain). At each site, we analyzed pollen from moss polsters and conducted vegetation surveys. Most forested vegetation types (pinewoods, oak woods, evergreen mixed thermophilous woodlands) presented rather distinct pollen assemblages dominated by the pollen equivalents of the major tree species. Nevertheless, enhanced taxonomic resolution within *Pinus* and *Quercus ilex*-type would represent significant progress, e.g., enabling to separate Mediterranean and mountain pinewoods. Pollen spectra from shrubland and steppic communities are in general less differentiated, due to high regional pollen input associated with low local pollen production and/or the dominance of insect-pollinated species (e.g., *Cytisus oromediterraneus* in mountain shrublands). The results presented here will readily assist the interpretation of regional fossil pollen records from small mires/bogs/lakes and forest hollows, given their comparable pollen catchments. Comparison of modern pollen assemblages with pollen records from larger lakes and marine settings is not so straightforward, but our results suggest that marine pollen assemblages might average the pollen signature of the entire basin.

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### 1. Introduction

Pollen-stratigraphic records from sedimentary archives represent one of the most powerful and widely used tools to reconstruct vegetation changes on long (decadal to millennial) timescales (e.g., van Zeist and Wright, 1963; Birks, 1965; Lotter, 1999; Tinner et al., 1999; Sánchez Goñi et al., 2008; Rey et al., 2019). The Iberian Peninsula and its margin is one of the European regions where the amount of palynological investigations has increased most significantly in recent times, stimulated by its diverse landscape, complex land-use history and sensitivity to climate change (Carrion et al., 2010; Sánchez Goñi et al., 2018). Paleocology has particularly developed in central Iberia, with the publication of a number of new multi-proxy studies addressing

diverse ecological questions like vegetation dynamics, fire history, fire ecology, human impact, or herbivore–vegetation interactions (e.g., Franco Múgica et al., 1998; López-Merino et al., 2010; Abel-Schaad and López-Sáez, 2013; Morales-Molino et al., 2017a, 2019; Luelmo-Lautenschlaeger et al., 2019). Likewise, pollen-based paleoclimatic research on marine sediments with strong influence of the River Tagus and River Sado plumes has largely moved forward in recent years (e.g., Sánchez Goñi et al., 1999, 2008, 2019; Roucoux et al., 2006; Oliveira et al., 2017).

Studies on the modern pollen representation of extant plant communities have long been recognized as playing a central role in assisting the interpretation of fossil palynological records, helping disentangle challenging issues concerning differential pollen production, dispersal and preservation (e.g., Davis and Goodlett, 1960; Wright, 1967; Stevenson, 1985; Bell and Fletcher, 2016). During the last decades, several studies have addressed modern vegetation–pollen relationships all over the Mediterranean region (e.g., Davies and Fall, 2001; Finsinger

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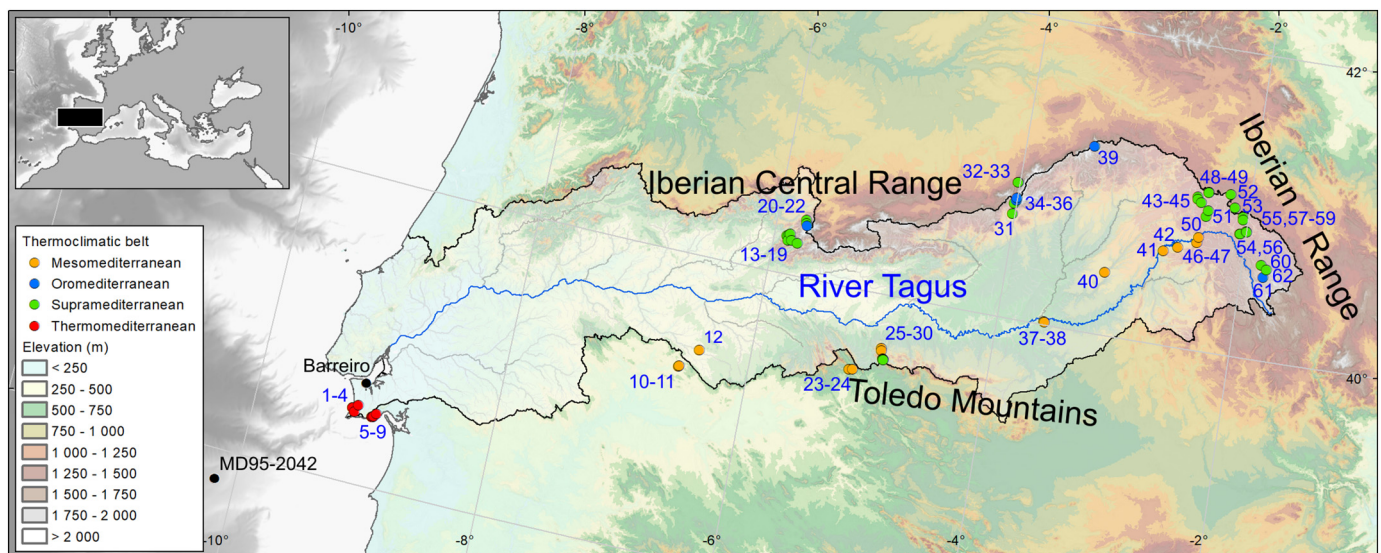
et al., 2007; Fall, 2012; Bell and Fletcher, 2016; López-Sáez et al., 2018), including the Iberian Peninsula (e.g., Stevenson, 1985; Díaz Fernández, 1994; Andrade Olalla et al., 1994; Aranbarri et al., 2015). The latter research has provided very valuable insights into the pollen representation of Iberian plant communities, but its geographical scope was usually rather narrow, i.e., transects across single mountain ranges (Díaz Fernández, 1994; Andrade Olalla et al., 1994; Sánchez Goñi and Hannon, 1999; Cañellas-Boltà et al., 2009; Aranbarri et al., 2015). In central Iberia, the main focus has been on specific plant communities such as *Pinus sylvestris*, *Quercus ilex* and *Quercus pyrenaica* woodlands (López-Sáez et al., 2010, 2013, 2015), or on geographically restricted areas such as the Gredos Mountains (Broothaerts et al., 2018). More general overviews on vegetation–pollen relationships over broad ecological and geographical gradients, i.e., those probably integrated in deep-sea pollen assemblages (Heusser and Balsam, 1977; Dupont and Wyputta, 2003; Mudie and McCarthy, 2006), are therefore lacking so far for the Iberian Peninsula.

In this paper, we aim at partially filling this gap by investigating the modern pollen representation of the Tagus Basin (Fig. 1). This area of central Iberia is not particularly rich in endemic plant species but it hosts an outstandingly diverse set of plant communities and is home to a diverse flora (Sainz Ollero et al., 2010; Moreno Saiz et al., 2013; Aedo et al., 2017), as a result of the wide environmental gradients and its location at the crossroad of several different floristic regions (Sainz Ollero and Sánchez de Dios, 2011; Moreno Saiz et al., 2013). In this setting, we sampled an array of (semi-)natural plant communities distributed throughout the Tagus Basin, from the Atlantic coast to the Iberian Range (Fig. 1). In our sampling, we included not only the most widespread woodlands and shrublands (e.g., pine and oak woods, maquis, garrigue) but also rarer vegetation types of great biogeographical interest such as beech and chestnut stands, *Prunus lusitanica*-dominated riparian forests, juniper woodlands, broom-dominated shrublands and steppic communities on gypsum (Table 1). Some of these currently rare vegetation types, for instance steppic communities, were dominant in the Iberian Peninsula during Quaternary cold and dry stages (e.g., Sánchez Goñi et al., 2002). At the study sites, we conducted vegetation surveys and collected surface samples (usually moss polsters) to analyze the modern pollen rain, with the main aim of assessing today's pollen–vegetation relationships and shedding new light into the interpretation of regional fossil pollen sequences.

## 2. Study area

The River Tagus flows south-westwards along more than 1000 km, from its springs in the Montes Universales at 1593 m asl to its mouth at the Atlantic Ocean near Lisbon (Fig. 1). The Tagus is indeed the longest of the Iberian rivers, and drains a basin of 81,600 km<sup>2</sup> across central Spain and Portugal. Most of the surface of the Tagus Basin is included within the Southern Iberian Plateau, where elevation is highest at the foothills of the Iberian Range on its north-eastern edge (ca. 1000 m asl) and then decreases westwards to ca. 200–300 m asl in the region of Extremadura, averaging 600–700 m asl. The mountainous borders of the Tagus Basin include the Iberian Central Range (“Sistema Central Ibérico” or “Cordillera Central Ibérica”) to the north, the Iberian Range (“Sistema Ibérico”) to the east, and the Toledo Mountains *sensu lato* (“Montes de Toledo”) to the south (Fig. 1). The Iberian Central Range is a ca. 600-km long mostly west-to-east oriented cordillera that mainly consists on siliceous bedrock (e.g., granite, gneiss, slate) and features notable peaks usually above 2000 m asl, particularly in its central and eastern sectors (e.g., Almanzor 2591 m asl, Peñalara 2428 m asl, or Pico del Lobo 2274 m asl). In contrast, although bedrock is outstandingly diverse, calcareous rocks clearly dominate in the section of the Iberian Range that delimits the Tagus Basin. Other major features of this mountainous area are: (i) the massive extension; (ii) the high plateau-like structure with relatively modest elevations mostly ranging between 1000 and 1800 m asl and lack of truly prominent peaks; and (iii) the abundance and length of impressive canyons (usually with several hundred metres high cliffs) carved by the River Tagus and its tributaries in the dominant limestone, dolostone and sandstone. Finally, the Toledo Mountains are a hilly landscape of mid-elevation mountains (highest peaks between 1000 and 1600 m asl: e.g., Pico Rocigalgo 1448 m asl and Pico Las Villuercas 1603 m asl) of usually gentle slopes built on acidic bedrock (e.g., schist, slate, quartzite).

The climate of the Tagus Basin is predominantly mediterranean, i.e., temperate with mild humid winters and dry and hot summers (climate Csa according to the Köppen-Geiger Climate Classification; AEMET/IMP, 2011). Although summer drought is a consistent feature all over the basin, cooler temperatures and convective rain attenuate it in the mountains (climate Csb), particularly in the Iberian Range where frequent convective rain episodes lead to an absence of dry season (climate Cfb; see  $P_{\text{summer}}$  values in Table 1). At the highest peaks of the Iberian Central Range, climate is cold with temperate/cool dry



**Fig. 1.** Location of the Tagus Basin in central Iberia and the sampling sites considered in this study (1–62), colored according to their thermoclimatic belt. The location of the estuarine (“Barreiro”) and marine (“MD95-2042”) surface samples used for comparison is indicated by black dots.

Table 1

Main features of the sampling sites in the Tagus Basin.

