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Don't lose sight of the forest for the trees! Discerning Iberian pine communities by means of pollen-vegetation relationships

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ABSTRACT

A set of 30 modern pollen samples collected in pine communities of the Gúdar Range (southeastern Iberian System) has been investigated to determine the relationships between pollen percentages and vegetation composition along a ~1000 m elevation transect. Pollen representation was estimated by comparing the presence of plant taxa from a recent vegetation survey with pollen spectra. Classification and ordination of modern pollen samples indicated the existence of eight vegetation units, which can be assigned to the six studied pine forest communities. Lowland forests are clearly discriminated from high-altitude ones. These analyses also allow separating *Pinus nigra* and *P. pinaster* communities according to their tree cover, and even those of *P. sylvestris* according to the bioclimatic belt they inhabit. We show that it is possible to obtain distinct pollen markers for Mediterranean pine forest communities. These results will also improve the reconstruction of pine forests from fossil pollen diagrams, as far as modern pollen rain studies are carried out in specific regions, an approach which can be extrapolated to other plant formations regardless the involved territory.

1. Introduction

The Mediterranean Basin, extending over more than 2 million km^2, is one of the main "hotspots" of plant diversity in the world (Médail and Quézel, 1997; Myers et al., 2000), containing approximately 30,000 plant species, i.e., 10% of all known higher vascular plants on Earth (Médail and Diadema, 2009), with an exceptional rate of endemicity (Thompson, 2005). For example, the region contains a great wealth of endemism in trees and shrubs, with 290 indigenous woody species and subspecies, 201 of which are endemic (Quézel and Médail, 2003). Such high biodiversity is the result of both environmental factors and historical processes that have determined the coexistence of taxa of very different origins (Quézel, 1985). However, this region is also one of the most threatened biodiversity hotspots of the world, largely as a result of human activity and ongoing aridification caused by climate warming (Blondel, 2006). The Mediterranean Basin ecosystems have undergone long continuous environmental degradation because of ancestral land-use practices, dependence on local socio-economic resources, natural fire regimes or intentional use of fire (Keeley et al., 2012). Forests of the Mediterranean Basin contain about 100 tree species (Fady-Welterlen, 2005), among which pines (*Pinus* sp.) and oaks (*Quercus* sp.) are dominant in most ecosystems (Blondel and Aronson, 1999; Fady and Médail, 2004). Pine forests cover about 13 million hectares in the Mediterranean Basin, which constitute ~5% of Mediterranean forested area (Barbéro et al., 1998). The extant pine flora of the Mediterranean Basin comprises 11 pine species, including the widespread *Pinus sylvestris* which, although abundant in the region where it forms the southernmost species distribution limit, is more characteristic of Eurosiberian sites (Klaus, 1989; Price et al., 1998). Thanks to their massive seed production and dispersal, fast growth, early maturity, longevity and large size, drought resistance and the ability to establish in harsh environmental conditions, pines are considered pioneer trees that make a major contribution to forest restoration and effective ecosystem conservation (Tapias et al., 2004). The Iberian Mediterranean territories are a good example of the importance of pine forests, which occupy ~43% of the forest area (Alía et al., 1999). In the Iberian Peninsula, six autochthonous pine species are present (Amaral-Franco, 1986; Blanco et al., 1997): *Pinus halepensis*, *P. nigra*, *P. pinaster*, *P. pinea*, *P. sylvestris* and *P. uncinata*.

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Pleistocene and Holocene Iberian pollen records have shown that pine forests were the dominant forest formations during the last 2.6 million years, especially in Mediterranean mountain environments and coastal areas (Franco-Múgica et al., 2000; Carrión et al., 2010; González-Sampériz et al., 2010; Camuera et al., 2019). However, most Iberian fossil pollen records hardly describe the temporal evolution of forests dominated by pines without taking into account the dominant species. Logically, these facts make it very difficult to differentiate in detail the evolution of high-mountain pine forests as opposed to those located at lower altitudes, as often the pollen signal of one and the other is indistinguishable. This is especially problematic concerning fossil pollen records located in areas where several pine species currently coexist (Franco-Múgica et al., 2001, 2005; García-Antón et al., 2011; Morales-Molino et al., 2013; Robles-López et al., 2018). Fortunately, some exceptions overcome these limitations in the interpretation of the palynological record discussed above. For example, Carrión et al. (2001a, 2001b, 2003, 2004, 2007) and Carrión (2002) have demonstrated the possibility of differentiating between the Holocene dynamics of high-mountain *Pinus nigra* forests of the Baetic Range (southern Iberia) and that followed by *P. pinaster* woodlands at lower altitudes. López-Sáez et al. (2014, 2018a) and Broothaerts et al. (2018) have shown the unequivocal relationship between the progressive disappearance of *Pinus sylvestris*/*nigra*-type forests in the central and western sectors of the Gredos Range highlands (Central Iberia) during the Christian period as opposed to the previous regression of the *P. pinaster* woodlands located in the lowlands in Roman times. Aranbarri et al. (2014) have documented the resilience of high-mountain pine forests in the Villarquemado pollen record (eastern Iberia) over the past 13 cal ka BP, despite the enormous climatic variability that characterized this entire period. A similar picture has been documented by Carrión and van Geel (1999) in Navarrés (southeastern Iberia), where *Pinus nigra* and *P. pinaster* forests dominated the glacial landscape 30,000 years ago and resisted invasion by other species until the Middle Holocene, when they were replaced by evergreen oak woodlands and scrub after local fire disturbance by Neolithic communities.

The aforementioned problems mainly derive from the difficulty of separating the existing pollen morphotypes within pine species. Within the genus *Pinus*, several studies currently allow to differentiate three pollen types within the six pine species that inhabit the Iberian Peninsula (Carrión et al., 2000; Beug, 2004; López-Sáez et al., 2010b, 2019a; Desprat et al., 2015). The first two include several inseparable species and the latter is monospecific: *Pinus nigra*/*sylvestris*/*uncinata*-type, *P. halepensis*/*pinea*-type, and *P. pinaster*. Thanks to the notable progress derived from such studies, it is feasible to follow the temporal evolution during the Quaternary of Iberian forests dominated by different species of pines, even if they constitute mixed woods among them or with oaks (Carrión, 2012; Sánchez de Dios et al., 2019). Obviously, in those areas where only one pine species of the morphotypes that share two or three occur, it is easy to assign this pollen type to the specific species, although it may be a risky exercise. Nevertheless, when the pine species that share the same pollen type cohabit in the same territory, the previous possibility does not exist and the interpretation of the paleoenvironmental record is severely restricted (Felde et al., 2014).

The greatest limitation that still persists is to diagnose whether in the past there were typologically different forests dominated by the same pine species, that is with a different floristic composition and even structure. This is particularly problematic when succinct comparisons are made between fossil pollen records from different biogeographical domains within the Iberian Peninsula. Although the plant dynamics may seem similar - dominance of high-mountain or lowland pinewoods - among them, it is likely that they are reporting completely different forests in their floristic composition and typology despite the fact that the dominant pine species is the same. For instance, we might ask ourselves: (i) are fossil pollen studies designed to distinguish between different high-mountain pine forests dominated by the same, different, or coexisting species?; (ii) are they suited to discriminate the dynamics of Mediterranean pine forests by differentiating which inhabits the highlands from the lowlands? At this respect, López-Sáez et al. (2010a, 2013, 2015) have demonstrated the possibility of discriminating between forest communities constituted indistinctly by oaks (*Quercus rotundifolia*, *Q. pyrenaica*) and *Pinus sylvestris* in the Iberian Peninsula by means of modern pollen rain analysis, focusing not so much on the dominant tree pollen type but rather on the pollen record of shrubs and herbs that proved to have greater diagnostic power (Fall, 2012). Similar contributions are given by Glais et al. (2016) and López-Sáez et al. (2019b), who have been able to differentiate Mediterranean cypress (*Cupressus sempervirens*) and beech (*Fagus sylvatica*) communities of Crete and northeastern Greece respectively through studies of modern pollen rain. Therefore, fossil pollen records provide information about the types of ecosystems and vegetation once present in an area (Hicks and Birks, 1996; Bennett and Hicks, 2005), while modern pollen and vegetation data within different vegetation types are essential keys for the interpretation of past vegetation from fossil pollen records and for paleoecological reconstruction (Bunting et al., 2004). In any case, it is plausible to insist on the need for making an effort in the morphological identification of herb pollen taxa with a diagnostic character (Felde et al., 2014), because if we focus on the identification of tree species, a certain perspective may be lost in the typological discrimination of forests. Pollen can often only be identified as a group of species (pollen-types), to genus level or even just to family level (Birks et al., 2016). This restricted taxonomic precision greatly limits the interpretation of fossil pollen records. Furthermore, over-represented pollen taxa such pine species occur usually in high percentages, but yield only local or regional signals. Under-represented taxa allow more detailed environmental reconstructions but are scarcely found (Moscol-Olivera et al., 2009; López-Sáez et al., 2018b).

In this paper, we have investigated modern pollen samples from the Iberian Peninsula to discriminate *Pinus* forest communities, that is, the exploration of how well local vegetation is represented in the pollen assemblages. To improve our knowledge of Iberian pine forests and to address research questions related to spatial aspects that cannot be answered by the analysis of site-specific taxa, an extended dataset of sample plots was collected in the southern Iberian System (Gúdar Range, Teruel, eastern Spain). These mountains constitute a key enclave for the development of this research, probably a unique case within the Mediterranean region, because in just 25 km of an altitudinal transect six Iberian pine species coexist (Camarero et al., 2015). The pollen content was then determined in relation to associated relevés in order to define relationships among vegetation and pollen data. The main objectives of our study are: (i) to explore how contemporary vegetation is depicted in surface pollen assemblages, (ii) to identify pollen indicators of *Pinus* forest communities, and, (iii) to establish statistic relationships between pollen rain and vegetation patterns on the basis of multivariate analysis in order to use them for paleoecological reconstruction in future studies.

2. Vegetation and climate of the Gúdar Range

The study was conducted in the Gúdar Range located in southern Aragón, eastern Spain (Fig. 1). This mountainous area belongs to the southern Iberian System, an alpine intraplate orogen in central-eastern Iberia. Regional geological bedrock is made of Upper Triassic-Jurassic limestones, Lower Cretaceous detrital rocks, and Upper Cretaceous limestones and dolostones that are affected by NW-SW and NE-SW trending folds, thrusts and faults (Gutiérrez and Peña, 1990). In the study area, basic loamy soils predominate. The highest altitudes of this whole massif are reached in the Gúdar Range (Peñarroya peak, 2028 m asl). (See Fig. 1.)

