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Modern analogues for understanding pollen-vegetation dynamics in a Mediterranean mosaic landscape (Balearic Islands, Western Mediterranean)

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1. Introduction

Mediterranean sylvo-agropastoral landscapes are the outcome of long-term, dynamic processes involving socio-environmental and climate variables, where the diversity of human practices has resulted in ecologically and socially valuable mosaic landscapes (Mercuri and Sadori, 2014; Rita and Magri, 2012; Woodbridge et al., 2018). Mosaic landscapes are patchy sets of habitats including woodlands and open areas, crop fields and pastures, imbricated in a fragile socio-ecosystem in which human, environmental and climate dimensions are fundamentally interlaced. Examining these diachronic relationships can tell us much about their long and complex history. When investigating such landscapes, islands provide vital insights for understanding cultural and environmental processes through time because they tend to amplify geographical and cultural determinants and appear more vulnerable and less resilient to change than their mainland counterparts (Blondel, 2008). This "amplification effect" is more tangible in small to medium-sized islands, such as the Balearic archipelago, making them amenable study locations. In the Balearic Islands, the mosaic-like landscape is represented by the alternation of wild-olive macchia and garrigues with open areas since approximately the 5th millennium cal BP. While several palynological studies in the Balearics have been carried out (Burjachs et al., 2017; Kaniewski et al., 2020; Pérez-Obiol et al., 2000; Servera-Vives et al., 2018; Yll et al., 1997), the vegetation dynamics in response to human practices and climate oscillation are not yet fully assessed.

The genesis and evolution of cultural landscapes is a key issue for the disentangling of present-day landscapes and to better define past, current, and future human-nature interactions (Dearing et al., 2006). Palynology is an important discipline in this field of study (Mercuri, 2014). In this sense, the study of modern pollen analogues has proven valuable in exploring pollen-vegetation relationships and advancing the interpretation of paleoenvironmental data (Ejarque

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et al., 2011; Mazier et al., 2006; Morales-Molino et al., 2020). Additionally, modern analogues have implications for understanding the triggers of past environmental changes induced by climate trends and human activities through advanced numerical approaches (Marquer et al., 2020) or defining Anthropogenic Pollen Indicators (Brun, 2009; Mazier et al., 2009; Mercuri et al., 2013). While these type of studies have increasingly been developed in many regions around the world, including northern European countries and Asia (Chen et al., 2017; Zanon et al., 2018), they are still relatively rare in Mediterranean Islands (Fall, 2012; López-Sáez et al., 2018).

We present the first study of modern pollen analogues in the Balearic Islands based on a combination of vegetation surveys, pollen counts and numerical analyses. The main objectives of this research are: 1) to study pollen-vegetation relationships in relation to environmental and land-use variables; 2) to understand modern pollen representation in a mosaic landscape structure; 3) to propose pollen indicators that characterize the main vegetation types from the Balearic Islands to better interpret past pollen records in Mediterranean island environments.

2. Study area

The Balearic Islands is an archipelago located in the Western Mediterranean Sea formed by a group of 151 islands and islets. The four major islands are inhabited, namely Mallorca, Menorca, Eivissa and Formentera. Mallorca is characterized by a basin-and-range topographical configuration. The range areas correspond to uplifted blocks of the Alpine fold belt, mainly composed by carbonate deposits. Menorca is composed by two geological regions: the Tramuntana, in the north, composed by Palaeozoic, Mesozoic, and Lower Tertiary rocks, and the Migjorn, in the south, with Upper Miocene carbonates. Eivissa is structured into three different units of carbonate thrusted deposits with inverse faults of NE - SW orientation. Formentera is formed by Miocene carbonate reef platforms with quaternary alluvial and wind deposits superimposed.

The Balearic Archipelago has a Mediterranean climate characterized by marked seasonality, with dry and hot summers and maximal precipitation in autumn season. Under these strong Mediterranean conditions, various climatic zones were defined by Guijarro (1986). In Mallorca, the Tramuntana Mountain Range experiences average annual precipitation of > 1000 mm, with peaks exceeding 1400 mm; conversely, precipitation only reaches 500-700 mm in the central and eastern portions of the island, and 300 mm on the meridional coast. The average annual temperature in Mallorca is 17°C, except for the Tramuntana Range, which experiences an average annual temperature of <16°C (Figure 1). Menorca has a gentler topography and experiences annual average precipitation of 500-600 mm and an annual average temperature of 16.5 to 17°C. Eivissa exhibits higher variability in precipitation and temperature due to topographic features. Annual average precipitation ranges from 250 mm in the drier southern areas to 600 mm in the northern mountain areas; annual average temperatures are 19° to 15°C, respectively. Formentera's annual precipitation ranges from 300 mm in the western part of the island to 450 mm in the east. The annual average temperature for the island is 18°C.