Site no.	Geographical coordinates	Altitude (m asl)	T (°C) <sup>a</sup>	Vegetation belt	Vegetation type and description
			P (mm) <sup>a</sup>		
			P <sub>summer</sub> (mm) <sup>a</sup>		
1	38°29.247'N 009°10.988'W	10	15.7 650 30	Thermo	Coastal dunes with <i>Artemisia campestris</i> subsp. <i>maritima</i> , <i>Elymus farctus</i> , <i>Arundo donax</i> , <i>Ammophila arenaria</i> , <i>Lotus creticus</i> , <i>Cyperus</i> sp., <i>Eryngium maritimum</i> , <i>Otanthus maritimus</i> , <i>Euphorbia paralias</i> , <i>Crithmum maritimum</i> , <i>Pancreaticum maritimum</i> , <i>Sedum sediforme</i> , <i>Armeria</i> sp., <i>Helichrysum</i> sp., <i>Thymus</i> sp. and <i>Stauracanthus</i> sp.
2	38°29.155'N 009°10.980'W	30	15.7 650 30	Thermo	Mediterranean pinewoods. Open <i>Pinus pinaster</i> stand on dunes with <i>Corema album</i> , <i>Ulex</i> sp., <i>Daphne gnidium</i> , <i>Juniperus phoenicea</i> , <i>Lavandula stoechas</i> and <i>Carpobrotus edulis</i>
3	38°27.715'N 009°09.752'W	90	15.6 680 30	Thermo	Mediterranean pinewoods. Disturbed woodland (40% tree cover) dominated by <i>Pinus pinea</i> , <i>P. pinaster</i> and <i>Quercus suber</i> , with <i>Quercus lusitana</i> , <i>Cistus crispus</i> , <i>Ulex</i> sp., <i>Calluna vulgaris</i> , <i>Cistus salvifolius</i> , <i>Oxalis pres-caprae</i> , <i>Acacia</i> gr. <i>melanoxyton</i> , <i>Quercus faginea</i> subsp. <i>broteroi</i> and <i>Eucalyptus</i>
4	38°30.611'N 009°08.588'W	20	15.9 650 30	Thermo	Mediterranean pinewoods. <i>Pinus pinea</i> and <i>P. pinaster</i> wood (40% tree cover) on sandy soils with <i>Quercus suber</i> , <i>Cistus crispus</i> , <i>Cistus salvifolius</i> , <i>Lavandula stoechas</i> , <i>Ulex</i> sp., <i>Halimium umbellatum</i> , <i>H. halimifolium</i> and <i>Daphne gnidium</i>
5	38°27.524'N 009°00.631'W	250	15.2 760 35	Thermo	Evergreen thermophilous woodlands. Maquis (1–3 m tall; 100% canopy cover): <i>Olea europaea</i> , <i>Phillyrea angustifolia</i> , <i>Pistacia lentiscus</i> , <i>Cistus albidus</i> , <i>C. monspeliensis</i> , <i>Arbutus unedo</i> , <i>Quercus coccifera</i> , <i>Juniperus phoenicea</i> , <i>Bupleurum fruticosum</i> , <i>Rhamnus oleoides</i> , <i>Rh. alaternus</i> , <i>Daphne gnidium</i> , <i>Smilax aspera</i> , <i>Erica arborea</i> and <i>Lonicera implexa</i> . Scattered <i>Pinus pinea</i> and <i>Quercus faginea</i> subsp. <i>broteroi</i> trees
6	38°27.704'N 009°00.294'W	190	15.5 730 30	Thermo	Evergreen thermophilous woodlands. Mixed forest (100% tree cover) with tree <i>Quercus coccifera</i> , <i>Q. faginea</i> subsp. <i>broteroi</i> , <i>Pistacia lentiscus</i> , <i>Phillyrea latifolia</i> , <i>Arbutus unedo</i> , <i>Viburnum tinus</i> , <i>Ceratonia siliqua</i> , <i>Juniperus phoenicea</i> , <i>Erica arborea</i> , <i>Rhamnus alaternus</i> and <i>Myrtus communis</i> . Abundant lianas ( <i>Smilax aspera</i> , <i>Lonicera implexa</i> ) and epiphytic ferns ( <i>Polypodium</i> , <i>Davallia</i> )
7	38°27.702'N 009°00.185'W	160	15.5 730 30	Thermo	Evergreen thermophilous woodlands. Mixed forest (100% tree cover) with tree <i>Quercus coccifera</i> , <i>Q. faginea</i> subsp. <i>broteroi</i> , <i>Pistacia lentiscus</i> , <i>Phillyrea latifolia</i> , <i>Arbutus unedo</i> , <i>Viburnum tinus</i> , <i>Ceratonia siliqua</i> , <i>Juniperus phoenicea</i> , <i>Erica arborea</i> , <i>Rhamnus alaternus</i> and <i>Myrtus communis</i> . Abundant lianas ( <i>Smilax aspera</i> , <i>Lonicera implexa</i> ) and epiphytic ferns ( <i>Polypodium</i> , <i>Davallia</i> )
8	38°27.989'N 008°59.825'W	120	15.9 680 30	Thermo	Evergreen thermophilous woodlands. Maquis (3 m tall; 80% canopy cover): <i>Quercus coccifera</i> , <i>Phillyrea latifolia</i> , <i>Ph. angustifolia</i> , <i>Pistacia lentiscus</i> , <i>Juniperus phoenicea</i> , <i>Erica arborea</i> , <i>Arbutus unedo</i> , <i>Viburnum tinus</i> , <i>Coronilla</i> sp., <i>Lonicera implexa</i> , <i>Osyris lanceolata</i> , <i>Rosmarinus officinalis</i> , <i>Smilax aspera</i> , <i>Daphne gnidium</i> and <i>Cistus</i> spp.
9	38°29.051'N 008°58.657'W	90	15.4 750 35	Thermo	Evergreen thermophilous woodlands. Maquis (6–10 m tall; 80% canopy cover): <i>Pistacia lentiscus</i> , <i>Ceratonia siliqua</i> , <i>Juniperus phoenicea</i> , <i>Phillyrea latifolia</i> , <i>Olea europaea</i> , <i>Myrtus communis</i> , <i>Jasminum fruticans</i> , <i>Viburnum tinus</i> and <i>Smilax aspera</i>
10	39°15.197'N 006°34.864'W	360	16.0 550 35	Meso	Evergreen thermophilous woodlands. Dehesa of <i>Quercus ilex</i> subsp. <i>ballota</i> (30–40% tree cover), with <i>Cistus crispus</i> , <i>C. ladanifer</i> , <i>C. salvifolius</i> , <i>Apiaceae</i> and <i>Celtica gigantea</i>
11	39°15.514'N 006°34.745'W	330	16.1 540 35	Meso	Evergreen oak woods. Dehesa of <i>Quercus ilex</i> subsp. <i>ballota</i> and <i>Q. suber</i> (30% tree cover) with <i>Cistus ladanifer</i> , <i>C. salvifolius</i> , <i>C. crispus</i> , <i>Ulex</i> sp., <i>Cytisus scoparius</i> and <i>Crataegus monogyna</i>
12	39°23.414'N 006°26.032'W	360	16.2 530 40	Meso	Evergreen oak woods. Dehesa of <i>Quercus ilex</i> subsp. <i>ballota</i> (20% tree cover) with <i>Cytisus multiflorus</i> and <i>C. cf. striatus</i>
13	40°14.775'N 005°53.554'W	960	11.9 800 70	Supra	Monospecific coppiced <i>Castanea sativa</i> stand (90–100% tree cover)
14	40°14.833'N 005°52.811'W	870	11.8 790 70	Supra	Deciduous oak woods. Grazed <i>Quercus pyrenaica</i> stand (70% tree cover) with <i>Pteridium aquilinum</i> , <i>Rosa</i> sp., <i>Rubus</i> gr. <i>ulmifolius</i> , <i>Crataegus monogyna</i> , <i>Clinopodium vulgare</i> and diverse <i>Poaceae</i>
15	40°15.510'N 005°52.508'W	770	13.3 650 60	Supra	Deciduous oak woods. <i>Quercus pyrenaica</i> - <i>Castanea sativa</i> forest (60–70% tree cover), with <i>Acer monspessulanum</i> , <i>Hedera helix</i> , <i>Cytisus scoparius</i> , <i>Ruscus aculeatus</i> , <i>Lonicera cf. periclymenum</i> , <i>Festuca elegans</i> , <i>Polypodium</i> and <i>Asplenium onopteris</i>
16	40°13.274'N 005°52.340'W	1440	9.2 1100 100	Supra	Mountain shrublands. Rather open <i>Cytisus oromediterraneus</i> shrubland on mountain pass
17	40°15.934'N 005°51.884'W	720	12.8 690 65	Supra	Deciduous oak woods. <i>Quercus pyrenaica</i> - <i>Castanea sativa</i> stand (70–80% tree cover) with <i>Daphne gnidium</i> , <i>Ruscus aculeatus</i> , <i>Hedera helix</i> , <i>Rubia peregrina</i> , <i>Teucrium scorodonia</i> , <i>Clinopodium vulgare</i> , <i>Acer monspessulanum</i> , <i>Crataegus monogyna</i> , <i>Cytisus scoparius</i> , <i>Arenaria montana</i> , <i>Luzula cf. forsteri</i> , <i>Brachypodium sylvaticum</i> and <i>Polypodium</i>
18	40°13.445'N 005°50.825'W	1370	9.9 990 90	Supra	Mountain shrublands. Broom-dominated shrubland ( <i>Genista florida</i> , <i>G. cinerascens</i> , <i>Cytisus oromediterraneus</i> , <i>Adenocarpus argyrophyllus</i> , <i>Erica arborea</i> , <i>Lavandula cf. stoechas</i> ) not far from the <i>Quercus pyrenaica</i> treeline
19	40°12.854'N 005°47.534'W	810	12.8 670 65	Supra	Deciduous oak woods. <i>Quercus pyrenaica</i> stand (70–80% tree cover) with <i>Cistus psilosepalus</i> , <i>Cytisus scoparius</i> , <i>Pteridium aquilinum</i> , <i>Lavandula pedunculata</i> , <i>Campanula rapunculoides</i> and <i>Brachypodium sylvaticum</i>
20	40°22.469'N 005°45.100'W	1030	10.7 770 80	Supra	Small <i>Castanea sativa</i> stand (90% tree cover) with <i>Rubus</i> sp., <i>Pteridium aquilinum</i> , <i>Quercus pyrenaica</i> (rare). Some <i>Betula</i> sp. and <i>Frangula alnus</i> closeby
21	40°21.117'N 005°44.713'W	1400	9.4 940 95	Supra	Mountain pinewoods. <i>Pinus sylvestris</i> afforestation (80% tree cover) with <i>Cytisus striatus</i> and <i>Festuca elegans</i> . Shrubland with <i>Erica arborea</i> , <i>Adenocarpus argyrophyllus</i> and <i>Adenocarpus</i> gr. <i>complicatus</i> nearby.
22	40°20.45'N 005°44.250'W	1670	7.6 1180 115	Oro	Mountain shrubland dominated by <i>Cytisus oromediterraneus</i> and <i>Echinopartum ibericum</i> , with <i>Santolina oblongifolia</i> , <i>Avenella hispanica</i> , <i>Nardus stricta</i> and sparse <i>Salix atrocinerea</i> . Extensive <i>Pinus sylvestris</i> afforestation closeby

(continued on next page)



Table 1 (continued)