The current climate of the region is continental-mountain Mediterranean, with high seasonal contrast between very hot summers (maximum mean temperature in August, the warmest month, is 32 °C) and very cold winters (minimum mean temperature in January, the coldest

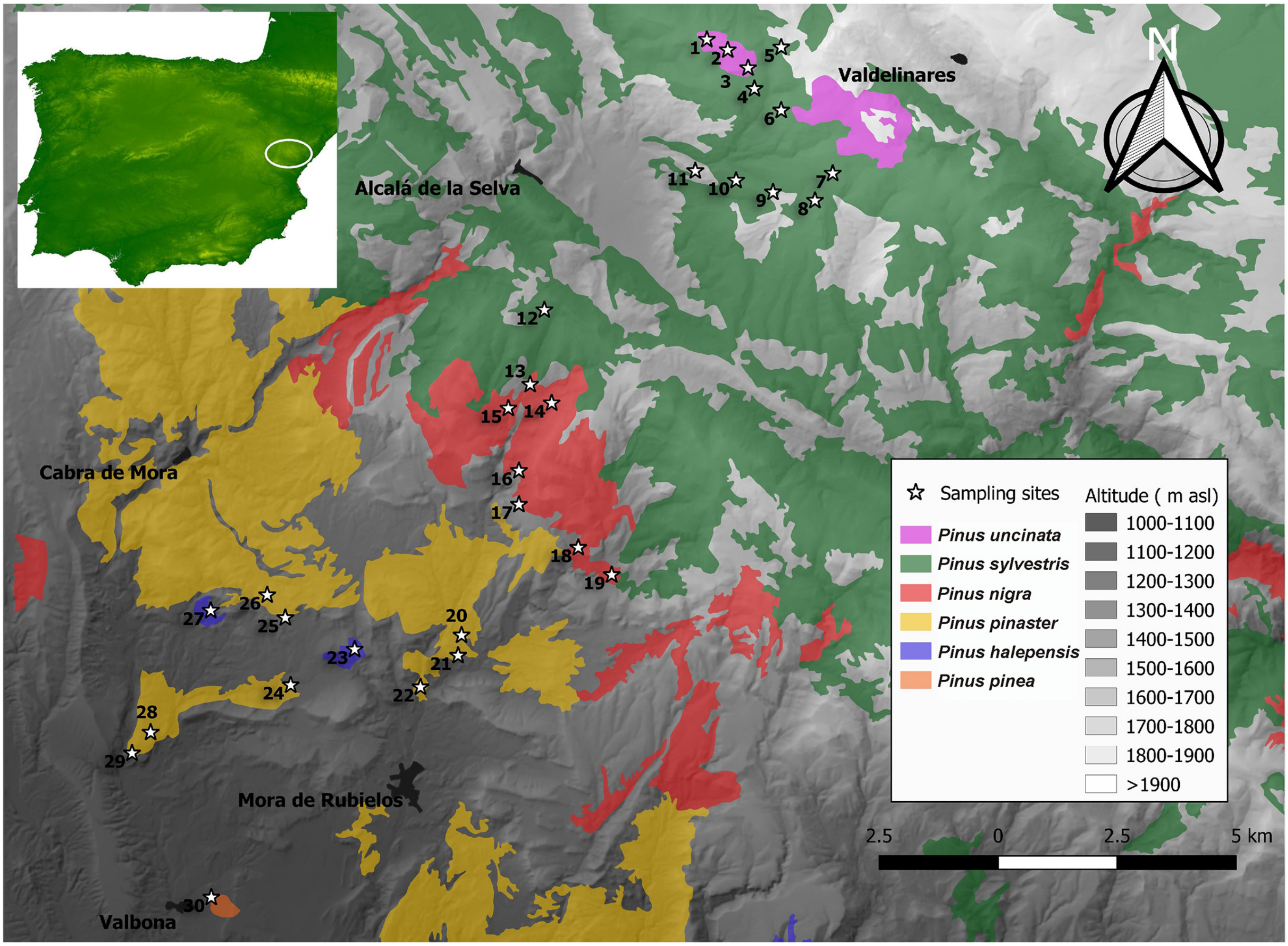

Fig. 1. Location map of the Gúdar Range (southern Iberian System) within the Iberian Peninsula (white circle), and modern surface pollen samples (1–30) according to pine communities and altitude. The gray-colored areas correspond to supramediterranean communities of holm oak (*Quercus ilex* subsp. *ballota*), as well as supramediterranean communities of *Quercus faginea* in north and west orientations.

month, is 0 °C) and 500 mm of mean annual precipitation, occurring from fall through spring, with a maximum in May. Regional-scale rainfall dynamics are controlled by the westerly winds, associated with cold fronts in spring and by eastern Mediterranean convections in summer and autumn. During the summer, the subtropical Azores anticyclone blocks the moisture from the west and brings warm and dry air masses from the south.

The mountains of the Gúdar Range constitute one of the main botanical enclaves of the Iberian Peninsula because this region is among the most sparsely populated areas in Europe, which has allowed a good conservation of its vegetation (Blanco, 1989). Six pine species are characteristics of the Gúdar woodlands. Across the southern Iberian System, *Pinus uncinata* forests, the southernmost population of the species in Europe, are considered a relict plant community occupying the highest hills (2028–1930 m asl) of the Gúdar Range (Peñarroya and Valdelinares peaks) on the oromediterranean bioclimatic belt on calcareous substrates (Camarero, 2009). These communities are dominated by a dense tree canopy, accompanied by mountain junipers (*Juniperus communis* subsp. *hemisphaerica*) and crawling junipers (*J. sabina*), while hygrophilous species abound in the undergrowth such as *Geum sylvaticum*, *Hepatica nobilis*, *Myosotis alpestris*, *Poa nemoralis* and *Viola willkommi*. The differential species of these relict groves are *Prunus prostrata*, *Berberis vulgaris* subp. *seroi*, *Galium idubadae* and *Veronica javalambrensis* (Peinado et al., 2017).

Oromediterranean Scots pine (*Pinus sylvestris*) forests occupy a lower altitude (until 1600 m asl) than those of *P. uncinata*, although both find their ecotone at ~1930 m asl. These forests have a more xerophytic character than the previous ones and often appear relatively open incorporating mountain and crawling junipers and thorny communities of *Erynacea anthyllis* and *Prunus spinosa*, as well as communities dominated by thyme (*Thymus leptophyllus* subp. *paui)* or pastures (*Festuca hystrix*, *Avenula pratensis*) in the driest and shallowest soils, or by *Ononis cristata* and *Coronilla minima* in wetter soils (Rivas-Goday and Borja, 1961; Rivas-Martínez et al., 2001). At lower altitudes (1600–1535 m asl), upper supramediterranean Scots pine forests acquire a more xeric character by incorporating xerophilous elements in their floristic courtship, such as *Coris monspeliensis*, *Genista scorpius*, *Lavandula latifolia*, *Lithodora fruticosa*, *Satureja montana* and *Thymus vulgaris*, while meadows are dominated by *Brachypodium retusum* and *Koeleria vallesiana* (Rivas-Martínez et al., 2002; Peinado et al., 2017).

Pinus nigra subsp. *salzmannii* (Spanish black pine) communities constitute low-density and open forests situated on the upper supramediterranean bioclimatic belt (1535–1225 m asl), developing in very dry areas (Regato and Del Río, 2009). Their undergrowth is dominated by heliophilous species such as *Juniperus communis* subsp. *hemisphaerica*, *Lavandula latifolia*, *Rubia peregrina*, *Salvia lavandulifolia*, *Thymus vulgaris* and *Aphyllanthes monspeliensis* (Regato et al., 1995).

These forests have suffered numerous fires, which have promoted the abundance of *Genista scorpius*.

Maritime pine communities correspond to a dense pinewood of *Pinus pinaster*, usually accompanied by *Quercus faginea* and *Juniperus oxycedrus*, and rarely by *Quercus ilex* subp. b*allota*, *Q. coccifera*, *Rhamnus alaternus* and *Juniperus phoenicea*. The understory is dominated by *Cistus laurifolius*, with varying densities, usually accompanied by *Ulex parviflorus*, *Dorycnium pentaphyllum*, *D. hirsutum*, *Helichrysum stoechas* and *Hypochaeris radicata* (Rivas-Goday and Borja, 1961). These communities occupy the lower supramediterranean bioclimatic belt (1225–1000 m asl) on sandstone outcrops in relatively dry environments.

The Aleppo pine (*Pinus halepensis*) is represented in the study area by two small, relict stands of 0.6 and 0.2 ha, respectively. These woodlands appear on the lower supramediterranean belt (1140–1015 m asl), they are located in southeastern oriented slopes, and are surrounded by dense Maritime pine forests. They correspond to low density forests where *Quercus ilex*, *Q. coccifera*, *Juniperus oxycedrus*, *J. phoenicea J. thurifera* and even some Spanish black pine are frequent. Its shrub suite is rich in *Rosmarinus officinalis* and *Ulex parviflorus*. The presence of these forest formations in the study area must be considered as range-edge populations, the last irradiations of the extensive Aleppo pine groves located in the eastern part of the Iberian Peninsula.

Finally, the presence of the Stone pine (*Pinus pinea*) in the study area corresponds to a small plantation (0.38 ha) carried out at the end of the 1980s on sandy clay soils since the species is not native to the study area. Its floristic composition is not very different from that of nearby Aleppo pine woodlands.

3. Material and methods

3.1. Field methods – vegetation and pollen sampling

The data concerning the vegetation and the relevant pollen material were collected in the spring and summer of 2019 from 30 locations (1–30) of the Gúdar Range situated along a NE-SW altitudinal gradient from 970 to 2028 m asl (Fig. 1; Table 1). Sampling sites were chosen to cover diversity of vegetation types in the whole range within a wide altitudinal interval, although the main purpose was the analysis of modern pollen rain related to pine communities. Pollen sampling was carried out on moss cushions, commonly used as surface samples in modern analogue studies (Hicks and Birks, 1996). The samples were collected at each location to provide modern pollen data, with positional and altitudinal data recorded using a portable Juno 3D Trimble Ltd. Global Positioning System (GPS) device. Several moss samples were randomly collected on the ground at each site within an area of 100 m^2, and blended into one sample. Each sample includes at least five subsamples to ensure an even representation, following Sugita (1994) and Hicks et al. (2001) recommendations. The collection approach ensured a representative sampling of plant elements with either long- or short-range pollen dispersion and also minimized over-representation of single species (Wang et al., 2004). The subsamples were sealed in plastic bags and mixed into one sample per site. A relevé of vegetation was also made at each sampling site (10 × 10 m) following the physotociological approach (Braun-Blanquet, 1979). Taxonomic nomenclature and authorities follow Castroviejo Castroviejo (1986-2015).

3.2. Laboratory methods

Moss polster samples of approximately 10 cm^3 were homogenized prior to extraction. The samples were sieved through 1 mm screens to remove larger particles (e.g., leaves, twigs and gravel) and then processed following the standard protocol developed by Faegri and Iversen (1989). Samples were stored in glycerol, mounted on microscope slides and examined with a Nikon Eclipse 50i light-microscope to identify pollen taxa. Routine counting was carried out at 600x magnification, with more difficult identifications made under oil immersion at 1000x magnification. Pollen grains were identified according to Moore et al. (1991) at the lowest currently possible taxonomical level. "Type" groups of several taxa that are morphologically indistinguishable were used (Table 2). *Pinus pinaster*, *P. halepensis*/*pinea* and *P. nigra*/*sylvestris*/

Table 1
Study samples (1–30) and sample characteristics for the 30 modern pollen surface samples from the Gúdar Range.