The vegetation of the Balearic Islands is characterized by a mosaic-like pattern, which is the result of local environmental conditions and human-induced fires, land uses and building activity

(Morey and Ruiz-Pérez, 2008). Therefore, the Balearic landscape is primarily composed of alternating woods/forests, macchia, garrigues, grasslands, agropastoral areas and olive orchards. The predominant tree vegetation is formed by evergreen forests, woodlands and sclerophyllous shrublands dominated by *Quercus ilex* L., *Pinus halepensis* Miller, *Olea europaea* L., *Pistacia lentiscus* L. and *Juniperus phoenicea* L. (Llorens and Gil, 2017). Main agropastoral uses are based on traditional dry extensive agriculture including annual cereal crops, with scattered fruit trees and post-cereal-harvest cattle grazing (Morey and Ruiz-Pérez, 2008). Arboreal crops have traditionally been based on fig, olive, carob, and almond tree cultivation. Since the second half of the 20th century many coastal areas were widely urbanized in response to the tourism boom. Since the end of the past century, agropastoral areas have been increasing used for non-agricultural and leisure activities, therefore modifying traditional uses of the territory.

3. Material and methods

3.1. Field methods: vegetation description and sampling

A total of 56 modern pollen samples were collected within the Balearic Archipelago from Mallorca, Menorca, Eivissa, Formentera and Cabrera in 2016 and 2018 (Servera-Vives et al., 2021). The sites were selected to record the diversity of main vegetation types of the Balearic mosaic-like landscapes. The studied samples consisted of moss cushions as they are prone to record several years of pollen rain on the sampling point (Räsänen, 2001; Räsänen et al., 2007). Surface sedimentary samples were collected when local environmental constraints did not allow moss cushions (Florenzano et al., 2017). At least 5 moss cushions or surface sedimentary samples were mixed into one sample from each sampling point. During fieldwork, GIS Cloud software was used on mobile devices to collect the GPS coordinates and record the associated information of each site. A total of nineteen environmental variables were collected for each sampling point, including vegetation type, meteorology, soil, landscape openness, fire activity, topography, and land use information (Table 1 and Supplementary Material). Vegetation descriptions were done in a 100m^2 square using the Braun-Blanquet (1979) phytosociological approach. Additionally, the occurrence of tree and shrub species in the surrounding area were also recorded. Botanical nomenclature follows specialized phytosociological research in the area (Table 2). The sampling sites were classified in nine “vegetation types” that encompass the most important types of plant communities in the archipelago, as described below:

- *Quercus ilex* L. forest (HOF) is an ecologically and floristically well-defined community. It currently covers an extended area (52,906.04 ha), mainly on the mountains and hills of the major islands and is often intergraded with pine tree and shrubs on open, rocky, or heavily disturbed areas. Both mesic and thermophilous oak forests were sampled.

- *Buxus balearica* (BUX) plant communities are currently found in different habitats. On the Serra de Tramuntana (Mallorca) this taxon is present on isolated areas of a woodland assemblages, cliff crevices or rocky peaks, whereas on Cabrera Island box grows on xeric and coastal shrubland formations.

- The *maquis* (MAQ) correspond to sclerophyllous woodlands predominantly on the archipelago, spreading mainly on dry plains and coastal areas, and often associated to the existence of pine clusters. This vegetation group also includes other coastal formations dominated by junipers, as defined by EUNIS habitat classification (https://www.eea.europa.eu/data-and-maps/data/eunis-habitat-classification). Mallorca, Menorca and Pityusic islands present specific varieties of *Oleo sylvestris-Ceratonion siliquae* Br.-Bl. 1936 communities, constituting differentiated botanical associations (Rivas Martínez et al., 1992). For this study, the main Balearic communities of *Oleo-Ceratonion* were retained to characterize these well-known floristics and structure differences.

- Garrigues (GAR) are shrubland formations present on all the islands. Garrigues are both related to local disturbance dynamics (e.g., intense or recurrent fires) and abiotic features (e.g., dry sandy soils of the Pithyusic islands and loamy soils of Mallorca). For instance, the extensive areas covered by *Ampelodesmos mauritanica* grass in Mallorca are the result of recurrent fires.