Site no.	Geographical coordinates	Altitude (m asl)	T (°C) <sup>a</sup>	Vegetation belt	Vegetation type and description
			P (mm) <sup>a</sup>		
			P <sub>summer</sub> (mm) <sup>a</sup>		
23	39°28.070'N 005°09.711'W	590	14.9 480 40	Meso	Evergreen oak woods. Coppiced dehesa of <i>Quercus ilex</i> subsp. <i>ballota</i> (20% tree cover) with <i>Arbutus unedo</i> , <i>Viburnum tinus</i> and abundant <i>Cistus ladanifer</i> and <i>Lavandula pedunculata</i> . <i>Eucalyptus</i> and <i>Pinus pinaster</i> afforestations in the surroundings
24	39°28.554'N 005°07.858'W	470	15.2 440 40	Meso	Evergreen oak woods. <i>Quercus ilex</i> subsp. <i>ballota</i> stand (60% tree cover) with <i>Pistacia terebinthus</i> , <i>Acer monspessulanum</i> , <i>Cistus ladanifer</i> , <i>Arbutus unedo</i> , <i>Phillyrea angustifolia</i> , <i>Rosmarinus officinalis</i> , <i>Juniperus oxycedrus</i> , <i>Lavandula stoechas</i> , <i>Thymus mastichina</i> and <i>Rumex cf. induratus</i>
25	39°38.799'N 004°55.456'W	790	13.8 470 50	Meso	Lowland shrublands. <i>Cistus ladanifer</i> shrubland with <i>Phillyrea angustifolia</i> , <i>Lavandula pedunculata</i> , <i>Genista triacanthos</i> , <i>Daphne gnidium</i> , <i>Asparagus acutifolius</i> and scattered and sparse <i>Quercus ilex</i> subsp. <i>ballota</i> trees (5–10% tree cover)
26	39°37.865'N 004°55.184'W	890	12.9 530 55	Meso	Evergreen oak woods. Mixed <i>Quercus ilex</i> and <i>Q. faginea</i> stand on scree, with <i>Pistacia terebinthus</i> (abundant), <i>Phillyrea angustifolia</i> , <i>Cistus ladanifer</i> , <i>C. populifolius</i> , <i>Viburnum tinus</i> and <i>Rubus gr. ulmifolius</i> . <i>Lonicera implexa</i> , <i>Cytisus scoparius</i> , <i>Arbutus unedo</i> , <i>Erica arborea</i> and <i>Genista florida</i> in the understory. Pine afforestations and olive groves closeby.
27	39°34.784'N 004°53.693'W	820	12.8 530 55	Supra	Riparian forest with <i>Prunus lusitanica</i> , <i>Frangula alnus</i> , <i>Erica arborea</i> and <i>Hedera helix</i> particularly rich in ferns (e.g., <i>Polystichum</i> , <i>Dryopteris</i> , <i>Osmunda</i> ). <i>Quercus pyrenaica</i> stands upslope
28	39°34.709'N 004°53.655'W	860	12.8 530 55	Supra	Deciduous oak woods. <i>Quercus pyrenaica</i> coppice (70% tree cover) with <i>Erica arborea</i> (abundant), <i>Cistus ladanifer</i> (rare) and <i>Daphne gnidium</i> . <i>Quercus ilex</i> stand on the opposite slope
29	39°34.567'N 004°53.541'W	900	12.8 530 55	Supra	Deciduous oak woods. Closed <i>Quercus pyrenaica</i> coppiced stand
30	39°34.462'N 004°53.357'W	900	12.1 580 60	Supra	Riparian forest with <i>Prunus lusitanica</i> (dominant), <i>Ilex aquifolium</i> , <i>Taxus baccata</i> , <i>Frangula alnus</i> and <i>Osmunda regalis</i> , surrounded by <i>Quercus pyrenaica</i> stands
31	40°41.077'N 004°01.130'W	1030	11.4 450 70	Supra	Evergreen oak woods. <i>Quercus ilex</i> subsp. <i>ballota</i> woodland (30% tree cover) with <i>Juniperus oxycedrus</i> , <i>Cistus ladanifer</i> , <i>C. laurifolius</i> , <i>Celtica gigantea</i> and <i>Lavandula pedunculata</i> . <i>Pinus pinaster</i> stands nearby.
32	40°45.108'N 004°00.971'W	1500	7.9 890 105	Supra	Mountain pinewoods. <i>Pinus sylvestris</i> forest (80–90% tree cover) with <i>Cytisus scoparius</i> , <i>Cistus laurifolius</i> , <i>Juniperus communis</i> , <i>Pteridium aquilinum</i> and <i>Rosa</i> sp.
33	40°53.501'N 004°00.933'W	1190	10.2 540 85	Supra	Deciduous oak woods. Dense <i>Quercus pyrenaica</i> stand (90% tree cover) with <i>Cistus laurifolius</i> and <i>Rubus gr. ulmifolius</i> (rare)
34	40°53.493'N 004°00.844'W	1180	10.1 550 85	Supra	Deciduous oak woods. <i>Quercus pyrenaica</i> stand (70% tree cover) with abundant <i>Cistus laurifolius</i>
35	40°46.536'N 004°00.298'W	1770	7.0 1130 120	Oro	Mountain pinewoods. <i>Pinus sylvestris</i> woodland (60–70%) with <i>Cytisus oromediterraneus</i> , <i>Genista cinerascens</i> and <i>Juniperus communis</i> subsp. <i>alpina</i>
36	40°47.339'N 003°59.938'W	1920	6.0 1330 135	Oro	Mountain shrubland dominated by <i>Cytisus oromediterraneus</i> and <i>Juniperus communis</i> subsp. <i>alpina</i>
37	40°01.176'N 003°35.995'W	560	14.8 390 45	Meso	Steppic vegetation dominated by <i>Macrochloa (Stipa) tenacissima</i> with <i>Salsola vermiculata</i> , <i>Atriplex halimus</i> , <i>Tamarix</i> sp. and <i>Lycium europaeum</i> . <i>Phragmites australis</i> communities nearby
38	40°01.142'N 003°35.789'W	580	14.8 390 45	Meso	Steppic vegetation dominated by <i>Macrochloa (Stipa) tenacissima</i> with <i>Ephedra</i> sp., <i>Helianthemum squamatum</i> , <i>Lepidium subulatum</i> , <i>Reseda suffruticosa</i> , <i>Frankenia thymifolia</i> , <i>Retama sphaerocarpa</i> , <i>Artemisia campestris</i> and <i>Artemisia herba-alba</i>
39	41°12.957'N 003°24.788'W	1700	7.1 840 115	Oro	<i>Fagus sylvatica</i> stand with <i>Ilex aquifolium</i> , <i>Sorbus aucuparia</i> , <i>S. aria</i> , <i>Erica arborea</i> , <i>Arctostaphylos uva-ursi</i> , <i>Vaccinium myrtillus</i> and <i>Cytisus scoparius</i> . <i>Quercus pyrenaica</i> and <i>Betula pendula</i> stands and pine afforestations nearby
40	40°24.721'N 003°09.214'W	710	13.5 430 45	Meso	Lowland shrublands. Garrigue on gypsum with <i>Quercus coccifera</i> and sparse <i>Quercus ilex</i> subsp. <i>ballota</i> and <i>Quercus faginea</i> (10% tree cover). <i>Ephedra</i> sp., <i>Genista scorpius</i> , <i>Macrochloa (Stipa) tenacissima</i> , <i>Salvia lavandulifolia</i> , <i>Euphorbia nicaeensis</i> , <i>Ononis tridentata</i> , <i>Thymus</i> sp., <i>Helianthemum squamatum</i> , <i>Lithodora fruticosa</i> , <i>Rosmarinus officinalis</i> , <i>Bupleurum fruticosum</i> and <i>Lepidium subulatum</i> . <i>Pinus halepensis</i> afforestation, <i>Quercus faginea</i> stands and cereal fields closeby
41	40°37.087'N 002°40.957'W	800	13.1 430 55	Meso	Deciduous oak woods. <i>Quercus faginea</i> - <i>Pinus halepensis</i> stands recolonizing old fields (60% tree cover) with <i>Quercus ilex</i> subsp. <i>ballota</i> , <i>Juniperus oxycedrus</i> , <i>Genista scorpius</i> , <i>Arctostaphylos uva-ursi</i> (abundant), <i>Ononis fruticosa</i> , <i>Dorycnium pentaphyllum</i> , <i>Bupleurum rigidum</i> , <i>Olea europaea</i> , <i>Crataegus monogyna</i> , <i>Lonicera etrusca</i> , <i>Lavandula latifolia</i> , <i>Thymus vulgaris</i> , <i>Lithodora fruticosa</i> , <i>Jasminum fruticans</i> and <i>Cornus sanguinea</i>
42	40°39.247'N 002°33.970'W	900	12.4 470 55	Meso	Evergreen oak woods. Open <i>Quercus ilex</i> subsp. <i>ballota</i> woodland (30% tree cover) with <i>Juniperus oxycedrus</i> , <i>Juniperus phoenicea</i> , <i>Rosmarinus officinalis</i> , <i>Rosa</i> sp., <i>Genista pumila</i> , <i>Crataegus monogyna</i> , <i>Genista scorpius</i> , <i>Jasminum fruticans</i> , <i>Rubia peregrina</i> , <i>Arctostaphylos uva-ursi</i> , <i>Galium fruticosum</i> , <i>Lavandula latifolia</i> , <i>Thymus vulgaris</i> , <i>Satureja intricata</i> and scattered <i>Pinus halepensis</i>
43	41°00.376'N 002°27.381'W	1150	10.6 520 75	Supra	Mediterranean pinewoods. Open <i>Pinus pinaster</i> woodland (60% tree cover) with <i>Quercus faginea</i> , <i>Calluna vulgaris</i> , <i>Erica scoparia</i> , <i>Cistus laurifolius</i> , <i>Crataegus monogyna</i> and <i>Arctostaphylos uva-ursi</i>
44	40°59.479'N 002°27.348'W	1120	10.8 520 75	Supra	Mediterranean pinewoods. Mixed <i>Pinus pinaster</i> - <i>Quercus faginea</i> stand (70–80% tree cover) with <i>Calluna vulgaris</i> , <i>Cistus laurifolius</i> , <i>Crataegus monogyna</i> , <i>Juniperus communis</i> and <i>Prunus spinosa</i> . <i>Erica scoparia</i> -dominated heathland nearby

Table 1 (continued)