Samples	Latitude N	Longitude W	Altitude (m asl)	Aspect	Bioclimatic belt	Main pine species
1	40°23′26.12″	0°39′54.76″	2028	N-NE	Oromediterranean	*Pinus uncinata*
2	40°23′21.44″	0°39′53.38″	1990	NW	Oromediterranean	*Pinus uncinata*
3	40°23′18.25″	0°39′45.80″	1960	NW	Oromediterranean	*Pinus uncinata*
4	40°23′16.74″	0°39′32.43″	1930	N	Oromediterranean	*Pinus sylvestris*
5	40°23′31.78″	0°39′14.40″	1885	SE	Oromediterranean	*Pinus sylvestris*
6	40°22′55.74″	0°39′7.38″	1935	SW	Oromediterranean	*Pinus sylvestris*
7	40°22′10.13″	0°38′21.27″	1900	SW	Oromediterranean	*Pinus sylvestris*
8	40°21′51.26″	0°38′38.33″	1815	SW	Oromediterranean	*Pinus sylvestris*
9	40°21′57.96″	0°39′16.96″	1750	SE	Oromediterranean	*Pinus sylvestris*
10	40°22′6.99″	0°39′50.83″	1700	SE	Oromediterranean	*Pinus sylvestris*
11	40°22′14.52″	0°40′28.34″	1600	SE	Supramediterranean	*Pinus sylvestris*
12	40°20′38.83″	0°42′51.34″	1580	S	Supramediterranean	*Pinus sylvestris*
13	40°20′18.86″	0°42′48.98″	1500	SW	Supramediterranean	*Pinus nigra*
14	40°19′41.56″	0°42′47.45″	1425	NW	Supramediterranean	*Pinus nigra*
15	40°19′36.84″	0°43′11.60″	1380	SW	Supramediterranean	*Pinus nigra*
16	40°18′45.46″	0°43′18.72″	1390	SW	Supramediterranean	*Pinus nigra*
17	40°18′21.49″	0°43′19.52″	1375	SW	Supramediterranean	*Pinus nigra*
18	40°17′39.52″	0°43′4.76″	1290	SE	Supramediterranean	*Pinus nigra*
19	40°17′29.23″	0°43′7.17″	1260	NW	Supramediterranean	*Pinus nigra*
20	40°16′49.94″	0°44′15.68″	1150	SE	Supramediterranean	*Pinus pinaster*
21	40°16′35.67″	0°44′19.33″	1120	SE	Supramediterranean	*Pinus pinaster*
22	40°16′7.03″	0°45′16.47″	1120	S	Supramediterranean	*Pinus pinaster*
23	40°16′41.85″	0°45′54.89″	1140	SE	Supramediterranean	*Pinus halepensis*
24	40°16′32.38″	0°46′26.08″	1100	S	Supramediterranean	*Pinus pinaster*
25	40°17′5.42″	0°46′58.28″	1170	SE	Supramediterranean	*Pinus pinaster*
26	40°17′21.89″	0°47′14.48″	1185	NE	Supramediterranean	*Pinus pinaster*
27	40°17′11.94″	0°48′7.02″	1015	SE	Supramediterranean	*Pinus halepensis*
28	40°15′46.64″	0°49′5.38″″	1065	NE	Supramediterranean	*Pinus pinaster*
29	40°15′26.99″	0°49′28.57″″	1000	W	Supramediterranean	*Pinus pinaster*
30	40°13′48.76″	0°48′13.10″	970	S	Supramediterranean	*Pinus pinea*

Table 2
Correspondence between pollen types and species found in relevés. Only those between which there is no unequivocal correspondence are listed.

Pollen type	Parent plants
Anthemis-type	*Achillea collina*, *Tanacetum corymbosum*
Apiaceae undiff.	*Bupleurum fruticescens*, *Pimpinella major*
Asparagus-type	*Aphyllanthes monspeliensis*, *Asparagus officinalis*
Brassicaceae	*Arabis turrita*, *Biscutella fontqueri*, *Erysimum gomezcampoi*
Carduoideae	*Rhaponticum coniferum*, *Staehelina dubia*
Caryophyllaceae	*Dianthus algenatus*, *Saponaria glutinosa*, *Silene legionensis*, *S. nutans*, *S. vulgaris*
Cichorioideae	*Hieracium glaucinum*, *H. murorum*, *Hypochaeris radicata*
Cyperaceae	*Carex halleriana*, *C. humilis*
Fabaceae undiff.	*Anthyllis montana*, *Astragalus austriacus*, *A. incanus*, *Coronilla minima*, *Medicago suffruticosa*
Fritillaria-type	*Anthericum liliago*
Galium-type	*Asperula aristata*, *Cruciata glabra*, *Dorycnium hirsutum*, *D. pentaphyllum*, *Galium estebanii*, *G. idubedae*, *Rubia peregrina*
Genisteae	*Erinacea anthyllis*, *Genista scorpius*, *Ulex parviflorus*
Gentiana pneumonanthe-type	*Gentiana cruciata*
Juniperus-type	*Juniperus communis* subsp. *hemisphaerica*, *J. oxycedrus*, *J. phoenicea*, *J. sabina*, *J. thurifera*
Lamiaceae	*Acinos alpinus*, *Lavandula latifolia*, *Rosmarinus officinalis*, *Salvia lavandulifolia*, *Satureja montana*, *Sideritis glacialis*, *S. hirsuta*, *Teucrium chamaedrys*, *T. expassum*, *Thymus leptophyllus*, *T. vulgaris*
Pinus halepensis/*pinea*-type	*Pinus halepensis*, *P. pinea*
Pinus nigra/*sylvestris*/*uncinata*-type	*Pinus nigra*, *P. sylvestris*, *P. uncinata*
Plantago major/*media*-type	*Plantago media*
Poaceae	*Arrhenatherum elatius*, *Avenula pratensis*, *Brachypodium retusum*, *Briza media*, *Festuca gautieri*, *F. hystrix*, *Koeleria vallesiana*, *Poa nemoralis*, *Stipa lagascae*
Potentilla-type	*Fragaria vesca*, *Potentilla cinerea*, *P. erecta*, *P. neumanniana*
Quercus (deciduous)	*Quercus faginea*
Quercus (evergreen)	*Quercus coccifera*, *Q. ilex*
Rosa-type	*Amelanchier ovalis*, *Rosa pimpenellifolia*
Scrophulariaceae	*Digitalis obscura*, *Macrosyringion longiflorum*
Viola arvensis-type	*Viola willkommi*, *V. riviniana*

*uncinata*were palynologically identified according to Carrión et al. (2000), Reille (1999) and Desprat et al. (2015), respectively, while *Viscum album* according to López-Sáez (1999). Asteraceae Asteroideae pollen types were palynologically discriminated according to Punt and Hoen (2009), and Cistaceae pollen types according to Sáenz (1979). A minimum of 600 pollen grains were identified and counted for each sample (pollen sums range 600–1152; mean = 812 pollen grains). Pollen percentages were calculated using a pollen sum excluding indeterminable pollen grains, and presented as bars in a pollen diagram. Tilia and TGView (Grimm, 1992, 2004) and CorelDraw software were used to plot the pollen diagrams.

3.3. Statistical analyses

To identify clusters of samples based on their pollen content we used multivariate analysis. Although 62 pollen taxa were identified, all statistical analyses were performed only on the pollen taxa with percentages ≥1% in at least two samples. The analyses were performed on recalculated percentages after all modifications had been made. Classification was performed by hierarchical cluster analysis (HCA) using the matrix of the Euclidean distance and Ward's minimum variance method (Ward, 1963) with software PAST (Hammer et al., 2001). The percentage values of the taxa were not transformed. Later, we used ordination analyses to estimate the relationships between pollen assemblages and pollen types. Principal component analysis (PCA) was used as a lineal interpretation method, because a previously applied detrended correspondence analysis (DCA) pointed to a linear response (gradient length <2 standard deviation of species turnover units) of pollen types (variables) instead of unimodal responses of taxa (ter Braak and Prentice, 1988). PCA was performed using square-root transformed percentage of pollen taxa and down-weighting of rare taxa with CANOCO version 4.5 (Anderson and Van Devender, 1991; ter Braak and Šmilauer, 2002).

To explore the relationship between pollen types and plant taxa (Tables 3–6) we used different indices such as the association (*A*) index (Davis, 1984), or the over-representation (*O*) and under-representation (*U*) indices (Hjelle, 1997; Bunting, 2003; Mazier et al., 2006), which measure if the presence of a pollen taxon in a modern surface sample gives an indication of the presence of the parent plant taxon in the vegetation relevés. These indices are based on presence-absence data and are defined as follows: $A = b_0 / (p_0 + p_1 + b_0)$; $O = p_0 / (p_0 + b_0)$; $U = p_1 / (p_1 + b_0)$, where b_0 is the number of samples in which both the pollen type and its parent plant are present, p_0 is the number of samples in which the pollen type is present and the parent plant absent, and p_1 is the number of samples in which the parent plant is present and the pollen type absent. All these indices range between 0 and 1. Using these parameters, pollen types were classified (Mazier et al., 2006; Cañellas-Boltà et al., 2009) into: SAT, Strongly Associated Types ($A > 0.65$); AT, Associated Types (*A* between 0.5 and 0.65); ORT, Over-Represented Types (low *A*, high *O* and $U = 0$); WAT, Weakly Associated Types (low *A* and relatively high *O* and *U*); UT, Unassociated Types ($A = 0$ and high *O* and *U*). As an extension of the abovementioned association index we also calculated the fidelity (*F*) and dispersability (*D*) indices (McGlone and Meurk, 2000; Fall, 2012) as follows: $F = (b_0 / P) \times 100$; $D = (p_0 / p) \times 100$, where P is the total number of samples where the plant was present in the relevés, and, p is the total number of samples where the plant was absent. The *F* index ranges from 100% where the pollen is always recorded when the parent plant is present, to 0%, when the pollen is never recorded when the source plant is present. The *D* index ranges from 100% where the pollen is always recorded in the absence of the parent plant, to 0%,

Table 3
Pinus uncinata forest relevés (samples 1–3).

Relevé number/Modern pollen sample	1	2	3
Pinus uncinata	5	5	5
Pinus sylvestris	−	−	+
Juniperus communis subsp. *hemisphaerica*	2	3	1
Juniperus sabina	1	2	1
Geum sylvaticum	+	1	+
Myosotis alpestris	+	+	−
Poa nemoralis	3	2	1
Viola willkommi	1	1	+
Sideritis glacialis	−	+	+
Thymus leptophyllus subsp. *paui*	+	+	−
Cruciata glabra	+	+	−
Polygala nicaeensis	−	+	+
Veronica tenuifolia subsp. *javalambrensis*	1	1	+
Galium idubedae	+	+	+
Hepatica nobilis	2	2	1
Fragaria vesca	+	+	+
Rosa pimpenellifolia	+	−	−
Potentilla erecta	+	+	−
Helleborus foetidus	1	+	1
Berberis vulgaris subsp. *seroi*	+	1	+
Prunus prostrata	1	1	+
Arabis turrita	+	−	+
Saponaria glutinosa	−	+	−
Silene nutans	+	+	−
Campanula rotundifolia	−	+	+
Allium sphaerocephalon	−	+	+
Epipactis atrorubens	−	+	−
Tanacetum corymbosum	+	+	−
Carex halleriana	1	1	+
Carlina vulgaris	+	+	+
Sedum acre	+	−	−

Table 4
Pinus sylvestris forest relevés (samples 4–12).