- In addition to the communities of fixed dunes sampled and classified here either in MAQ or GAR vegetation types, we studied a location corresponding to an hemicryptophytes community in a grey mobile dune (DUN).

- Xeroacanthic Balearic communities includes some endemic spiny cushion-like species (SPH) such as *Launaea cervicornis*, *Astragalus balearicus* or *Teucrium marum*. They are exclusively located on the rocky summits of the Serra de Tramuntana mountains and on narrow coastal areas of the shore platform of Gymnesic islands. Heavy desiccation by winds, soil erosion, high insolation and ruminants, allow a common physiognomy of the vegetation and the presence of the main characteristic taxa on both sectors (Bolòs and Molinier, 1958; Llorens and Gil, 2017).

- Wetlands located mainly near the shoreline are heterogeneous habitats with floristic compositions that belong to a wide range of different communities. The coastal saltmarshes and saline riverine scrubs category (CSV) include representative samples from coastal halophilous scrubs assemblages.

- Meadows of grasses and sedges located on the margins of freshwater streams are included in the Mediterranean tall humid grassland and freshwater riverine scrubs (HSV).

- Human-induced vegetation (ANT) can include different habitats and plant communities such as the class *Stellarietea mediae* Tüxen, Lohmeyer & Preising ex von Rochow 1951 including archaeophytes and neophytes, annual herbs of crop fields, orchards, pastures, and edges. We did not assign detailed phytosociological descriptions to all these samples due to the spatial and temporal heterogeneity of modern agricultural land use in most of the studied areas, which mix ruderal and nitrophilous taxa with the surrounding communities.

3.2. Pollen analysis

Moss cushions were dried overnight and were treated following the standard procedures in palynology, including KOH, 200µm sieving and acetolysis (Erdtman, 1960; Faegri et al., 1989). Surface sedimentary samples were dried and subjected to the laboratory routine extraction described by Florenzano et al. (2012).This treatment uses 2g of dry sediment for deflocculation with Na-pyrophosphate 10%, sieving (7µm-mesh nylon mesh), HCl 10%, acetolysis, heavy liquid separation (Sodium metatungstate hydrate) and HF 40%. The final residue was mounted in permanent slides using glycerin jelly and sealed with paraffin. Pollen counts and identification were done using a x400, x600 and x1000 light microscope. A mean pollen sum of 383 grains were counted in the samples. Pollen percentages are based on pollen sum excluding *Pinus* due to its overrepresentation. The taxonomic identification of pollen grains was based on pollen atlases (Beug, 2004; Reille, 1992-1998), morphological keys (Chester and Raine, 2001; Punt et al., 1976-2009) and the pollen reference collection of the Laboratorio di Palinologia e Paleobotanica (Università degli Studi di Modena e Reggio Emilia). In this work, cereal grains are described as Poaceae pollen grains with diameter ≥40µm, porus+annulus ≥12µm (Faegri et al., 1989) and scabrate ornamentation pattern of the exine (Beug, 2004; Tweddle et al., 2005). The name Cichorieae is used to refer fenestrate pollen within the Cichorioideae subfamily (Florenzano et al., 2015). In this study, Chenopodiaceae is used as equivalent to Chenopodiaceae/Amaranthaceae pollen classification. Vegetation to pollen type correspondence of selected taxa is shown in Table 2, together with phytosociological adscription of collected samples. Pollen diagrams were elaborated using the C2 software (Juggins, 2007).

3.3. Numerical analysis

3.3.1.Data selection and transformation

To identify relationships between modern vegetation communities and the composition of directly related pollen datasets, we employed a suite of multivariate analyses, including cluster analysis and ordination. To reduce dataset noise and increase the sensitivity of our analysis, all rare taxa and pollen clumps were excluded from the pollen dataset. The criteria for determining a rare taxon were defined as a taxon that occurred in 2 or fewer samples and constituted less than 1% of the total pollen percentage. Additionally, multiple species or pollen types from the same genus were aggregated in a single taxon (e.g., *Quercus ilex*-t, *Quercus robur/pubescens*-t, and *Quercus* sp. are aggregated to *Quercus*) to facilitate pollen types and vegetation taxa identified in the field during vegetation surveys. The identified 160 pollen and spore types were reduced to 54 selected taxa. A square-root transformation was performed on the percentage of taxa data to reduce the influence of the most abundant taxa, as used in other modern analogue studies (Ejarque et al., 2011; López-Sáez et al., 2018). All data cleaning, analysis, and visualization was performed using R, version 4.1.0 (R Core Team, 2021), the vegan package, version 2.5-7 (Oksanen et al., 2020), and the ggplot2 package version 3.3.3 (Wickham, 2016).