Site no.	Geographical coordinates	Altitude (m asl)	T (°C) <sup>a</sup>	Vegetation belt	Vegetation type and description
			P (mm) <sup>a</sup>		
			P <sub>summer</sub> (mm) <sup>a</sup>		
45	40°58.417'N 002°25.388'W	1100	10.8 520 75	Supra	Mediterranean pinewoods. <i>Pinus pinaster</i> woodland (70% tree cover) with <i>Quercus faginea</i> , <i>Juniperus communis</i> , <i>Cistus laurifolius</i> and <i>Lavandula pedunculata</i>
46	40°42.509'N 002°24.524'W	890	12.3 470 55	Meso	Mediterranean pinewoods. Open <i>Pinus nigra</i> - <i>Quercus ilex</i> subsp. <i>ballota</i> woodland (40% tree cover) with abundant <i>Rosmarinus officinalis</i> , <i>Juniperus phoenicea</i> , <i>Juniperus oxycedrus</i> , <i>Arctostaphylos uva-ursi</i> , <i>Salvia lavandulifolia</i> , <i>Brachypodium retusum</i> , <i>Lavandula latifolia</i> , <i>Thymus vulgaris</i> , <i>Genista scorpius</i> , <i>Lithodora fruticosa</i> , <i>Helianthemum</i> sp. And sparse <i>Pinus halepensis</i>
47	40°44.672'N 002°23.904'W	810	12.4 460 55	Meso	Mediterranean pinewoods. <i>Pinus nigra</i> - <i>P. halepensis</i> forest (90% tree cover), with a dense understory of <i>Arctostaphylos uva-ursi</i> , <i>Rosmarinus officinalis</i> , <i>Juniperus phoenicea</i> and <i>Juniperus oxycedrus</i>
48	41°02.905'N 002°22.179'W	1220	10.4 540 80	Supra	Deciduous oak woods. Small stand of <i>Quercus faginea</i> (70–80% tree cover) with <i>Cistus laurifolius</i> , <i>Quercus ilex</i> subsp. <i>ballota</i> , <i>Genista scorpius</i> , <i>G. pumila</i> subsp. <i>pumila</i> , <i>Juniperus communis</i> and <i>Euphorbia nicaeensis</i> . Pine afforestation closeby
49	41°02.704'N 002°22.084'W	1200	10.4 540 80	Supra	Evergreen oak woods. Open <i>Quercus ilex</i> subsp. <i>ballota</i> woodland (40% tree cover) with <i>Quercus faginea</i> , <i>Thymus vulgaris</i> , <i>Juniperus communis</i> , <i>Helianthemum cinereum</i> , <i>Crataegus monogyna</i> , <i>Genista scorpius</i> , <i>Cistus laurifolius</i> and <i>Euphorbia nicaeensis</i>
50	40°53.091'N 002°21.835'W	1180	11.1 540 70	Supra	Evergreen oak woods. <i>Quercus ilex</i> subsp. <i>ballota</i> woodland with <i>Juniperus thurifera</i> , <i>Quercus faginea</i> , <i>Genista scorpius</i> , <i>Lavandula latifolia</i> , <i>Thymus vulgaris</i> , <i>Satureja intricata</i> , <i>Amelanchier ovalis</i> and <i>Santolina chamaecyparissus</i>
51	40°55.535'N 002°21.092'W	1060	11.2 530 70	Supra	Deciduous oak woods. <i>Quercus faginea</i> woodland (60% tree cover) with <i>Juniperus communis</i> , <i>Amelanchier ovalis</i> , <i>Genista scorpius</i> , <i>Crataegus monogyna</i> , <i>Euphorbia nicaeensis</i> , <i>Lavandula latifolia</i> , <i>Salvia lavandulifolia</i> , <i>Thymus</i> sp. and <i>Rosa</i> sp.
52	41°03.506'N 002°10.726'W	1340	9.6 590 95	Supra	Juniper woodlands. Open <i>Juniperus thurifera</i> woodland with <i>Juniperus communis</i> , <i>Genista scorpius</i> , <i>Rosa</i> sp., <i>Thymus vulgaris</i> , <i>Helianthemum</i> sp., <i>Genista pumila</i> subsp. <i>pumila</i> and sparse <i>Quercus faginea</i> and <i>Q. ilex</i> subsp. <i>ballota</i>
53	40°58.478'N 002°07.596'W	1210	10.4 550 85	Supra	Deciduous oak woods. Mixed <i>Quercus pyrenaica</i> - <i>Q. faginea</i> stand (70% tree cover) with <i>Viburnum lantana</i> , <i>Juniperus communis</i> , <i>Lonicera xylosteum</i> , <i>Crataegus monogyna</i> , <i>Prunus mahaleb</i> , <i>Lonicera periclymenum</i> , <i>Cistus laurifolius</i> , <i>Prunus spinosa</i> and <i>Ligustrum vulgare</i>
54	40°48.655'N 002°03.194'W	1040	11.2 510 75	Supra	Mountain pinewoods. Closed <i>Pinus nigra</i> forest (90% tree cover) with <i>Amelanchier ovalis</i> , <i>Rosa</i> sp., <i>Prunus mahaleb</i> , <i>Juniperus thurifera</i> , <i>Juniperus communis</i> , <i>Quercus faginea</i> , <i>Euphorbia</i> sp. and shrubby <i>Lamiaceae</i> ( <i>Satureja</i> , <i>Thermomyus</i> , <i>Salvia</i> , <i>Lavandula</i> )
55	40°55.328'N 002°02.834'W	1280	9.9 570 90	Supra	Juniper woodlands. Rather dense <i>Juniperus thurifera</i> woodland (40% tree cover) with <i>Juniperus communis</i> , <i>Genista scorpius</i> , <i>Lavandula latifolia</i> , <i>Satureja intricata</i> , <i>Thymus vulgaris</i> , <i>Helianthemum cinereum</i> , <i>H. apenninum</i> , <i>H. oelandicum</i> subsp. <i>incanum</i> and <i>Artemisia pedemontana</i>
56	40°48.671'N 002°02.785'W	990	11.3 500 75	Supra	Mountain pinewoods. <i>Pinus nigra</i> woodland with <i>Juniperus thurifera</i> (60–70% tree cover) with <i>Genista scorpius</i> , <i>Rosa</i> sp., <i>Juniperus communis</i> , <i>Ligustrum vulgare</i> , <i>Digitalis obscura</i> , <i>Satureja intricata</i> , <i>Berberis vulgaris</i> subsp. <i>seroi</i> , <i>Lavandula latifolia</i> , <i>Salvia lavandulifolia</i> , <i>Euphorbia nicaeensis</i> and <i>Clematis vitalba</i>
57	40°54.192'N 002°02.624'W	1320	9.6 580 95	Supra	Juniper woodlands. Rather dense <i>Juniperus thurifera</i> woodland (40% tree cover) with sparse <i>Quercus faginea</i> and <i>Q. ilex</i> subsp. <i>ballota</i> , <i>Juniperus communis</i> , <i>Genista scorpius</i> , <i>Lavandula latifolia</i> , <i>Satureja intricata</i> , <i>Thymus vulgaris</i> , <i>Helianthemum cinereum</i> , <i>H. apenninum</i> , <i>H. oelandicum</i> subsp. <i>incanum</i> and <i>Artemisia pedemontana</i>
58	40°49.826'N 002°00.126'W	1120	10.8 520 80	Supra	Mediterranean pinewoods. <i>Pinus pinaster</i> woodland (50% tree cover) with <i>Quercus faginea</i> , <i>Q. pyrenaica</i> , <i>Q. ilex</i> subsp. <i>ballota</i> , <i>Arctostaphylos uva-ursi</i> , <i>Cistus laurifolius</i> , <i>Lavandula pedunculata</i> and <i>Crataegus monogyna</i>
59	40°49.753'N 001°59.811'W	1000	10.8 520 80	Supra	Mediterranean pinewoods. <i>Pinus pinaster</i> forest (70–80% tree cover) with <i>Acer monspessulanum</i> , <i>Corylus avellana</i> , <i>Lonicera etrusca</i> , <i>Prunus mahaleb</i> , <i>Sambucus nigra</i> , <i>Ulmus minor</i> , <i>Ligustrum vulgare</i> , <i>Cistus laurifolius</i> and <i>Berberis vulgaris</i> subsp. <i>seroi</i> )
60	40°37.583'N 001°49.814'W	1440	9.2 600 110	Supra	Mountain pinewoods. Mixed woodland (50% tree cover) dominated by <i>Pinus nigra</i> , with <i>P. sylvestris</i> , <i>Quercus faginea</i> , <i>Q. ilex</i> subsp. <i>ballota</i> , <i>Buxus sempervirens</i> , <i>Juniperus sabina</i> , <i>J. thurifera</i> , <i>Juniperus communis</i> , <i>Berberis vulgaris</i> subsp. <i>seroi</i> , <i>Artemisia pedemontana</i> , <i>Rosa</i> sp., <i>Thymus vulgaris</i> and <i>Lavandula latifolia</i>
61	40°33.017'N 001°48.112'W	1560	8.4 650 120	Oro	Mountain pinewoods. Open <i>Pinus sylvestris</i> woodland with <i>Juniperus sabina</i> , <i>J. communis</i> , <i>Buxus sempervirens</i> , <i>Rosa</i> sp. and <i>Berberis vulgaris</i> subsp. <i>seroi</i>
62	40°36.106'N 001°46.774'W	1350	9.3 590 110	Supra	Mountain pinewoods. <i>Pinus sylvestris</i> forest with <i>Quercus pyrenaica</i> , <i>Rosa pimpinellifolia</i> , <i>Prunus spinosa</i> and <i>Cistus laurifolius</i>

Abbreviations: T = Mean annual temperature, P = mean annual precipitation, P<sub>summer</sub> = mean summer precipitation (June–August), Thermo = Thermomediterranean, Meso = Mesomediterranean, Supra = Supramediterranean, Oro = Oromediterranean.

<sup>a</sup> Values obtained from WorldClim 2 (Fick and Hijmans, 2017).

summers (climates Dsb and Dsc). Similarly, particularly dry conditions translate into a cold steppe climate (climate BSk) in the lowlands of the central sector of the Tagus Basin. Mean annual temperature ranges from ca. 15–17 °C close to the Atlantic Ocean and on the Extremaduran plains to ca. 5 °C at the highest mountains of the Iberian Central Range and the Montes Universales area in the Iberian Range. Mean annual precipitation is also quite variable, from less than 400 mm in the central section of the River Tagus valley bottom to more than 1000 mm at the highest elevations of the Iberian Central Range (Table 1). In general, mean annual precipitation follows two main gradients: (i) decreasing

rainfall with increasing distance to the Atlantic coast, and (ii) increasing precipitation at higher elevation in the mountains due to orographic rain.

Today's vegetation cover of the Tagus Basin, like elsewhere in the Mediterranean region, is heavily disturbed after millennia of human activities, and the landscape is mainly dedicated to rather intensive farming and industrial activities. Natural and semi-natural vegetation is mostly restricted to mountainous terrain where agricultural activities and livestock raising were always extensive and have been largely abandoned during the last decades. Despite these constraints, the Tagus Basin currently

hosts a unique richness of plant species and communities. This paper does not intend to provide a detailed description of the many different plant communities that currently inhabit this region of central Iberia. We will rather describe briefly the main plant communities thriving in each of the four major vegetation belts represented in the Tagus Basin, i.e., the Thermomediterranean, the Mesomediterranean, the Supramediterranean, and the Oromediterranean, based on Costa et al. (2005), Loidi (2017) and the authors' field expertise. The Thermomediterranean belt consists of a narrow strip of land along the Atlantic coast where the most relevant woody plant communities are evergreen thermophilous woodlands and maquis (with *Quercus coccifera*, *Ceratonia siliqua*, *Pistacia lentiscus*, *Phillyrea latifolia*, *Arbutus unedo*, *Olea europaea* and *Erica arborea* among others), Mediterranean pinewoods (*Pinus pinaster*, *Pinus pinea*) on coastal dunes and sand sheets, psammophilous communities on the coastal dunes, and some *Quercus suber*-dominated "dehesas" ("montados" in Portuguese; open oak woods with agro-silvo-pastoral use). Evergreen oak (*Quercus ilex subsp. ballota*, *Quercus suber*) woods and "dehesas" are the most frequent forest communities in the Mesomediterranean belt, widespread in the central and western sectors of the study area, with notable variations in the floristic composition of their understory driven by local soil features, climatic conditions, historical biogeography, and land-use history. At the foothills of the Iberian Central Range and the Iberian Range, evergreen oaks mixed with Mediterranean pines (mostly *Pinus pinaster* and to a lesser extent *Pinus pinea* and *Pinus halepensis*) and deciduous oaks (*Quercus pyrenaica*, *Quercus faginea subsp. faginea*). The Supramediterranean belt covers extensive mid-elevation areas of the Iberian Central Range and the Iberian Range, and the highest areas of the Toledo Mountains. This vegetation belt hosts the highest diversity of wooded plant communities of the entire Tagus Basin, namely deciduous oak woods (*Quercus pyrenaica* on siliceous bedrock, and *Quercus faginea subsp. faginea* on calcareous bedrock and gypsum), mountain pinewoods (*Pinus nigra subsp. salzmannii*, *Pinus sylvestris*), *Pinus pinaster* woodlands, juniper (*Juniperus thurifera*) woodlands, sweet chestnut (*Castanea sativa*) stands, and evergreen oak woodlands (*Quercus ilex*), just to mention the most broadly distributed ones. Finally, *Pinus sylvestris* woods are the dominant forest communities at the highest elevations of the central and eastern sectors of the Iberian Central Range and the Iberian Range, i.e., in the Oromediterranean belt, both on siliceous and calcareous bedrock. The understory of these Oromediterranean mountain pinewoods is usually dominated, particularly near the timberline and at the tree line ecotone, by creeping shrubs like *Juniperus communis subsp. alpina*, *Juniperus sabina* and *Cytisus oromediterraneus*, which are actually the most frequent species in the shrublands located above the tree limit. The Oromediterranean belt of the Iberian Central Range, specifically on the Ayllón Mountains, is also home to some of the southern-edge populations of *Fagus sylvatica* in western Europe, where European beech is accompanied by a diverse set of mesophilous trees like *Quercus petraea*, *Ilex aquifolium*, *Betula pendula*, *Sorbus aria* or *S. aucuparia*. Another differential feature of the vegetation of the Ayllón Mountains, partially shared with the westernmost massifs of the Central Iberian Range (e.g., Serra da Estrela), is the abundance of Ericaceae (e.g., *Calluna vulgaris*, *Erica arborea*, *Erica australis*, *Arctostaphylos uva-ursi*) in the understory of the deciduous forests typical of the Supra- and Oromediterranean vegetation belts, above the timberline, and in the serial shrublands. Riparian vegetation is very diverse in the Tagus Basin (Lara et al., 2007), with *Salix* spp., *Populus* spp., *Fraxinus angustifolia* and *Ulmus minor* as the usually dominant taxa and also the remarkable presence of some communities dominated by the rare Tertiary evergreen broadleaved *Prunus lusitanica*, particularly in the western sector of the Toledo Mountains (Calleja et al., 2009). Concerning non-forested vegetation, the shrublands that have replaced forests and woodlands following anthropogenic or natural intense and/or frequent disturbance mostly consist of *Cistus* spp., *Erica* spp., *Calluna vulgaris* and different genera of Genisteae (e.g., *Cytisus*, *Genista*, *Pterospartum*) and Lamiaceae (e.g., *Lavandula*, *Thymus*, *Salvia*, *Satureja*). Finally, it is noteworthy the presence of steppic communities with abundant *Macrochloa (Stipa)*

*tenacissima*, Amaranthaceae (Chenopodiaceae), *Ephedra* spp., *Helianthemum squamatum* and *Artemisia herba-alba* on gypsum in some areas of the central Tagus Basin.