Relevé number/Modern pollen sample	4	5	6	7	8	9	10	11	12
Pinus sylvestris	4	4	5	5	5	5	5	3	4
Pinus uncinata	+	−	−	−	−	−	−	−	−
Juniperus communis subsp. *hemisphaerica*	+	1	+	+	+	1	1	1	1
Juniperus sabina	3	3	1	1	1	1	1	−	−
Thymus leptophyllus subsp. *paui*	+	1	1	+	1	−	−	+	+
Cruciata glabra	+	+	+	−	−	+	1	−	−
Polygala nicaeensis	+	−	−	−	−	−	−	−	−
Veronica tenuifolia subsp. *javalambrensis*	1	−	−	−	−	−	−	−	−
Hepatica nobilis	−	+	+	+	−	1	2	−	−
Fragaria vesca	−	−	−	−	−	2	3	−	−
Rosa pimpenellifolia	+	−	−	−	−	−	−	−	−
Helleborus foetidus	1	1	+	+	+	1	1	−	−
Berberis vulgaris subsp. *seroi*	−	+	+	+	−	−	−	+	+
Arabis turrita	+	−	−	−	−	−	−	−	−
Campanula rotundifolia	−	+	+	−	+	+	+	−	−
Carlina vulgaris	+	−	−	−	−	−	−	−	−
Viola riviniana	+	−	−	−	−	+	−	−	−
Carex humilis	+	−	−	−	−	−	−	1	1
Cephalanthera rubra	+	+	−	−	−	+	−	−	−
Cephalanthera damasonium	−	−	−	−	−	+	+	−	−
Geranium sanguineum	+	−	−	−	−	−	−	−	−
Rhamnus alpina	1	−	−	−	−	−	−	−	−
Rhamnus saxatilis	+	−	−	−	−	−	−	+	+
Hieracium murorum	+	−	−	−	−	−	−	−	−
Arrhenaterum elatius	+	−	−	−	−	−	−	−	−
Acinos alpinus	+	−	−	−	−	−	−	−	−
Ononis cristata	+	1	1	1	+	−	−	−	−
Erinacea anthyllis	−	1	1	1	+	+	+	−	−
Avenula pratensis	−	1	1	1	+	−	+	−	−
Potentilla cinerea	−	+	+	−	+	−	+	1	1
Potentilla neumanniana	−	−	+	+	−	+	+	+	+
Koeleria vallesiana	−	+	−	+	+	−	+	2	1
Erysimum gomezcampoi	−	−	+	+	−	−	+	−	−
Hippocrepis comosa	−	1	1	+	+	−	−	−	−
Anthyllis montana	−	+	+	+	−	−	−	−	−
Briza media	−	−	+	+	+	−	−	−	−
Klasea nudicaulis	−	1	+	1	+	−	−	−	−
Helianthemum apenninum	−	+	+	+	−	−	−	−	−
Onobrychis argentea subp. *hispanica*	−	+	+	+	+	+	+	+	+
Astragalus austriacus	−	−	+	−	+	−	−	−	−
Prunus spinosa	−	+	+	+	−	+	+	−	−
Galium estebanii	−	+	−	−	+	−	−	−	−
Globularia vulgaris	−	−	+	+	+	−	−	+	+
Carduncellus hispanicus	−	+	+	−	+	−	−	−	−
Teucrium chamaedrys	−	+	+	−	+	+	+	+	+
Sedum acre	+	+	−	+	+	−	+	−	+
Festuca hystrix	−	1	1	1	+	−	−	−	−
Coronilla minima	−	+	+	1	+	−	+	−	−
Festuca gautieri	−	−	−	+	+	1	+	−	+
Ononis spinosa	−	−	−	−	−	+	+	−	−
Ribes uva-crispa	−	−	−	−	−	+	+	−	−
Lonicera etrusca	−	−	−	−	−	+	+	−	−
Achillea collina	−	−	−	−	−	+	+	−	−
Asperula aristata	−	−	−	+	−	+	+	+	+
Trifolium repens	−	−	−	−	−	+	+	+	−
Monotropa hypopitys	−	−	−	−	−	+	−	−	−
Gentiana cruciata	−	−	−	+	−	+	+	−	−
Geranium pyrenaicum	−	−	−	−	+	+	+	−	−
Plantago media	−	−	−	−	−	+	+	−	−
Pimpinella major	−	−	+	−	−	+	+	−	+
Genista scorpius	−	−	−	+	−	+	+	2	2
Viscum album	−	−	−	−	−	+	−	1	−
Brachypodium retusum	−	−	−	−	−	−	+	3	3
Thymus vulgaris	−	−	−	−	−	−	+	2	2
Lavandula latifolia	−	−	−	−	−	−	−	2	1
Satureja montana	−	−	−	−	−	−	−	1	1
Lithodora fruticosa	−	−	−	−	−	+	−	1	1
Teucrium expassum	−	−	−	−	−	−	−	+	+
Astragalus incanus	−	−	−	−	−	−	−	+	+
Fumana procumbens	−	−	−	−	−	−	−	+	+
Digitalis obscura	−	−	−	−	−	−	−	−	+
Eryngium campestre	−	−	−	−	−	−	−	+	+
Aphyllanthes monspeliensis	−	−	−	−	−	−	−	+	+
Macrosyringion longiflorum	−	−	−	−	−	−	−	+	+
Amelanchier ovalis	−	−	−	+	−	+	−	+	+

Table 4 (*continued*)

Relevé number/Modern pollen sample	4	5	6	7	8	9	10	11	12
Asphodelus albus	−	−	−	−	+	−	−	+	+
Coris monspeliensis	−	−	−	−	−	−	−	+	+
Silene legionensis	−	−	−	−	−	−	−	+	+
Sideritis hirsuta	−	−	−	−	−	−	−	+	+
Helianthemum marifolium subsp. *molle*	−	−	−	−	−	+	−	+	+
Linum appressum	−	−	−	−	−	−	+	+	+
Scabiosa columbaria	−	−	−	−	−	−	+	+	+
Cephalaria leucantha	−	−	−	−	−	−	−	+	−

Table 5

Pinus nigra subsp. *salzmannii* forest relevés (samples 13–19).

Relevé number/Modern pollen sample	13	14	15	16	17	18	19
Pinus nigra subsp. *salzmannii*	4	4	3	4	4	3	3
Juniperus communis subsp. *hemisphaerica*	3	2	2	1	2	2	1
Juniperus phoenicea	−	−	+	+	+	−	+
Salvia lavandulifolia	2	2	3	3	2	3	2
Genista scorpius	2	2	3	3	3	3	3
Galium maritimum	1	1	+	1	+	1	1
Avenula pratensis	1	1	2	1	1	2	2
Lavandula latifolia	1	+	1	1	1	2	1
Potentilla cinerea	1	1	1	+	+	1	+
Rubia peregrina	+	+	+	1	+	+	1
Euphorbia nicaeensis	+	+	−	+	+	+	−
Aphyllanthes monspeliensis	−	+	+	−	+	+	+
Quercus ilex subsp. *ballota*	−	−	+	+	−	+	+
Digitalis obscura	+	+	−	−	+	+	+
Prunus spinosa	−	−	+	+	−	+	−
Eryngium campestre	+	+	1	+	−	+	+
Erinacea anthyllis	+	−	−	+	−	−	−
Thymus vulgaris	1	+	+	1	+	+	+
Helleborus foetidus	−	−	+	+	−	+	−
Lotus corniculatus	+	+	−	+	+	−	+
Amelanchier ovalis	+	−	−	−	+	−	−
Hieracium murorum	−	−	+	+	−	−	−
Carlina vulgaris	−	−	+	+	+	−	−
Staehelina dubia	+	+	−	−	−	+	−
Medicago suffruticosa	−	−	−	+	+	−	−
Helianthemum marifolium subsp. *molle*	+	−	+	+	−	−	−
Bupleurum fruticescens	−	−	−	+	+	−	−
Rhaponticum coniferum	−	+	−	−	+	−	−
Helianthemum apenninum	−	−	+	−	−	−	−
Hedera helix	−	−	−	+	−	−	+
Sedum sediforme	+	−	−	−	−	−	−
Cephalanthera rubra	−	−	−	+	−	−	−
Prunus mahaleb	−	−	−	−	+	−	−
Malus sylvestris	−	−	+	−	−	−	−

Table 6

Pinus pinaster forest (samples 20–22, 24–26, and 28–29), *P.halepensis* (samples 23 and 27) and *P. pinea* (sample 30) woodland relevés.

Relevé number/Modern pollen sample	20	21	22	24	25	26	28	29	23	27	30
Pinus pinaster	3	4	3	2	4	4	5	4	−	−	−
Pinus halepensis	−	−	−	−	−	−	−	−	4	4	−
Pinus nigra subsp. *salzmannii*	+	−	−	+	−	−	−	−	+	+	−
Pinus pinea	−	−	−	−	−	−	−	−	−	−	4
Cistus laurifolius	2	2	3	+	1	2	2	1	1	1	−
Juniperus oxycedrus	−	−	−	2	1	−	+	+	1	+	+
Juniperus phoenicea	−	−	+	+	−	−	−	−	3	1	+
Juniperus thurifera	−	−	−	−	−	−	−	−	+	+	−
Brachypodium retusum	1	+	+	2	1	+	+	1	3	3	3
Ulex parviflorus	+	+	+	1	+	1	+	+	3	2	1
Helichrysum stoechas	1	1	+	2	1	1	1	1	+	+	+
Rhamnus alaternus	+	+	−	+	+	−	+	+	−	−	−
Quercus faginea	−	+	+	+	−	−	−	−	−	−	+
Quercus ilex subsp. *ballota*	1	+	+	1	1	1	+	1	+	+	+
Helianthemum marifolium subsp. *molle*	−	−	+	1	+	+	1	1	−	−	−
Rosmarinus officinalis	1	1	+	1	1	1	+	+	1	2	−
Hypochaeris radicata	1	1	1	+	+	1	1	+	−	−	−
Bupleurum fruticescens	+	+	+	−	+	+	+	+	−	−	−
Thymus vulgaris	1	1	+	+	1	+	+	1	−	−	2
Eryngium campestre	+	+	−	−	+	+	+	+	1	1	+
Galium maritimum	+	+	1	+	+	1	+	+	−	−	−
Staehelina dubia	−	−	+	+	+	+	−	+	−	−	−
Rhaponticum coniferum	+	+	−	−	−	+	+	−	−	−	−
Biscutella fontqueri	+	+	+	−	−	+	−	−	−	−	−
Sedum sediforme	−	−	+	+	+	+	+	+	−	−	−
Sedum album	−	−	−	−	−	+	−	−	−	−	−
Fumana ericifolia	−	−	−	+	−	−	−	+	−	−	−
Carlina corymbosa	+	+	−	−	−	−	+	−	−	−	−
Lavandula latifolia	−	+	+	−	−	−	−	−	+	1	1
Dianthus algenatus subsp. *turolensis*	−	−	−	−	+	−	−	−	−	−	−
Carex halleriana	−	−	−	−	−	+	+	−	+	+	−
Silene vulgaris	−	−	+	−	−	−	−	−	−	−	−
Quercus coccifera	−	−	−	−	−	−	−	+	+	+	−
Dorycnium hirsutum	−	−	−	−	−	−	−	+	−	−	−
Dorycnium pentaphyllum	−	−	−	−	−	−	+	+	−	−	+
Anthericum liliago subsp. *liliago*	−	−	−	−	−	−	+	+	−	−	−
Hieracium glaucinum	−	−	−	−	−	−	−	+	−	−	−
Asparagus officinalis	+	+	−	−	−	−	−	+	+	+	+
Digitalis obscura	−	−	−	−	−	−	−	−	+	+	−
Euphorbia arvalis subsp. *longistyla*	−	−	−	−	−	−	−	−	−	−	2
Stipa lagascae	−	−	−	−	−	−	−	−	−	−	+

where the pollen is never recorded if the parent plant is absent. Individual pollen-plant relationships were studied using the Spearman rank-order correlation coefficient (Siegel and Castellan, 1988; Mazier et al., 2006), because the data on plant abundance are semi-quantitative.

4. Results

The pollen percentage data of the 30 modern surface samples (Fig. 1; Table 1) are summarized in a pollen diagram (Fig. 2). A total of 62 pollen taxa were identified during the analysis. The 30 modern surface pollen samples were classified by means of HCA into eight sample groups, which correspond to ecologically and floristically distinct and interpretable pine communities (Fig. 3). Fig. 4 presents the PCA scatter plots for both samples (circles) and the most contributing pollen taxa into the PCA axis 1 and PCA axis 2, in which the contribution of axes 1 and 2 to the total variance are 61.9% and 11.9%, respectively. The first four axes of the PCA explain 88.8% of variance in the pollen surface dataset. The PCA biplot of modern pollen dataset allows identifying five distinct groups (A–E).

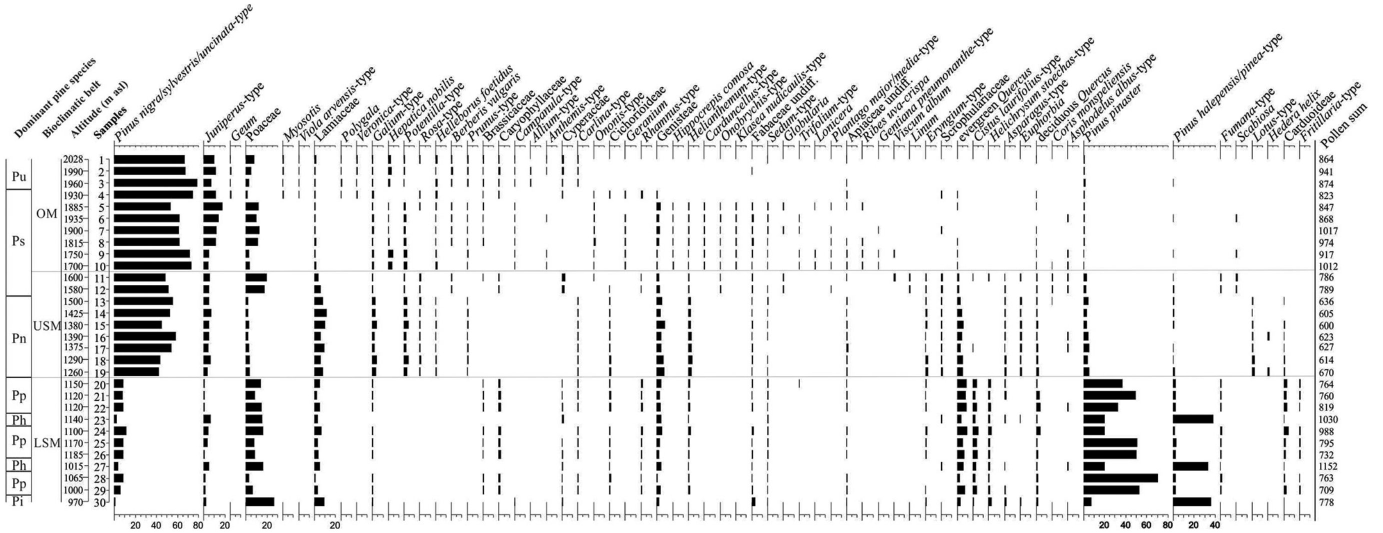

Fig. 2. Percentage pollen diagram of the 30 modern surface samples of the Gúdar Range following an altitudinal transect. Bioclimatic belts: OM (oromediterranean), USM (upper supramediterranean), LSM (lower supramediterranean). Dominant pine species: Pu (*Pinus uncinata*), Ps (*P. sylvestris*), Pn (*P. nigra*), Pp (*P. pinaster*), Ph (*P. halepensis*), Pi (*P. pinea*).

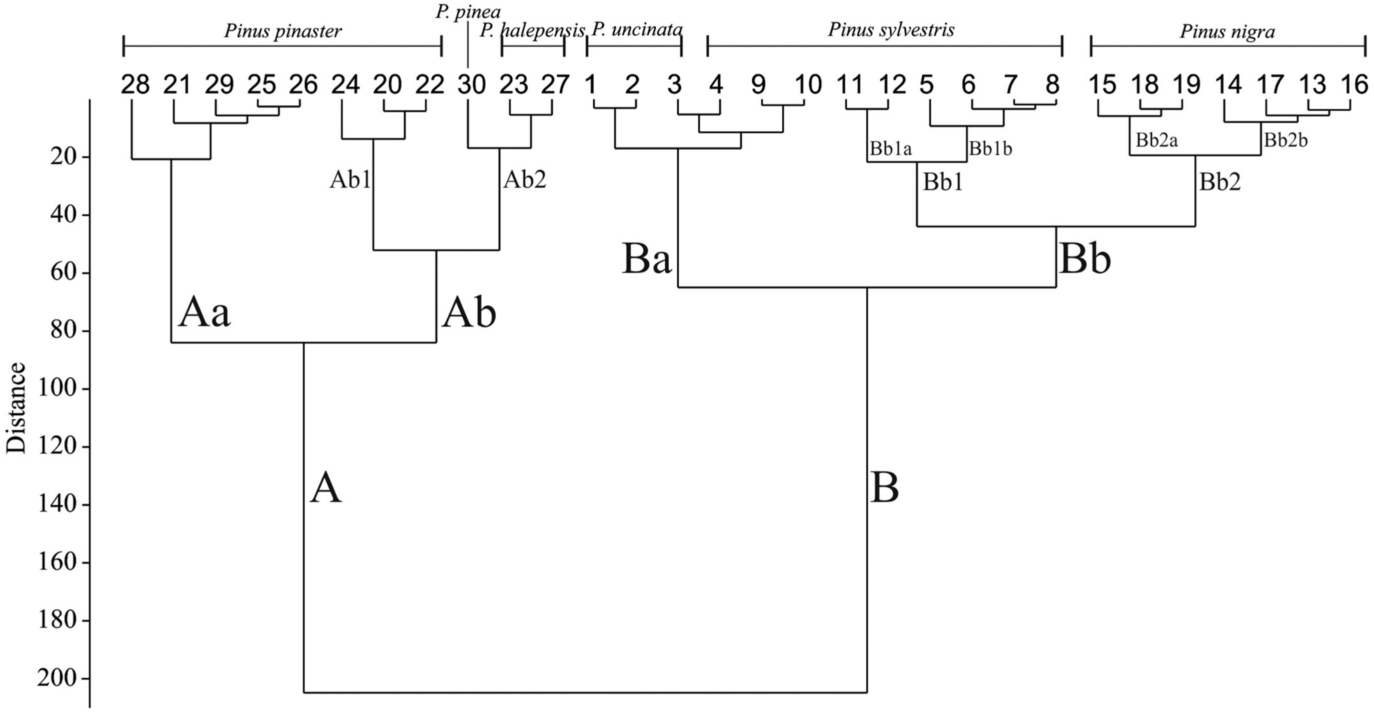

Fig. 3. Hierarchical cluster analysis (HCA) dendrogram of the 30 modern pollen spectra.

5. Discussion

5.1. Representation of pine communities by pollen – hierarchical cluster analysis (HCA) of pollen spectra

On the first division level, the dendrogram of the HCA performed on pollen data (Fig. 3) shows a good differentiation between Mediterranean pine communities (cluster A) and high-mountain pine communities (cluster B). This division is probably related to higher pollen frequencies of *Pinus nigra/sylvestris/uncinata*, *Galium*, *Hepatica nobilis*, *Potentilla*, *Rosa*, *Helleborus*, *Berberis vulgaris*, *Prunus* and *Lotus* pollen types in samples from cluster B, as well as higher values of Caryophyllaceae, evergreen *Quercus*, Carduoideae, *Cistus laurifolius*, *Helichrysum stoechas*, *Pinus pinaster* and *P. halepensis/pinea* pollen types (Fig. 2) in samples from cluster A. The next two clusters within cluster A are distinguished on the basis of high percentages (>50%) of *Pinus pinaster* in samples from cluster Aa, representing supramediterranean Maritime pine communities. Inside cluster Ab, we can detach, at a smaller range, the sub-clusters Ab1 from Ab2; respectively separating samples with *Pinus halepensis/pinea* values lower that 10% (sub-cluster Ab1) from those ~40% (local origin; sub-cluster Ab2). Sub-cluster Ab1 represents samples from supramediterranean