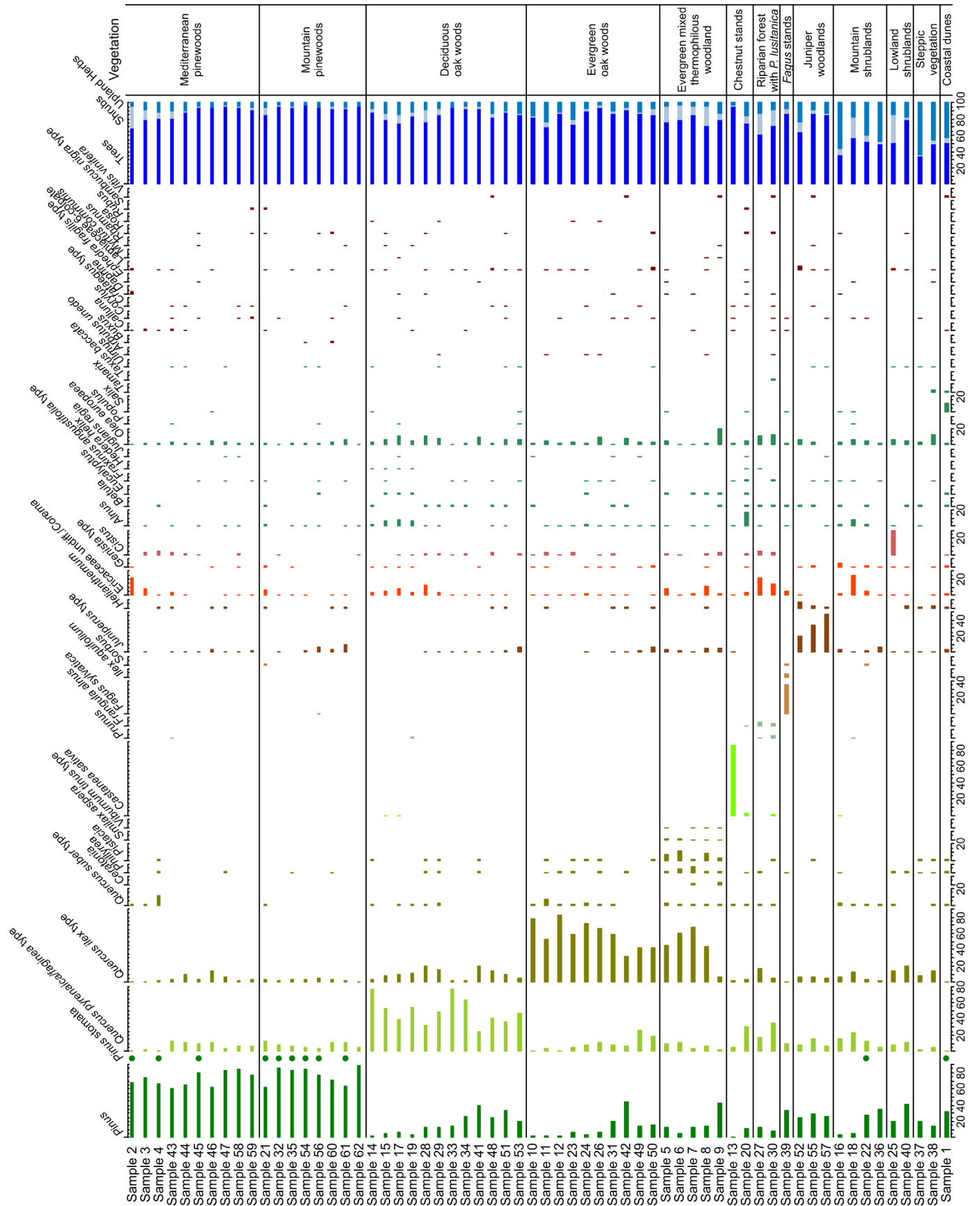
### 3. Material and methods

#### 3.1. Fieldwork: Sample collection and vegetation surveys

In November 2016, we conducted fieldwork throughout the Tagus Basin, collecting 62 samples from the coastal dunes and sand sheets close to the River Tagus estuary to the headwaters of the River Tagus and its main tributaries (Fig. 1). Fieldwork planning aimed at sampling a wide set of the extant (semi-)natural plant communities of central Iberia (Table 1), from the Thermomediterranean to the Oromediterranean vegetation belt. The environmental gradients covered were thus notably broad, with the sampling sites located along a large elevation gradient (from sea level to ca. 1900 m asl), under contrasting climatic conditions (from the mild Atlantic shore to one of the coldest and most seasonal area of the Iberian Peninsula, the central Iberian Range), and on diverse bedrock (e.g., granite, schist, limestone, sandstone).

The sampling sites were classified in 13 groups according to their present "vegetation type" to facilitate the latter representation and discussion of the results (see Table 1, Fig. 2): (1) "Mediterranean pinewoods" includes forest and woodland communities dominated by *Pinus pinea*, *Pinus halepensis* and/or *Pinus pinaster* ( $n = 10$ ); (2) "Mountain pinewoods" consists of *Pinus sylvestris*- and/or *Pinus nigra*-dominated forests and woodlands ( $n = 8$ ); (3) "Deciduous oak woods" comprises woodlands where *Quercus pyrenaica* and/or *Quercus faginea* dominate ( $n = 12$ ); (4) "Evergreen oak woods" groups the *Quercus ilex subsp. ballota*- and/or *Quercus suber*-dominated woodlands and "dehesas" ( $n = 10$ ); (5) "Evergreen mixed thermophilous woodland" refers to shrub and forest communities dominated by several species of Mediterranean evergreen trees and shrubs (often referred to as sclerophyllous) like *Quercus coccifera*, *Pistacia lentiscus*, *Olea europaea*, *Ceratonia siliqua*, *Phillyrea latifolia*, *Arbutus unedo*, *Erica arborea*, *Juniperus phoenicea* or *Viburnum tinus* ( $n = 5$ ); (6) "Chestnut stands" are communities with *Castanea sativa* as the dominant tree ( $n = 2$ ); (7) "Riparian forest with *Prunus lusitanica*" sites are within stands of *Prunus lusitanica* inhabiting narrow gorges of the Toledo Mountains surrounded by *Quercus pyrenaica* woodlands ( $n = 2$ ); (8) "Beech stands" site was located in one of the three main *Fagus sylvatica* sub-populations of the Iberian Central Range ( $n = 1$ ); (9) "Juniper woodlands" refers to more or less open woodlands dominated by *Juniperus thurifera* with an understory rich in chamaephytes ( $n = 3$ ); (10) "Mountain shrublands" are located above the modern tree line and the dominant species are usually *Cytisus oromediterraneus* and *Juniperus communis subsp. alpina* ( $n = 4$ ); (11) "Lowland shrublands" includes communities resulting from the degradation of mid-elevation woodlands where Cistaceae and Lamiaceae are dominant ( $n = 2$ ); (12) "Steppic vegetation" refers to *Macrochloa (Stipa) tenacissima*-dominated communities growing on gypsum in particularly dry settings, where other typical steppic plants such as *Artemisia*, *Ephedra*, *Helianthemum* and Amaranthaceae (Chenopodiaceae) are relevant ( $n = 2$ ); and (13) "Coastal dunes" includes a single site from a dune system on the Portuguese coast ( $n = 1$ ).

Surface samples mostly consisted of moss polsters but in some cases some litter and/or the topmost soil layer were also collected. At each site we picked up several moss fragments (usually 5) within a plot of ca. 20 × 20 m<sup>2</sup> following the recommendations in Pardoe et al. (2010). The only exception was at Site no. 1, where we collected the uppermost soil layer. In these plots we recorded vegetation structure and composition, with a particular focus on the woody taxa (i.e., trees, shrubs, dwarf shrubs, and lianas). Local tree cover (%) and, in some cases, shrub cover (%) were also visually estimated in most cases. We also recorded the



**Fig. 2.** Percentage pollen diagram of the surface samples from the Tagus Basin: selected trees and shrubs. Samples are arranged according to the dominant extant vegetation around the sampling sites. *Pinus stomata*: dots denote “presence.”



extra-local vegetation (some hundred metres around the sampling site) when this was different from the local.

### 3.2. Pollen analysis

In the laboratory, we carefully homogenized each sample to prevent overrepresentation of plants growing next to each individual moss polster. Moss sub-samples of ca. 5–10 cm<sup>3</sup> then underwent physical (wet sieving with a 150 µm mesh, decanting) and chemical (HCl, HF, KOH, acetolysis) to concentrate pollen. We finally mounted slides using glycerol as mounting medium and counted pollen and spores using an optical microscope at 400× magnification. Terrestrial pollen sum (excluding spores and pollen from aquatic plants) was always above 500 pollen grains (Mean ± SE: 531 ± 35) with the exception of Sample no. 1 ( $n = 413$ ) due to poorer pollen preservation. For pollen identification we used photographic atlases (e.g., Reille, 1992), identification keys (e.g., Punt et al., 1976–2009; Beug, 2004) and the reference collection at the University of Bordeaux (UMR EPOC). The Tilia software (<https://www.tiliait.com/>) was used for pollen data handling and plotting of percentage pollen diagrams.

### 3.3. Numerical analyses

We grouped the sampling sites according to the similarity of their modern pollen assemblages using Ward's minimum-variance agglomerative clustering (Ward, 1963; Legendre and Birks, 2012a) running in PAST 3.18 (Hammer et al., 2001). We then used ordination to summarize and assess the compositional variation of the pollen dataset (Legendre and Birks, 2012b). First, we ran detrended correspondence analysis (DCA) on untransformed pollen percentages to quantify the compositional turnover in the surface pollen sample dataset in standard deviation (SD) units and to assess whether ordination methods based on linear or unimodal response models were better suited for further analysis (ter Braak and Prentice, 1988; Šmilauer and Lepš, 2014). As the length-of-gradient of the first axis of the DCA was 2.11 SD, we selected the linear method for unsupervised ordination, i.e., Principal Component Analysis (PCA; Legendre and Birks, 2012b). One surface pollen sample from the Tagus Estuary ("Barreiro") and another marine core-top sample from the Iberian margin off-Portugal ("MD95-2042"; Fig. S1; Naughton et al., 2007) were added passively to the ordination plots to explore the relationships between the modern pollen spectra at these sites and the pollen representation of extant plant communities of central Iberia. Ordination analyses were conducted in Canoco 5 (ter Braak and Šmilauer, 2012).

## 4. Results

### 4.1. Pollen data

The most striking feature of the pollen spectra from Mediterranean pinewoods is the dominance of *Pinus* pollen (ca. 60–85%), in some cases accompanied by pine stomata (Fig. 2). *Quercus* pollen is usually relevant in these pollen assemblages, with the main *Quercus* pollen type (type = t.) changing according to the elevation (i.e., *Quercus suber*-t. on coastal communities, *Quercus ilex*-t. at mid-elevation, and *Quercus pyrenaica/faginea*-t. further up). Tree pollen percentages are therefore rather high (70–95%) and there are few shrubs and herbs truly important (Ericaceae undiff./*Corema*, *Cistus*, Poaceae; Figs. 2, 3). Mountain pinewoods show a very similar picture, with *Pinus* pollen largely dominating the assemblages (ca. 60–90%) and regular findings of *Pinus* stomata (Fig. 2). *Quercus pyrenaica/faginea*-t. pollen is relatively abundant (>10%) in some samples, and it is worth to note the representation of *Juniperus*-t. in some samples from the Iberian Range (5–10%; Fig. 2). In summary, tree pollen percentages are very high (ca. 85–95%) and the pollen representation of herbs is extremely reduced (3–5%).