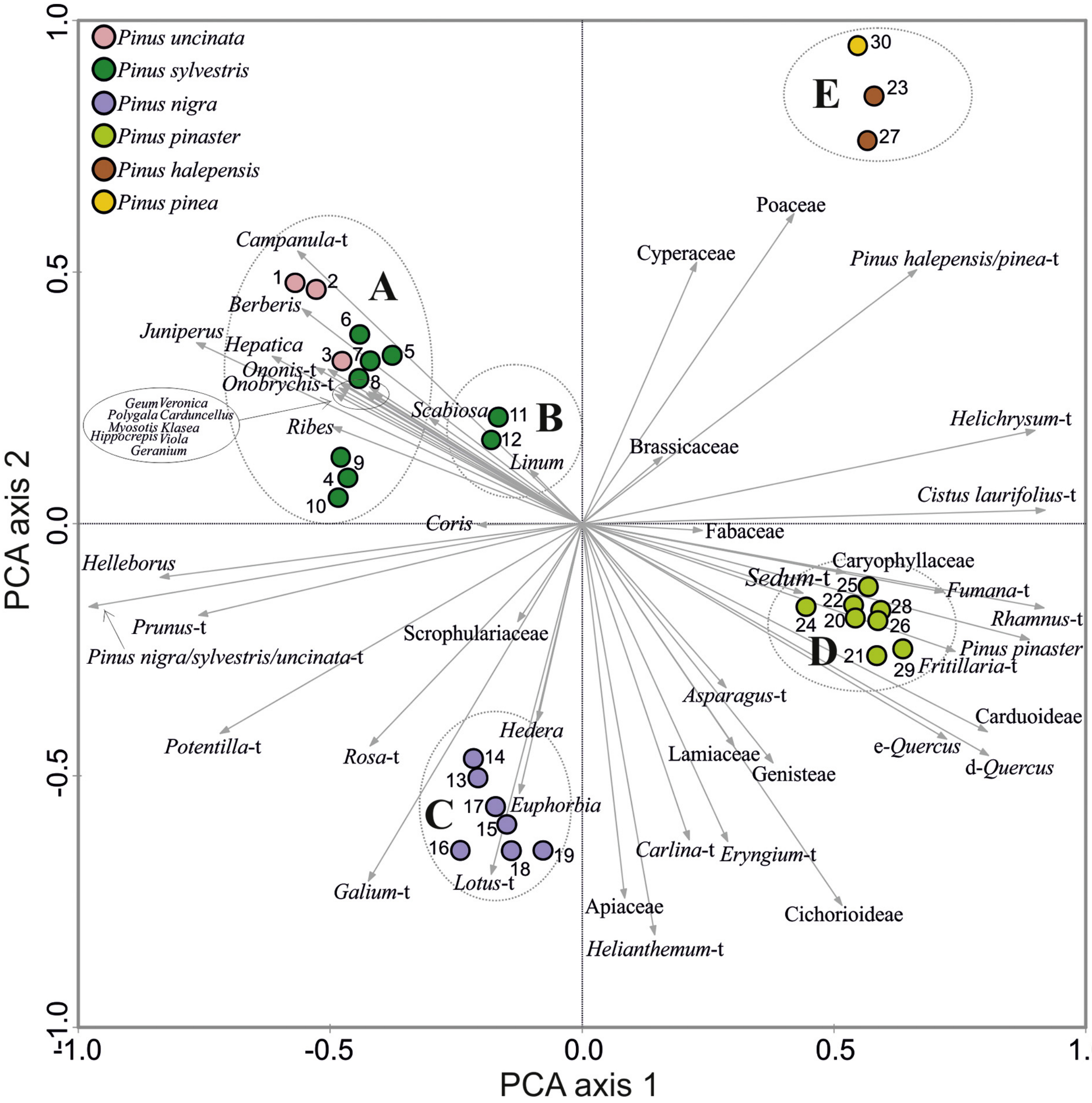

Fig. 4. Principal Component Analysis (PCA) ordination biplot of the 30 study sites (circles) and the dominant pollen taxa (arrows). Each sample is expressed by the observed pine forest community (see Table 1).

Maritime pine communities with low tree cover (Table 6). Sub-cluster Ab2 represents two samples from supramediterranean Aleppo pine communities and also includes the sample from the Stone pine reforestation, which is clearly separated from the previous ones (Fig. 2) by its higher values of Poaceae (>30%) and Lamiaceae (~10%), as well as by lower values of *Pinus pinaster* (<10%).

Relating to cluster B, the major segregation separates Ba from Bb clades. The main disjunction promoted here is due to the high percentages (>60%) of *Pinus nigra/sylvestris/uncinata*, *Hepatica nobilis* and *Helleborus foetidus* pollen types in cluster Ba. This cluster represents three samples from oromediterranean *Pinus uncinata* communities as well as three other samples from oromediterranean *P. sylvestris* communities, which are not clearly segregated from each other in the HCA. The division of cluster Bb produced two main clades (Bb1 and Bb2). The first sub-cluster Bb1 includes the rest of samples coming from *Pinus sylvestris* communities. Inside sub-cluster Bb1, the sub-clusters Bb1a and Bb1b are segregated by lower values of *Pinus nigra/sylvestris/uncinata* (<50%) and *Juniperus* (<10%) as well as higher ones of Poaceae and Lamiaceae in the former (Fig. 2). Sub-cluster Bb1a represents supramediterranean *Pinus sylvestris* communities, while sub-cluster Bb1b represents oromediterranean ones. Finally, sub-cluster Bb2 represents supramediterranean *Pinus nigra* communities and can be subdivided into two sub-clusters (Bb2a and Bb2b), segregated by the abundance (>50%) of *P. nigra/sylvestris/uncinata* pollen type in the latter as it corresponds to samples with a wider tree cover (Table 5).

5.2. Principal component analysis (PCA) of pollen spectra

On the first axis (PCA axis 1) high-mountain pine communities (groups A, B and C) are separated from Mediterranean pine communities (groups D and E). Thus, PCA axis 1 is probably related to altitude. Many pollen taxa are discriminated along this axis; those displaying the highest species scores were typical of highland areas (negative values: e.g. *Pinus nigra/sylvestris/uncinata*, *Helleborus*, *Prunus*) or from lowlands (positive values: e.g., *Cistus laurifolius*, *Pinus halepensis/pinea*,

Table 7
Degree of association between abundance of pollen in moss samples and abundance of parent plants in vegetation relevés (see Fig. 2 and Tables 3-6). The coincidence (*A*), over-representation (*O*) and under-representation (*U*) parameters and its derived classification into SAT (Strongly Associated Types), AT (Associated Types), ORT (Over-Represented Types) and WAT (Weakly Associated Types) measure the degree of association based on presence/absence data (see methods for more details). The fidelity (*F*) and dispersability (*D*) indices are also indicated. I = prevailing insect dispersal syndrome; W = prevailing wind dispersal syndrome.

Pollen taxa	*A*	*O*	*U*	*F*	*D*	Association	Pollination syndrome
Allium-type	1.0	0.0	0.0	100.0	0.0	SAT	I
Anthemis-type	0.8	0.2	0.0	100.0	3.8	SAT	I
Apiaceae undiff.	0.4	0.5	0.2	84.6	76.5	WAT	I
Asparagus-type	0.9	0.1	0.0	100.0	11.8	SAT	I
Asphodelus albus-type	0.2	0.8	0.3	66.7	25.9	WAT	I
Berberis vulgaris	0.9	0.1	0.0	100.0	4.5	SAT	I
Brassicaceae	0.5	0.5	0.1	90.0	40.0	AT	I
Campanula-type	0.7	0.3	0.0	100.0	13.0	SAT	I
Carduncellus-type	0.5	0.5	0.0	100.0	11.1	AT	I
Carduoideae	0.6	0.3	0.1	92.3	35.3	AT	I
Carlina-type	0.5	0.5	0.1	90.0	45.0	AT	I
Caryophyllaceae	0.4	0.6	0.0	100.0	33.3	ORT	I
Cichorioideae	0.6	0.4	0.0	100.0	36.8	AT	I
Cistus laurifolius-type	0.8	0.2	0.0	100.0	15.0	SAT	I
Coris monspeliensis	0.5	0.5	0.0	100.0	7.1	AT	I
Cyperaceae	0.6	0.4	0.0	100.0	30.0	AT	W
Eryngium-type	0.7	0.2	0.1	87.5	21.4	SAT	I
Euphorbia	0.6	0.4	0.0	100.0	16.7	AT	I
Fabaceae undiff.	0.3	0.7	0.0	100.0	81.0	OTR	I
Fritillaria-type	0.3	0.8	0.0	100.0	21.4	OTR	I
Fumana-type	0.3	0.7	0.0	100.0	30.8	ORT	I
Galium-type	1.0	0.0	0.0	100.0	0.0	SAT	I
Genisteae	1.0	0.0	0.0	100.0	20.0	SAT	I
Gentiana pneumonanthe-type	1.0	0.0	0.0	100.0	0.0	SAT	I
Geranium	0.7	0.3	0.0	100.0	7.7	SAT	I
Geum	0.8	0.3	0.0	100.0	3.7	SAT	I
Globularia	0.3	0.5	0.6	40.0	8.0	WAT	I
Hedera helix	1.0	0.0	0.0	100.0	0.0	SAT	I
Helianthemum-type	0.6	0.4	0.0	100.0	66.7	AT	I
Helichrysum stoechas-type	0.9	0.1	0.0	100.0	5.3	SAT	I
Helleborus foetidus	0.8	0.2	0.0	100.0	23.5	SAT	I
Hepatica nobilis	0.9	0.1	0.0	100.0	4.5	SAT	I
Hippocrepis comosa	0.7	0.3	0.0	100.0	7.7	SAT	I
Juniperus-type	0.9	0.1	0.0	100.0	100.0	SAT	W
Klasea nudicaulis-type	0.7	0.3	0.0	100.0	7.7	SAT	I
Lamiaceae	1.0	0.0	0.0	100.0	0.0	SAT	I
Linum	0.7	0.0	0.3	66.7	0.0	SAT	I
Lonicera	0.7	0.3	0.0	100.0	3.6	SAT	I
Lotus-type	0.7	0.3	0.0	100.0	8.0	SAT	I
Myosotis	0.5	0.5	0.0	100.0	7.1	AT	I
Onobrychis-type	1.0	0.0	0.0	100.0	0.0	SAT	I
Ononis-type	0.8	0.1	0.0	100.0	4.3	SAT	I
Pinus halepensis/pinea-type	0.1	0.9	0.0	100.0	70.4	ORT	W
Pinus nigra/sylvestris/uncinata-type	0.8	0.2	0.0	100.0	100.0	SAT	W
Pinus pinaster	0.3	0.7	0.0	100.0	100.0	ORT	W
Plantajo major/media-type	0.3	0.7	0.0	100.0	20.0	ORT	W
Poaceae	1.0	0.0	0.0	100.0	0.0	SAT	W
Polygala	0.8	0.3	0.0	100.0	3.7	SAT	I
Potentilla-type	1.0	0.0	0.0	100.0	0.0	SAT	I
Prunus-type	0.8	0.3	0.0	100.0	22.2	SAT	I
deciduous *Quercus*	0.1	0.9	0.0	100.0	88.5	ORT	W
evergreen *Quercus*	0.6	0.4	0.0	100.0	66.7	AT	W
Rhamnus-type	0.8	0.3	0.0	100.0	14.3	SAT	I
Ribes uva-crispa	0.5	0.5	0.0	100.0	7.1	AT	I
Rosa-type	0.4	0.5	0.3	75.0	27.3	WAT	I
Scabiosa	0.4	0.5	0.3	66.7	7.4	WAT	I
Scrophulariaceae	0.7	0.3	0.0	100.0	19.0	SAT	I
Sedum-type	0.5	0.5	0.1	92.9	75.0	AT	I
Trifolium-type	0.3	0.6	0.3	66.7	11.1	WAT	I
Veronica-type	1.0	0.0	0.0	100.0	0.0	SAT	I
Viola arvensis-type	0.8	0.0	0.2	80.0	0.0	SAT	I
Viscum album	1.0	0.0	0.0	100.0	0.0	SAT	I

P. pinaster, evergreen and deciduous *Quercus*, *Fumana*, *Fritillaria*, *Helichrysum*, Carduoideae).

Group A includes samples from oromediterranean *Pinus uncinata* and *P. sylvestris* forest communities, which are located on the negative side of PCA axis 1 showing negative scores. The most important pollen types in group A correspond to taxa only or mostly present in the oromediterranean bioclimatic belt (*Berberis*, *Campanula*, *Carduncellus*, *Geranium*, *Geum*, *Hepatica*, *Hippocrepis*, *Klasea*, *Myosotis*, *Onobrychis*, *Ononis*, *Polygala*, *Ribes*, *Veronica* and *Viola*) or to others (*Juniperus*) with a wider distribution but with higher in that bioclimatic belt (Fig. 2; Tables 2–6). *Pinus uncinata* and *P. sylvestris* samples are discriminated on the positive side of PCA axis 2.