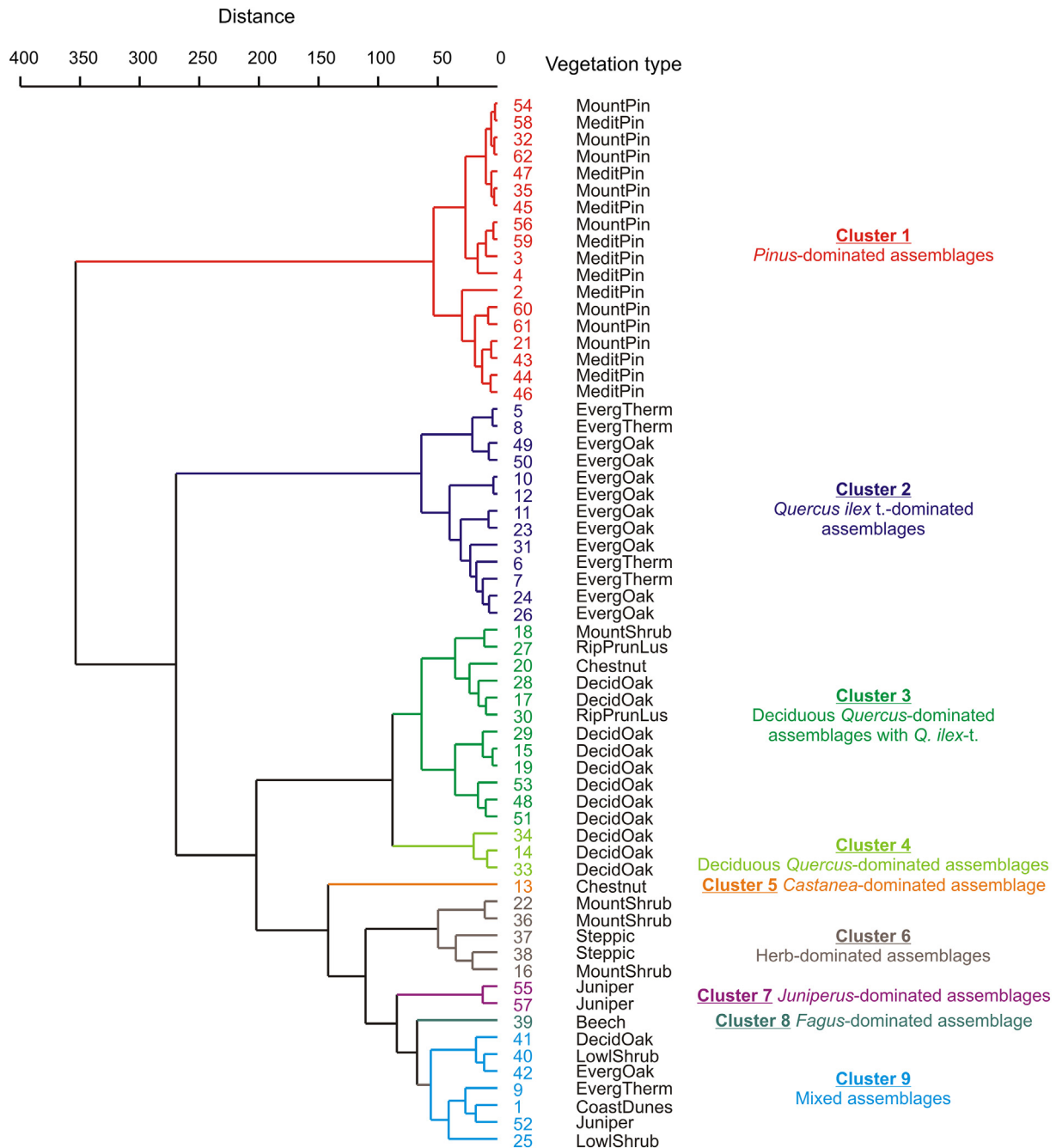
Pollen assemblages of deciduous oak woods are characterized by high percentages of tree pollen (75–95%), mostly corresponding to *Quercus pyrenaica/faginea*-t. (usually 30–75%) but with notable representation of *Quercus ilex*-t. (usually ca. 5–20%) and *Pinus* (ca. 5–40%; Fig. 2). Ericaceae undiff./*Corema* and *Alnus* are well represented in several samples from the western sector of the Tagus Basin with >5%. Another remarkable feature of the western deciduous oak woods is the relative abundance of *Plantago lanceolata*-t. (ca. 2–5%; Fig. 3). Tree pollen percentages are also high in samples from evergreen oak woods (70–95%), mainly *Quercus ilex*-t. (ca. 30–80%) but also *Pinus*, especially to the east of the study area (15–45%), and *Quercus pyrenaica/faginea*-t., also in the central and eastern sectors of the Tagus Basin (5–25%; Fig. 2). The abundance of Cichorioideae pollen (ca. 10%) in a pair of samples from "dehesas" is highly remarkable, together with moderate abundances of *Plantago lanceolata*-t. (2–4%; Fig. 3). Evergreen mixed thermophilous woodland pollen assemblages are also dominated by tree pollen (ca. 70–85%), with a moderate representation of shrub pollen (ca. 10–25%; Fig. 2). *Quercus ilex*-t. is usually the most abundant pollen type (ca. 40–65%) with the exception of Site no. 9 where *Pinus* is dominant (ca. 40%) alongside *Olea europaea* (ca. 20%). But the most remarkable feature of the pollen assemblages of this vegetation type is probably the diversity and moderate abundances of evergreen woody taxa (broadleaved and conifers), e.g., *Juniperus*, *Ceratonia*, *Phillyrea*, *Pistacia*, *Smilax aspera* or *Viburnum tinus*-t.

The two samples from chestnut stands have very different pollen signatures, as one of them bears a strong dominance of *Castanea sativa* pollen (no. 13, ca. 85%) while the other has a minimum representation of this pollen type (no. 20, ca. 2%; Fig. 2). Sample no. 20 has actually a rather mixed composition with *Alnus* (ca. 15%), *Pinus* (ca. 10%) and *Quercus pyrenaica/faginea*-t. (ca. 30%) as best represented taxa. Similarly, pollen assemblages from riparian communities where *Prunus lusitanica* is dominant or co-dominant record low proportions of *Prunus* pollen (0.5 and 3.5%), and are rather dominated by *Quercus pyrenaica/faginea*-t. (ca. 15–35%) and Ericaceae undiff./*Corema* (ca. 15–20%; Fig. 2). *Pinus* (ca. 10%) and *Quercus ilex*-t. (ca. 5–15%) are also important taxa of the assemblages, while *Frangula alnus* and *Cistus* reach ca. 5% and 3–4% of the terrestrial pollen sum respectively. In Sample no. 49, *Osunda regalis* spores reach an outstanding 15% (Fig. 3). The only sample collected from *Fagus sylvatica*-dominated stands show co-dominance of *Fagus* (ca. 35%) and *Pinus* (ca. 30%) in a pollen assemblage where other relevant woody taxa are *Quercus pyrenaica/faginea*-t. (ca. 10%), *Ilex aquifolium* (ca. 3%), *Sorbus* (1%) and Ericaceae undiff./*Corema* (ca. 5%; Fig. 2). Open juniper woodland (Sample no. 52) shows moderate tree pollen percentage (65%) while the closed stands of *Juniperus thurifera* (Samples no. 55 and 57) reach ca. 85% of tree pollen (Fig. 2). *Juniperus*-type is the most abundant pollen type (ca. 20–45%) with notable percentages of *Pinus* (ca. 25%), *Quercus pyrenaica/faginea*-t. (7–15%) and *Quercus ilex*-t. (ca. 5%). In Sample no. 52, *Helianthemum* and Lamiaceae 6-colpate are remarkably well-represented, 7% and 4% respectively.

Mountain shrubland samples feature rather low tree pollen percentages (ca. 35–55%) and usually low proportions of shrub pollen (2–8 (25%); Fig. 2). The representation of trees is quite variable depending on the site but, in general, *Pinus*, *Quercus* and *Alnus* are the main ones. *Juniperus*-t. (0.5–7%), Ericaceae undiff./*Corema* (1–24%) and *Genista*-t. (0.5–4%) are the most relevant shrubs. Among the herbs, Poaceae (ca. 10–40%), *Rumex acetosa/acetosella*-t. (1–1.5%), and 20% in Sample no. 16) and *Anthemis*-t. (1–3%) are the best represented (Fig. 3). Lowland shrubland samples are very different (Figs. 2, 3): Sample no. 25 is dominated by *Cistus* (30%) and regional tree pollen (*Pinus* 20%, *Quercus ilex*-t. 15%, *Quercus pyrenaica/faginea*-t. ca. 10%), whereas tree pollen dominates in Sample no. 40 (*Pinus* 40%, *Quercus ilex*-t. 20%, *Quercus pyrenaica/faginea*-t. 10%) with the remarkable abundance of *Gypsophila*-t. (ca. 10%). Pollen assemblages from steppic communities show the lowest values of tree pollen (35–50%) because herbs dominate (ca. 45–65%). It is important to note the relative abundance of regional





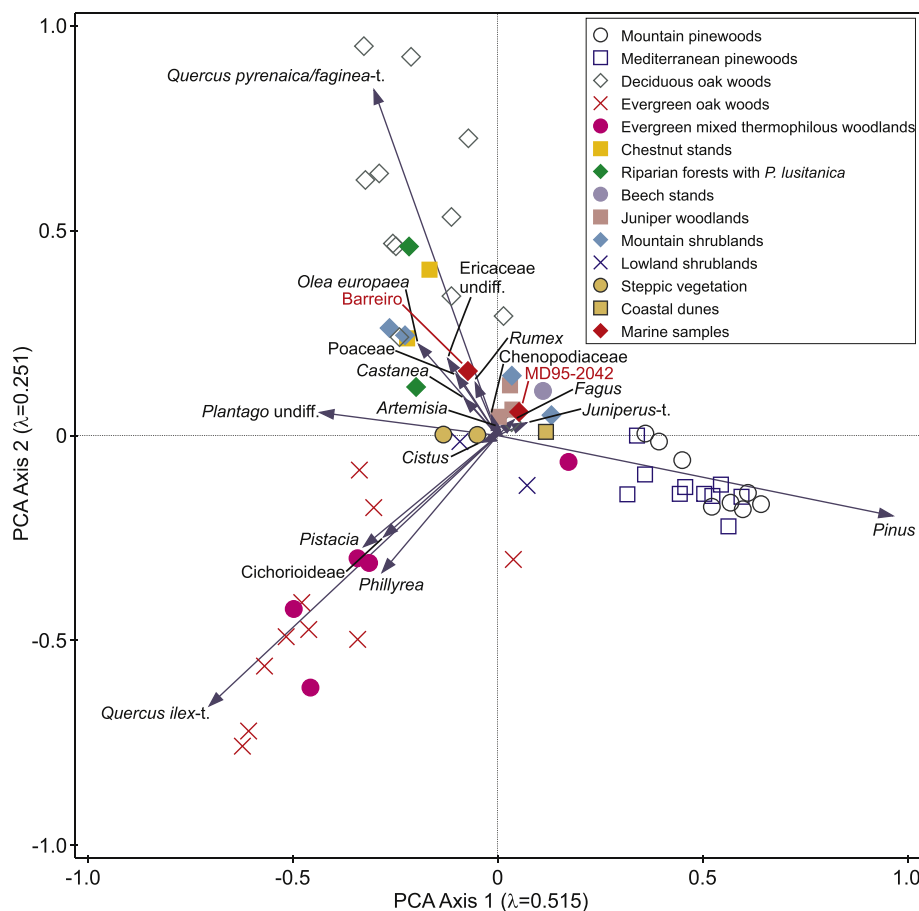


**Fig. 4.** Dendrogram showing the results of Ward's hierarchical clustering applied to the percentage pollen data from the surface samples collected in the Tagus Basin. The dataset has been split into nine clusters, which are represented in different colors. The "vegetation type" column shows the dominant extant vegetation around each of the sampling sites, while a brief description of each of the nine clusters is provided to the right of the figure.