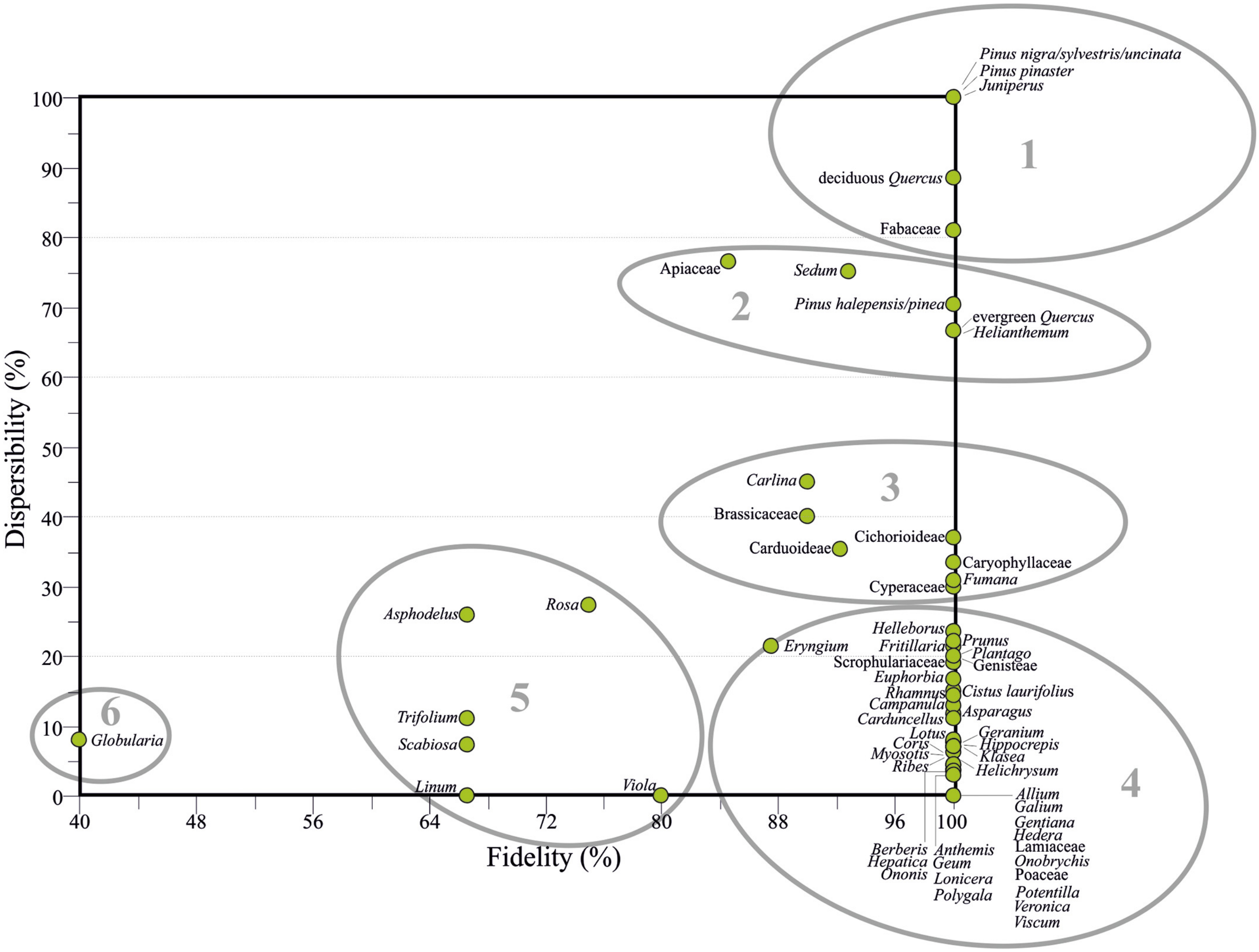

Fig. 5. Pollen taxa plotted by fidelity (*F*) vs. dispersability (*D*) indices. Six patterns are identified (gray circle on graph): (1) taxa with very high fidelity and dispersability (80–100%); (2) taxa with very high fidelity (80–100%) and high dispersability (60–80%); (3) taxa with very high fidelity (80–100%) and moderate dispersability (30–60%); (4) taxa with very high fidelity (80–100%) and low dispersability (0–30%); (5) taxa with high fidelity (60–80%) and low dispersability (0–30%); and (6) taxa with moderate fidelity (40%) and low dispersability (0–30%).

Group B includes samples from supramediterranean *Pinus sylvestris* forest communities, clearly separated from the corresponding oromediterranean ones, with low values on the negative side of PCA axis 1. The most characteristic pollen types in group B are *Coris*, *Linum* and *Scabiosa*, which correspond to plant taxa predominantly or exclusively present in these forests (Table 4).

Group C comprises samples from supramediterranean *Pinus nigra* forest communities sited on the negative sides of both PCA axes. *Euphorbia*, *Galium*, *Hedera* and *Lotus* are the most important pollen types of this group. Interestingly, samples in groups B and C are clearly separated on both sides of PCA axis 2. Pollen taxa strongly associated with this axis are Poaceae, Cyperaceae and *Campanula* on the positive side, and *Helianthemum*, *Galium*, Apiaceae and Cichorioideae on the negative side. Therefore, the interpretation of this axis is difficult, despite the evident segregation between the two abovementioned groups. In fact, a similar segregation occurs between groups D and E also discriminated in PCA axis 2.

Group D lies on the positive side of PCA axis 1 entailing samples taken in *Pinus pinaster* forest communities. The most characteristic pollen types of group D are *Pinus pinaster*, *Rhamnus*, *Fritillaria*, *Fumana*, Caryophyllaceae and Carduoideae.

Finally, group E, with the highest positive values on PCA axis 2, includes two samples from *Pinus halepensis* woodland communities and one sample from the *P. pinea* plantation. *Pinus halepensis/pinea*, Poaceae and Cyperaceae are the most important pollen types of this group.

5.3. Pollen–vegetation relationships

In order to estimate pollen representativity on the basis of the pollen rain, modern pollen data were combined for each relevé (Tables 3–6). Considering the degree of association between pollen abundance in moss samples and abundance of parent plants in vegetation relevés (Table 7), the more strongly associated types (SAT) are *Allium*, *Galium*, Genisteae, *Gentiana pneumonanthe*, *Hedera helix*, Lamiaceae, *Onobrychis*, Poaceae, *Potentilla*, *Veronica* and *Viscum album* ($A = 1$), followed by ($1 > A > 0.65$) *Anthemis*, *Asparagus*, *Berberis vulgaris*, *Campanula*, *Cistus laurifolius*, *Eryngium*, *Geranium*, *Geum*, *Helichrysum stoechas*, *Helleborus foetidus*, *Hepatica nobilis*, *Hippocrepis comosa*, *Juniperus*, *Klasea nudicaulis*, *Linum*, *Lonicera*, *Lotus*, *Ononis*, *Pinus nigra/sylvestris/uncinata*, *Polygala*, *Prunus*, *Rhamnus*, Scrophulariaceae and *Viola arvensis*. That is, from 62 identified pollen types, 35 (56.45%) appear strongly associated (SAT). On the other hand, 13 pollen types (Brassicaceae, *Carduncellus*,

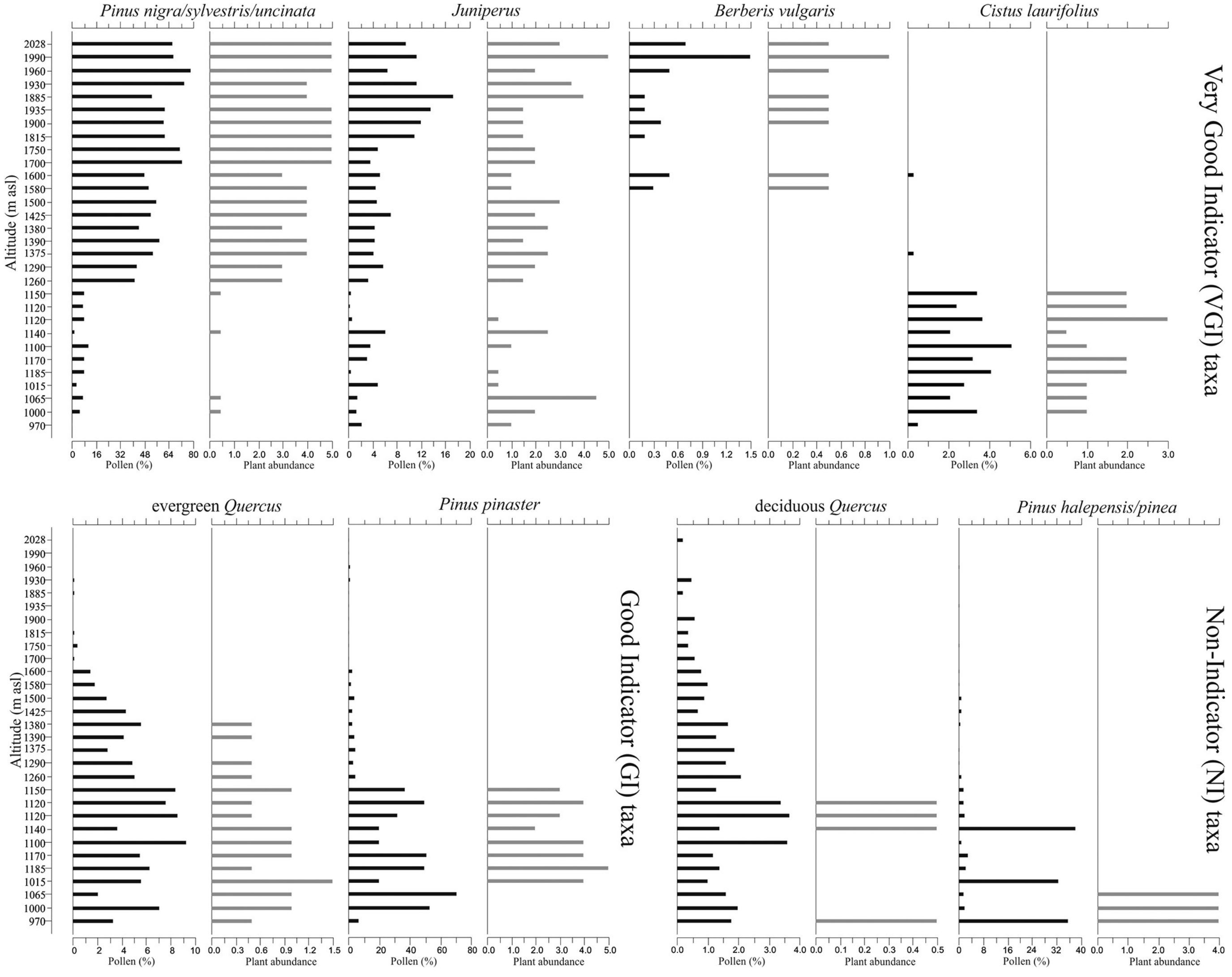

Fig. 6. Comparison of pollen percentages (black bars) and plant abundance (gray bars) of some examples for very good indicator (VGI) (*Pinus nigra/sylvestris/uncinata*, *Juniperus*, *Berberis vulgaris*, *Cistus laurifolius*), good indicator (GI) (evegreen *Quercus*, *P. pinaster*) and non-indicator (NI) (deciduous *Quercus*, *P. halepensis/pinea*) pollen taxa. Rare elements (those designed with "+" in the vegetation relevés) were quantified with a value of 0.5.