proportions of *Quercus ilex*-t., from *Quercus ilex* woodlands and "dehesas" as well as mixed thermophilous evergreen forests where *Quercus coccifera* is usually abundant; (iii) Cluster 3 is composed of 12 samples with pollen assemblages dominated by *Quercus pyrenaica/faginea*-t. and moderate abundances of *Quercus ilex*-t., from plant communities where deciduous *Quercus* (mostly *Quercus faginea* and *Quercus pyrenaica*) are dominant or co-dominant (e.g., riparian forests with *Prunus lusitanica*); (iv) Cluster 4 embraces three samples with a more prominent dominance of deciduous *Quercus* pollen (= *Quercus pyrenaica/faginea*-t.); (v) Cluster 5 actually corresponds to Sample no. 13, strongly dominated by *Castanea sativa* pollen and collected in a monospecific chestnut stand; (vi) Cluster 6 encompasses 5 samples with dominance of herb pollen from mountain shrublands and steppic

communities; (vii) Cluster 7 consists of 2 samples with *Juniperus*-t-dominated assemblages from relatively closed *Juniperus thurifera* stands; (viii) Cluster 8 has only 1 sample (no. 39) with high percentages of *Fagus sylvatica* and notable representation of other deciduous trees, collected from one of the few beech stands of the Iberian Central Range; and (ix) samples with mixed assemblages without clearly dominant pollen types amalgamate into Cluster 9, which comprises 7 samples from several vegetation types.

Axis 1 of the PCA explains 51.5% of the variation in the pollen dataset and mostly discriminates assemblages dominated by *Quercus* (negative values) and *Pinus* (positive values; Fig. 5). Meanwhile, Axis 2 explains 25.1% of the variation in the pollen dataset and mainly separates pollen assemblages where *Quercus ilex*-t. is most abundant (negative values)



**Fig. 5.** Ordination biplot of the principal component analysis (PCA) on untransformed pollen percentage data of the surface samples collected in the Tagus Basin. Axes 1 and 2 explain 51.5 and 25.1% of the variation in this dataset, respectively. Blue arrows denote species scores of the main pollen types. Colored symbols represent the composition of the dominant local to extra-local extant vegetation at the sampling sites (see legend). Two core-top samples from the River Tagus estuary (“Barreiro”) and a deep-sea core off the Portuguese margin (“MD95-2042”) were passively added to the ordination to assess the modern pollen representation of the sediments coming from the Tagus Basin (“Marine samples,” represented by red diamonds).

from those where *Quercus pyrenaica/faginea-t.* occurs most frequently (positive values; Fig. 5). In the ordination bi-plot, samples from pine-woods define a clear cluster but there is no distinction between those dominated by Mediterranean and mountain species. Likewise, pollen assemblages from evergreen oak woods and evergreen mixed thermophilous woodlands largely overlap although are mostly well-separated from the rest. Deciduous oak wood samples form a well-defined group with some samples from other plant communities where deciduous oaks are co-dominant. Finally, the rest of moss polster samples are quite intermingled in the central part of the ordination plot, with a particularly central placement for those from relatively open plant communities, “Barreiro” and “MD95-2042.” Interestingly, “MD95-2042” is closer to the *Pinus*-dominated assemblages than “Barreiro,” which is notably richer in Poaceae.

## 5. Discussion

The results suggest that the moss polsters have mainly collected pollen from the local to extra-local plant communities (up to several hundred metres away), although there was always certain regional representation (Figs. 2, 3; Table 1), which is in agreement with previous results from temperate and boreal Europe (Bunting et al., 2004; Broström et al., 2005; Mazier et al., 2008). In this regard, the abundance of *Olea* pollen in all the studied samples should be noted (Fig. 2), especially considering that sites on the Iberian Central Range and the Iberian Range are tens of kilometres away from the closest olive orchards. Modern pollen samples from other Mediterranean areas where olive

cultivation is regionally widespread also showed regular presence and even moderate abundances of *Olea* far away from the nearest orchards (e.g., Díaz Fernández, 1994; Sánchez Goñi and Hannon, 1999; Finsinger et al., 2007; Fall, 2012; Aranbarri et al., 2015; Bell and Fletcher, 2016) including montane to alpine sites in the Pyrenees (Cañellas-Boltà et al., 2009; Leunda et al., 2017).

### 5.1. Modern pollen signature of widespread forest communities

Major forest communities of the Tagus Basin (i.e., pinewoods and oak woodlands) had rather distinct pollen assemblages according to the results of hierarchical clustering and PCA (Figs. 4, 5), which reflected the high percentages of the dominant tree species, i.e., *Pinus*, *Quercus pyrenaica/faginea-t.* and *Quercus ilex-t.* respectively (Figs. 2, 3). Nevertheless, the fact that closely related vegetation types clustered together in both the hierarchical clustering and the PCA highlights certain limitations of the taxonomic resolution of pollen analysis (Figs. 4, 5).

Mediterranean and mountain pinewood samples shared high percentages of *Pinus* pollen as the most distinctive feature, as in most previous studies investigating the pollen rain of these communities elsewhere in the Mediterranean (e.g., Sánchez Goñi and Hannon, 1999; Gerasimidis et al., 2006; López-Sáez et al., 2013). Consequently, they were intermingled in Cluster 1 (Fig. 4) and largely overlapped in the PCA bi-plot (Fig. 5) despite the very different dominant species and floristic composition of the understory (Table 1). Quantitative morphological analysis of *Pinus* pollen grains might have provided more precise identifications (Desprat et al., 2015) and thus have improved



the discrimination of *Pinus*-dominated communities (e.g., Broothaerts et al., 2018), but it is extremely time-consuming and not applied in routine palynological analyses. Further, the high pollen production of *Pinus* may have often hindered the identification of indicator pollen types (Felde et al., 2014) specific to pinewoods dominated by a given pine species (e.g., which pollen types and/or in which abundances are closely related to *Pinus nigra* communities). However, the results still suggest that *Juniperus*-type was particularly frequent in the *Pinus nigra*- and *Pinus sylvestris*-dominated woods of the Iberian Range (Fig. 2), in agreement with the abundance of *Juniperus thurifera*, *Juniperus communis* and *Juniperus sabina* in the sampling sites (Table 1). Likewise, Ericaceae undiff./*Corema* pollen is remarkably abundant in the sample from a *Pinus pinaster* wood from the coastal dunes of central Portugal where *Corema album* dominates the understory (Sample no. 2; Fig. 2 and Table 1). Precising the composition of ancient pinewoods has long been a major research question in Mediterranean paleoecology and several palynological records identified different typologies of *Pinus* pollen based on quantitative and qualitative features (e.g., Carrión et al., 2000; López-Merino et al., 2010). However, unless thorough quantitative analyses are accomplished (Desprat et al., 2015), macrofossil analysis seems to continue as the most reliable tool to track pine species changes through time if this kind of remains are preserved in the sedimentary sequence (Morales-Molino et al., 2013).

Deciduous oak woods showed *Quercus pyrenaica/faginea*-t.-dominated pollen assemblages, in most cases with a significant representation of *Quercus ilex*-t. pollen (Cluster 3 in Fig. 4) although the dominance of deciduous *Quercus* pollen (= *Quercus pyrenaica/faginea*-t.) was particularly prominent in certain samples (Cluster 4 in Fig. 4). This more conspicuous dominance of deciduous *Quercus* pollen (named *Quercus pyrenaica*-t. there) was more frequent in samples from *Quercus pyrenaica* stands from the Iberian Central Range studied by López-Sáez et al. (2015), probably because some of our samples included in this vegetation type came from sites where the vegetation around was mosaic-like (Table 1). In contrast, lower representation of deciduous *Quercus* and moderate abundance of *Pinus* characterized Sánchez Goñi and Hannon (1999)'s samples from deciduous oak woods, making them more comparable to our samples from the Iberian Range (Fig. 2). However, our samples showed in general higher abundances of *Quercus ilex*-t. pollen, probably because of the more Mediterranean setting. Interestingly, Cluster 3 not only embraced samples from deciduous oak woods but also several ones from other plant communities scattered within widespread *Quercus pyrenaica* woods (Fig. 4). For instance, *Prunus lusitanica* stands (Samples no. 27, 30) form narrow bands along a stream that is completely surrounded by extensive *Quercus pyrenaica* woodlands on the adjacent slopes, and something similar occurs with one of the studied chestnut stands (Sample no. 20). There is also one sample from a broom-dominated mountain shrubland where deciduous oak pollen is dominant (Sample no. 18), most probably because of the close proximity to the *Quercus pyrenaica* timberline (Table 1). State-of-the-art palynology does not allow separating the different species included in the *Quercus pyrenaica/faginea*-t., but the slight ecological overlap has led some authors to use the names *Q. pyrenaica*-t. and *Q. faginea*-t. in sites where one of these oak species is expected to have been dominant (e.g., López-Merino et al., 2010; Morales-Molino et al., 2017a, 2017b). Recent research on the chemical composition of *Quercus* pollen has revealed promising results for enhanced taxonomic identification (Muthreich et al., 2020), and one should not discard that further refinement of this technique in the near future ends up in the distinction of the different species of white oaks. Western Iberian deciduous oak woods, which develop on acidic soils and under more oceanic conditions (Costa et al., 2005), showed moderate abundances of Ericaceae pollen, in agreement with the relevance of heaths in the understory of the sampled woodlands. The rather intense use of these western deciduous *Quercus* woodlands for free-ranging cattle could account for the consistently moderate percentages of *Plantago lanceolata*-t. observed in their pollen assemblages, in agreement with

previous research on the *Quercus pyrenaica* communities of the Iberian Central Range (López-Sáez et al., 2015). Finally, the only sample from deciduous oak woods outside Clusters 3 and 4 (Sample no. 41, in Cluster 9) did not show a clear dominance of any tree pollen type, probably as a result of the rather mixed composition of the stand where it was collected and the mosaic-like structure of the regional vegetation.

Overall, pollen assemblages from evergreen oak woods were clearly dominated by *Quercus ilex*-t. pollen, although *Quercus pyrenaica/faginea*-t., *Pinus* and to a lesser extent *Juniperus*-t. reached notable representation in the samples from the Iberian Range (Fig. 2). As previously explained for deciduous *Quercus* woods of the same area, this pattern may be due to the widespread occurrence of mixed stands and the mosaic-like landscape (Costa et al., 2005; Sainz Ollero et al., 2010). Interestingly, evergreen mixed thermophilous woodlands had pollen assemblages dominated by *Quercus ilex*-t. as well (Fig. 2), and this contributes to explain why most of the samples from this vegetation type clustered together with those from evergreen oak woods in Cluster 2 of the hierarchical clustering and the PCA (Figs. 4, 5). *Quercus ilex*-t. pollen found abundant and usually dominant in the evergreen mixed thermophilous woodland samples (Fig. 2) may actually have been produced mostly by *Quercus coccifera* (Beug, 2004), which is (co-)dominant in several of the sampled evergreen mixed thermophilous woodland sites (Table 1). As indicated above for deciduous oak pollen, ongoing research on pollen chemistry for taxonomical identification of *Quercus* (Muthreich et al., 2020) might bring along relevant implications for paleoecological research if it eventually allowed distinguishing between *Quercus ilex* and *Quercus coccifera*. In any case, despite that multivariate quantitative analyses showed a significant overlap between the pollen assemblages of these two vegetation types, *Pistacia*, *Phillyrea*, *Ceratonia siliqua*, *Viburnum tinus*-t. and *Smilax aspera* seemed to be good indicators to identify these thermophilous woodlands (Fig. 2). It is also worth to note here the unexpectedly high tree pollen percentages found in some "dehesa" samples despite the rather low tree cover (Figs. 2, 3; Table 1), higher than those previously reported from these agro-silvo-pastoral systems (López-Sáez et al., 2010). The traditional management of the "dehesas," which involves tillage, grazing and tree pruning (Olea and San Miguel, 2006), may account for this as it seeks to favor shrub removal and tree blooming while preventing herbaceous plants from flowering. The abundance of Cichorioideae might result from their remarkable tolerance to disturbance but also from differential preservation due to the resistance of this pollen type to degradation (Lebreton et al., 2010), while heavy grazing would explain the abundance of *Plantago lanceolata*-t. (Fig. 3; López-Sáez et al., 2010). The presence of *Quercus suber*-t. seemed to work in separating western holm oak woods from those typical of the Iberian Range, growing at higher elevation and on limestone (Fig. 2). Again, co-dominance of different tree species and mosaic-like landscape could be the underlying reasons why Sample no. 42 was included within Cluster 9 instead of Cluster 2 with the rest of evergreen oak wood samples (Fig. 5).