Carduiodeae, *Carlina*, Cichorioideae, *Coris monspeliensis*, Cyperaceae, *Euphorbia*, *Helianthemum*, *Myosotis*, evergreen *Quercus*, *Ribes uva-crispa* and *Sedum*) were recorded as Associated Types (AT; $A = 0.65–0.5$), which represents 20.97% of the total pollen types. The remaining 14 identified pollen types correspond to over-represented types (ORT; 8 types = 12.90%) and weakly associated types (WAT; 6 types = 9.68%). No unassociated pollen type (UT) was recorded. These patterns agree with previous studies carried out in the Pyrenees (Mazier et al., 2006; Cañellas-Boltà et al., 2009), where most coincident taxa show the same degree of association.

Among the 48 strongly associated (SAT) and associated (AT) types (Table 7), most of them (45) correspond to insect-pollinated plants (Herrera, 1987; Bosch et al., 1997; Aguado et al., 2017). These data demonstrate an unequivocal correspondence between the presence of the parent plant and its respective pollen, given the scarce pollen dispersion of entomophilous taxa (Faegri and Van der Pijl, 1979). However, 5 SAT and AT types (Table 7) correspond to wind-pollinated plants (Cyperaceae, evergreen *Quercus*, *Juniperus*, *Pinus nigra/sylvestris/uncinata*, Poaceae), probably indicating that their high degree of association is related to high pollen production and dispersal (López-Sáez et al., 2010a, 2013, 2015), as well as to the fact that these pollen types correspond to several parent plants rather than just one (Table 2), which are also more or less evenly distributed along the transect (Tables 3–6). As indicated in previous studies, in particular those of Hjelle (1997), Bunting (2003) and Mazier et al. (2006), who give indices for main taxa from Norwegian, Scottish and French vegetation communities, respectively, Poaceae and Cyperaceae are strongly associated pollen taxa. In short, entomophilous pollen taxa belonging to the SAT and AT groups are the most important in the differentiation of pine forest communities in the study area, and are, in fact, the ones that would have the greatest interpretative value in the application of a similar methodology to other future modern pollen rain studies and even in its application to the fossil record. In contrast, most anemophilous pollen taxa have a low degree of association, particularly *Pinus halepensis/pinea* and *P. pinaster*, which would mean that these are probably the least interesting in the typological diagnosis of pine forest communities according to their modern pollen rain. It is important to note the different degree of association between *Pinus nigra/sylvestris/uncinata* (SAT) vs. *P. halepensis/pinea* and *P. pinaster* (ORT), probably because the former represents three parent plants (Table 2) and has a wider distribution in the studied transect, while the latter two are represented by two and one parent plants, respectively, and have a more restricted distribution. Usually, strongly associated types (SAT) have low over-representation (*O*) and under-representation (*U*) values, between 0 and 0.3; while associated types (AT) can reach *O* values of 0.5 (Table 7). In contrast, over-represented types (ORT) and weakly associated types (WAT) can reach *O* values of 0.9 and 0.8, respectively; hence their low coincidence index (*A*). These data indicate that these indices can be applied widely to different regions and also to different habitats.

Comparison between fidelity (*F*) and dispersibility (*D*) indices produce six distinct patterns (Fig. 5). Obviously, the relationship between both indices is strongly linked to the plant's pollination strategy (Faegri and Van der Pijl, 1979; Moscol-Olivera et al., 2009; Fall, 2012). Pollen taxa with the lowest dispersability usually correspond to insect-pollinated parent plants (Table 7), except *Plantago major*/*media* and Poaceae (patterns 4, 5 and 6), while most of the pollen taxa with the highest dispersability are wind-pollinated plant species (patterns 1 and 2). Patterns 1 and 2 represent those pollen taxa with very high to high fidelity and dispersability, i.e., they are found in every modern pollen sample collected (Fig. 2). Parent plants in these patterns are common anemophilous trees and shrubs in the Gúdar Range (Table 7). Fabaceae undiff. is included in pattern 1, probably because it represents five parent plants (Table 2) that together are evenly distributed along the altitudinal transect and are also relatively abundant in relevés. Pattern 2 displays a mixture of insect and wind pollination mechanisms. Apiaceae, *Helianthemum* and *Sedum* are insect-pollinated taxa, while *Pinus halepensis*/*pinea* and evergreen *Quercus* are wind-pollinated. All of pollen taxa in pattern 3 show very high fidelity and moderate dispersability. Plants in this pattern are also common in the Gúdar Range and their pollen is reasonably well dispersed. Thus, plants in pattern 3 are well represented in the modern pollen rain (Fig. 2) and are good indicators of nearby growing source plants. Pollen taxa in patterns 4 and 5 have very high to high fidelity but low dispersability indices (below 30%). Pattern 4 includes most of the pollen taxa identified in this study, predominantly pollinated by insects, and appears as strongly associated (SAT) or associated types (AT), except *Fritillaria* (Table 7), which corresponds to the parent plant *Anthericum liliago* subsp. *liliago*, only present in two relevés (Table 6). Interestingly, two pollen taxa in pattern 4, Poaceae and *Plantago major*/*media*, are wind-pollinated. In contrast, pattern 5 includes two strongly associated types (SAT; *Linum*, *Viola arvensis*) with $D = 0$, as well as four weakly associated types (WAT; *Asphodelus*, *Rosa*, *Scabiosa* and *Trifolium*) with *D* between 7.4 and 27.3%. Finally, pattern 6 is only represented by the outlier *Globularia*, an insect-pollinated plant, with moderate fidelity and low dispersability, showing that there is not always a direct relationship between the appearance of pollen and the presence of the parent plant in the relevés.

According to the Spearman correlations (*rs*) calculated between pollen percentages and abundance data of parent plant along the altitudinal gradient, all taxa shown in Fig. 6 presented very high positive correlations ($rs = 0.63$–0.94, $p < .001$) excepting *Juniperus* ($rs = 0.52$, $p = .003$), deciduous *Quercus* ($rs = 0.45$, $p = .01$) and *Pinus halepensis*/*pinea* ($rs = 0.38$, $p = .04$). The comparison between pollen percentages (Fig. 2) and parent plant values (Tables 3–6) by taxon along the transect allowed the establishment of the next pollen groups (Fig. 6), following Cañellas-Boltà et al. (2009):

(i) Very good indicator pollen types (VGI), when the local occurrence and abundance of both the pollen type and the parent taxa show the same altitudinal patterns. This is the case, among the major pollen taxa, of *Pinus nigra*/*sylvestris*/*uncinata* and *Juniperus*, both with a great altitudinal range between the oromediterranean and the supramediterranean bioclimatic belts, as they correspond to three and five different parent taxa, respectively (Table 2). In addition, *Berberis vulgaris*, Caryophyllaceae, *Coris monspeliensis*, Cyperaceae, *Galium*, Genisteae, *Globularia*, *Helleborus foetidus*, Lamiaceae, *Onobrychis*, *Ononis*, Poaceae, *Potentilla*, *Prunus*, *Rhamnus* and the hemiparasite *Viscum album* also belong to this group, with pollen and parent plants restricted to both the oromediterranean and supramediterranean bioclimatic belts. This is also the case, among minority taxa, of *Allium*, *Anthemis*, *Carduncellus*, *Gentiana pneumonanthe*, *Geranium*, *Geum*, *Hepatica nobilis*, *Hippocrepis comosa*, *Klasea nudicaulis*, *Lonicera*, *Myosotis*, *Ribes uva-crispa*, *Viola*, *Veronica* and *Polygala*, all of them restricted to the oromediterranean bioclimatic belt; or of *Asparagus*, *Cistus laurifolius*, *Eryngium*, *Euphorbia*, *Hedera helix*, *Helichrysum stoechas*, *Linum* and *Lotus*, all of them restricted to the supramediterranean bioclimatic belt. Therefore, the number of very good indicator (VGI) pollen taxa representative of the corresponding bioclimatic belt and, consequently, of the existing pine forest community is very high (41 out of 62, or 66.1%) in the studied altitudinal transect.

(ii) Good indicator pollen types (GI), when the local occurrence of pollen types and parent taxa show similar altitudinal patterns although they disagree in some samples. The best examples are evergreen *Quercus* species and *Pinus pinaster*, which pollen and species (*Q. ilex*, *Q. coccifera*, *P. pinaster*) are concentrated in the lower supramediterranean belt. In both cases, the parent plant is absent from the upper supramediterranean and the oromediterranean belts, but their pollen is present in low abundances, likely because of an extensive wind dispersal. Other pollen types of this group are Apiaceae, *Asphodelus albus*, Brassicaceae, *Campanula*, Carduoideae, *Carlina*, Cichorioideae, *Fritillaria*, *Fumana*, *Helianthemum*, *Plantago major*/*media*, *Rosa*, *Scabiosa*, Scrophulariaceae, *Sedum* and *Trifolium*.

(iii) Non-indicator pollen types (NI), if there is no relationship between the altitudinal patterns of occurrence and abundance of pollen types and their parent taxa. This is the case of deciduous *Quercus* and *Pinus halepensis*/*pinea*, whose parent plants (*Q. faginea*, *P. halepensis*, *P. pinea*) are restricted to the lowermost part of the supramediterranean belt (up to 1150 m asl), but their pollen reach the upper supramediterranean and the oromediterranean belts, likely due to their great pollen dispersal by wind. Fabaceae shows a similar pattern, with its parent species (*Anthyllis montana*, *Astragalus austriacus*, *A. incanus*, *Coronilla minima*, *Medicago suffruticosa*) growing broadly at intermediate altitudinal levels (upper supramediterranean and oromediterranean belts), and, consequently, with its pollen evenly distributed along the transect.

6. Conclusions

Classification and ordination of modern pollen samples indicated the existence of eight vegetation units, which can be assigned to the six studied pine forest communities. Lowland forests are clearly discriminated from high-altitude ones. These analyses also allow separating *Pinus nigra* and *P. pinaster* communities according to their tree cover, and even those of *P. sylvestris* according to the bioclimatic belt they inhabit. Consequently we conclude that it is certainly possible to obtain distinct pollen markers for Mediterranean pine forest communities. These results will also improve the reconstruction of pine forests from fossil pollen diagrams, as far as modern pollen rain studies are carried out in specific regions. This approach can be extrapolated to other plant formations regardless the involved territory. Therefore, we strongly advise not to exclusively focus on the dominant arboreal pollen taxa or keystone species ("trees"), as this could lead to a loss of perspective on the true typological nature of the different types of plant communities ("forests").

Declaration of Competing Interest

None.

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