## 5.2. Modern pollen representation of other plant communities of biogeographical interest

As stated in the previous sub-section, the pollen representation of riparian forests with *Prunus lusitanica* did not differ significantly from that of the surrounding *Quercus pyrenaica* woods, with the exception of the noticeable representation of *Frangula alnus* and Ericaceae (Fig. 2). *Osmunda regalis*, a fern typical of riparian environments of western Iberia (Costa et al., 2005), also attained rather high abundances in one of the studied samples. In contrast, *Prunus* pollen was quite rare despite the (co-)dominance of *Prunus lusitanica*, most probably because this tree is insect-pollinated. *Prunus lusitanica*-dominated communities have a great biogeographical interest and are seriously threatened (Calleja et al., 2009), so tracking their past occurrence and dynamics using paleoecological research would be desirable to improve their present and future management. However, our data suggest that an

unambiguous palynological footprint for these communities is lacking, and this would in turn hamper addressing this question. In contrast to the sample from a small chestnut stand surrounded by deciduous oak woods where we reported that *Castanea sativa* pollen was rare (Sample no. 20), the closed *Castanea sativa*-dominated stand had a very distinct palynological signature because of the high percentages of *Castanea* pollen, which resulted in a separate cluster (Cluster 5; Fig. 4).

Pollen assemblages from mountain shrublands above the timberline revealed a notable representation of the regional vegetation, particularly of the forests forming the timberline (Figs. 2, 3). Our results also show that local pollen production was rather low, mainly because *Cytisus oromediterraneus*, the dominant shrub in most of our “Mountain shrubland” sites (Table 1), is insect-pollinated. Neither was *Juniperus*-t. abundant in any of the pollen assemblages of this vegetation type despite its relevance at Site no. 36. In contrast, Poaceae pollen was abundant in good agreement with their abundance in these mountain landscapes (Figs. 2, 3; Table 1). Likewise, our data suggest that the pollen representation of Ericaceae accounted better for their true abundance in the surrounding vegetation, not only in mountain shrublands but also in the understory of woodland communities (see Fig. 2). Previous research in the Oromediterranean belt of the Iberian Central Range had reported such striking underrepresentation of *Genista*-t. pollen in the extensive *Cytisus oromediterraneus*-dominated shrublands of the Gredos Mountains (Andrade Olalla et al., 1994). In marked contrast, certain pollen spectra of *Pinus sylvestris* stands from the Iberian Central Range where *Cytisus*, *Genista* and *Echinopartum* were dominant in the understory showed much higher percentages of Genisteae pollen (up to 20%; López-Sáez et al., 2013). Less “controversial” is the modern pollen representation of Ericaceae, as previous research also suggested a good correlation between the abundance of Ericaceae in the extant vegetation and the proportion of pollen found in surface samples (Stevenson, 1985; Díaz Fernández, 1994; López-Sáez et al., 2013, 2015). However, we must note that Ericaceae pollen was underrepresented in samples from *Pinus sylvestris* forests with *Erica australis*-dominated understory (Sánchez Goñi and Hannon, 1999). The palynological signature of steppic vegetation was not only determined by the abundance of grasses and other herbaceous taxa present locally such as Chenopodiaceae, *Artemisia*, *Gypsophila*-t. and Apiaceae, but also by long-distance transported pollen (Figs. 2, 3). In similar settings, López-Sáez et al. (2010) found higher abundances of Poaceae and lower input of long-distance transported tree pollen, although the main features of the pollen assemblages were similar.

Despite *Juniperus thurifera*-dominated woodlands are currently one of the most characteristic and unique forested communities of the western Mediterranean (Costa et al., 2005), to our knowledge no previous study had addressed their pollen representation. Our data show that the structure of the community, more or less open, had a certain influence in the abundance of *Juniperus*-t. pollen, but this is still largely dominant in the assemblages (Fig. 2). Indeed, *Juniperus*-t. pollen dominated conspicuously in the two samples from relatively closed woodlands (no. 55, 57), which grouped together in a separate cluster (Cluster 7), whereas *Juniperus*-t. was not so dominant in Sample no. 52, which was placed in Cluster 9 (Fig. 4). *Juniperus thurifera* is also one of the most relevant trees in the High Atlas (Morocco), but its pollen representation was minimum in surface samples probably because of its rarity at the sampling sites (Bell and Fletcher, 2016). Interestingly, modern pollen representation studies in the ecologically and structurally equivalent juniper communities of the eastern Mediterranean and south-western Asia (dominated by *Juniperus excelsa*, *Juniperus foetidissima*, and to a lesser extent *Juniperus phoenicea*) have reported a range of *Juniperus*-t. pollen percentages similar to the samples from the Iberian Range (Davies and Fall, 2001; Hajar et al., 2008; Djamali et al., 2009; Fall, 2012). Last but not least, it is worth to note the abundance of *Helianthemum* and Lamiaceae pollen in the pollen assemblage from the open juniper stand (Fig. 2), in agreement with their relevance in the extant plant community.

*Fagus* pollen dominated in the sample from the beech-dominated stand of the Hayedo de la Pedrosa but high percentages of *Pinus*, deciduous *Quercus* and Ericaceae pollen were also found (Fig. 2). This can be explained considering two features of the site: (i) the rather open structure of this beech wood, coppiced and with a dense understory where several *Erica* species, *Arctostaphylos uva-ursi* and *Vaccinium myrtillus* were abundant (see Table 1); and (ii) the spatial distribution of forest communities at the extra-local scale (several kilometres radius), with widespread *Quercus pyrenaica* (and *Quercus petraea*) woods and *Pinus sylvestris* afforestations. Despite the local abundance (even co-dominance) of *Ilex aquifolium* and *Sorbus* spp., the pollen of these insect-pollinated trees was quite rare. Similar abundances have been reported for *Ilex aquifolium* in *Pinus sylvestris*-*Ilex aquifolium* stands of the northern Iberian Range (Sánchez Goñi and Hannon, 1999) and in *Quercus pyrenaica*-*Fagus sylvatica* forests of the Ayllón Mountains (López-Sáez et al., 2015).

Finally, our results showed rather high percentages of *Cistus* in extensive shrublands dominated by *Cistus ladanifer* (Fig. 2), despite rockroses are insect-pollinated. Stevenson (1985) obtained similar results in the rather similar *Halimium*-dominated shrublands of the Doñana National Park (south-western Spain). Nevertheless, high regional tree pollen representation was quite high and led this sample to be placed within the undifferentiated Cluster 9 (Fig. 4). In any case, more samples from this vegetation type would be needed to properly assess the abundances of *Cistus* pollen that define these shrublands.

### 5.3. Some implications for the interpretation of fossil records

Our moss samples reflected mostly the composition of the local to extra-local plant communities (up to several hundred metres away from the sampling site), particularly when the surrounding vegetation was relatively closed and the dominant plant species were wind-pollinated. Consequently, they certainly provide relevant insights into the interpretation of fossil pollen records from forest hollows and small mires/bogs/lakes, which have a similar source area of pollen (Bradshaw, 2013) and are probably the most widely used archive for vegetation reconstruction (e.g., López-Merino et al., 2010; Abel-Schaad and López-Sáez, 2013; Ramos-Román et al., 2016; Morales-Molino et al., 2017a, 2019). Additionally, moss samples accumulate pollen rain during several years, time-averaging pollen deposition in a similar way to mires (Pardoe et al., 2010). On the contrary, comparison of pollen assemblages from larger lakes with the moss surface samples can be done but must be necessarily cautious because previous research has pointed out significant differences in their pollen catchments (Lisitsyna et al., 2012).

The comparison between pollen assemblages from moss polsters and estuarine/deep-sea sediments deserves even more attention, but there are some aspects worth to highlight. First, the closer location of “MD95-2042” to samples from pinewoods in the PCA plot compared to “Barreiro” suggests overrepresentation of *Pinus* pollen in the marine realm, supporting previous research on pollen representation in deep-sea sediments (e.g., Heusser and Balsam, 1977) and the common practice in marine palynology of excluding *Pinus* from the main sum used to calculate percentages (e.g., Sánchez Goñi et al., 1999). Second, the quite central position of both “Barreiro” and “MD95-2042” in the PCA plot could be pointing towards a relatively balanced representation of the main forested communities inhabiting the Tagus Basin today. Moreover, marine/estuarine samples grouped together with pollen assemblages from rather open environments (Fig. 5). This brings further support to marine sediments averaging the pollen representation of the entire basin as anthropogenic open vegetation (e.g., crops, pastures) is dominant in the study area (Cordovil et al., 2018), but its pollen representation largely underinvestigated here as we focused on (semi-) natural plant communities. Our results are therefore in line with previous results suggesting that pollen assemblages from deep-sea sedimentary sequences of the European margin integrate the pollen signal from

the vegetation of the adjacent hydrographic basins (e.g., Sánchez Goñi et al., 1999; Roucoux et al., 2006; Naughton et al., 2007). Nevertheless, only *ad hoc* studies based on a sampling design of high spatial resolution and stratified according to vegetation types and latter weighting of the pollen representation taking into account the surface covered by each vegetation type will contribute to elucidate this question in a robust manner. Last but not least, the different timespan potentially covered by marine surface samples (several centuries; Naughton et al., 2007) and moss polsters (several years; Lisitsyna et al., 2012) adds further complexity to the picture.

## 6. Conclusions

The main forested ecosystems of central Iberia show rather distinct pollen assemblages with high proportions of the pollen equivalents to the dominant tree species (basically pines and oaks). Nevertheless, taxonomical refinement within major pollen types such as *Quercus ilex*-t. and *Pinus* would notably improve the discrimination of ecologically relevant plant communities such as: (i) *Quercus ilex*-dominated woodlands and forests versus *Quercus coccifera*-dominated maquis and mixed evergreen thermophilous woodlands, and (ii) Mediterranean pinewoods versus mountain pinewoods. In contrast, rare narrowly distributed communities dominated by *Prunus lusitanica* does not have any distinctive pollen signature from the surrounding vegetation, probably because of the low pollen production and/or poor dispersal of this insect-pollinated species. Shrubland and stepic communities have less differentiated pollen spectra because regional pollen is dominant, which is in turn probably related to lower local pollen production and/or to the dominance of insect-pollinated species (e.g., mountain shrublands dominated by *Cytisus oromediterraneus*). An outstanding exception concerns *Cistus*, as *Cistus ladanifer*-dominated shrubland showed high percentages of pollen from this insect-pollinated plant. Pollen assemblages from moss polsters collected in central Iberia provide relevant information to improve the interpretation of fossil pollen data from mires and bogs. These results can also be useful for lake and marine records but must be taken with caution, and the need for carefully designed studies to assess the relationships between vegetation cover and the pollen representation of continental and marine samples must be highlighted.

## Declaration of Competing Interest

The authors declare no conflict of interest.

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## Appendix A. Supplementary data

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