3.3.2. Hierarchical clustering and Redundancy Analysis (RDA)

Based on the composition of their pollen assemblages, sample sites were grouped into clusters to initially evaluate their similarities and differences. Hierarchical Cluster Analysis (HCA) using Ward's minimum variance method (Ward, 1963), was performed on a matrix of Euclidean distances derived from the transformed pollen percentage datasets. The optimal number of cluster solutions was identified using the scree plot method and all cluster classifications were retained for subsequent ordination analyses.

Ordination techniques were then used to evaluate the relationship between individual and clusters of sample sites, pollen taxa, and environmental variables associated with each site. As a preliminary procedure, detrended correspondence analysis (DCA) was performed to determine an appropriate ordination technique, following the suggested protocol outlined in Šmilauer & Lepš (2014) and other recent published examples (e.g., Ejarque et al., 2011; López-Sáez et al., 2020; Mazier et al., 2006). The resulting gradient length of the pollen dataset was 2.11 standard deviation of species turnover units, meaning a linear ordination method is most appropriate for this dataset.

Redundancy analysis (RDA), a linear, constrained ordination technique, was performed on the 54 selected and transformed taxa, along with the environmental variables outlined in section 3.1 and Table 1. Following Li et al. (2015), variance inflation factors (VIF) were calculated for each of the environmental variables to evaluate the degree multicollinearity among each of these predictors. High collinearity among multiple environmental variables can cause unwanted redundancy and can make interpreting the ordination results difficult. Environmental variables that exhibited a VIF value greater than 10.0 were considered highly collinear and removed from the RDA. For the remaining environmental variables, a combination forward/backward stepwise model selection using permutation tests was performed to identify the most significant environmental variables associated with the pollen dataset.

3.3.3. Davis and Fidelity-Dispersibility Indices

Davis indices and Fidelity-Dispersibility indices were calculated for all taxa based on their presence or absence in both the pollen and observed vegetation datasets. These indices help evaluate the relationship between pollen types and the vegetation through several dimensions. Davis' (1984) indices include measures of association (A), underrepresentation (U), and overrepresentation (O) to assess how representative each pollen type is of the vegetation that occurs within each plot. To extend this interpretation, the fidelity index measures the rate at which taxa are observed in both the pollen and vegetation datasets. The dispersibility index measures the rate at which taxa are only recorded in the pollen dataset (as pollen rain) and absent from the observed vegetation (Fall, 2012; McGlone and Meurk, 2000). Hierarchical clustering techniques using Ward's method and Principal Components Analysis (PCA) were then used to evaluate the combined relationship between Davis indices, Fidelity-Dispersibility indices, and taxa. Indices were calculated using the pollen dataset prior to removing rare taxa, but after removing pollen clumps and aggregating some pollen types to a higher taxonomic level. A total of 64 taxa were represented in the final pollen dataset.

4. Results

4.1. Pollen from modern samples

A total of 160 pollen types and spores were identified. Pollen percentage diagrams with selected taxa and pollen clumps are shown in the pollen diagram Figure 2. Main palynological features of the samples, listed according to the vegetation types described in the field surveys, are shown in Table 3:

Vegetation type	Pollen spectra	Characteristic pollen flora
Broadleaved evergreen woodland: Holm-oak forests (HOF)	AP prevails (>73%). *Quercus ilex*-t is the main tree taxon (20-91%), and *Quercus* pollen clumps are recurrent in samples from this vegetation group. Also, *Pinus* has moderate to high pollen values (9-60%); *Olea* ranges from 5 to 24%. *Pistacia* is the only shrub >1%. Amongst the herbaceous taxa, Poaceae undiff. is the only one with values >1%.	*Quercus ilex*-t; *Taxus; Rhamnus*; *Hypericum; Daphne*; *Rubia*; *Plantago afra*-t; *Arbutus unedo* *Quercus ilex*-t clumps
***Buxus balearica* - Box woodlands (BUX)**	AP makes up to 96%. *Quercus ilex*-t and *Pinus* are characteristic tree taxa, despite their values are irregular variable ranging between 4-69% and 9-55% respectively. *Buxus* reaches values up to 69%, but uneven across the samples; pollen clumps of *Buxus* cf *balearica*, together with *Quercus* are frequent. *Olea* ranges from 6 to 24%, and *Juniperus* is recorded in all samples. The main shrubby taxa are *Pistacia, Hypericum* cf *balearicum* and *Erica* cf *multiflora*. Among herbs, Poaceae undiff., *Plantago* types, *Globularia* cf *alypum* and *Hornungia*-t are common.	*Quercus ilex-t; Buxus; Rhamnus; Hypericum; Daphne; Globularia* cf *alypum* *Buxus* clumps
Maquis, arborescent matorral and thermo-Mediterranean brushes (MAQ)	AP ranges from 22 to 87%, with *Pinus, Juniperus* and *Olea* as the foremost tree taxa, while *Quercus ilex*-t has low to moderate values (2-20%). This formation is also characterized by significant values of *Pistacia* (up to 27%), while noticeable values of *Myrtus, Rhamnus, Genista/Cytisus, Erica* cf *multiflora, Erica arborea-t, Cistus monspeliensis* and *C. albidus-t* reach moderate values in some samples. Poaceae undiff. prevail among herbaceous taxa, with a diversified spectrum including *Hordeum*-t, *Avena/Triticum*-t, *Plantago lanceolata*-t, *P. coronopus*-t, Cichorieae, *Senecio*-t, Apiaceae undiff., Chenopodiaceae undiff. and Scrophulariaceae undiff. *Pinus, Olea* and *Pistacia* clumps are recurrent. *Selaginella* spores can record high values (35%).	*Olea; Pinus; Juniperus-t; Ceratontia siliqua; Pistacia; Erica* cf *multiflora; Hordeum*-t; *Plantago afra*-t; *Senecio*-t; Apiaceae undiff; *Teucrium*; Scrophulariaceae undiff; *Selaginella* *Pinus, Pistacia* and *Olea* clumps
Garrigues (GAR)	AP values are between 64 and 84%. *Pinus, Olea* and *Juniperus* are the main tree taxa,	*Olea; Pinus; Juniperus*-t; *Ceratonia siliqua; Cistus*

	while *Quercus ilex*-t has low values (max. 12%). *Olea* and *Pinus* clumps are common. Among shrubs, *Pistacia* is <5%, a value lower than in the MAQ samples, while *Cistus monspeliensis* is well represented. Other taxa well represented are *Erica* cf *multiflora* and *Ephedra fragilis*-t. Poaceae undiff. dominates among herbs with values up to 12%. Other significant herb taxa are: *Plantago lanceolata*-t, *P. coronopus*-t, Cichorieae, *Euphorbia, Salvia*-t and *Globularia* cf *alypum. Selaginella* spores reach moderate values in some samples (max. 9%).	pollen types; *Globularia* cf *alypum; Cistus* pollen types; *Vitis*; Cichorieae; *Salvia/Rosmarinus*-t *Pinus* and *Olea* clumps
Coastal stable dune grassland: grey dunes (DUN)	AP in the only sample of this category is low (27%), with *Quercus ilex*-t, *Olea, Pinus* and *Juniperus* <5%. Shrubby taxa are almost absent, with only *Pistacia* >1%. Chenopodiaceae undiff. and *Verbascum* are the better represented herbs (18 and 12%, respectively). Also, Poaceae undiff., Rubiaceae undiff, *Plantago* cf *crassifolia*, *Lotus*-t, Cichorieae, Cyperaceae undiff., and *Hornungia*-t show values >1%.	*Centranthus*; *Lotus*-t; Rubiaceae undiff; Chenopodiaceae undiff.
West Mediterranean spiny heaths (SPH)	AP ranges from 45 to 75%, with high *Pinus* (32-67%) and moderate values of *Olea* and *Quercus ilex*-t (<20%). *Hypericum* cf *balearicum* dominates amongst shrubs, with values peaking at 52%. *Pistacia* and *Erica* cf *multiflora* also record moderate values. Herb assemblages are characterized by Poaceae undiff., Cichorieae, *Euphorbia* and *Matricaria*-t.	*Hypericum* cf *balearicum; Matricaria*-t
Anthropogenic herb stands (ANT)	AP is variable in this group (15-87%), with *Quercus ilex*-t, *Olea,* and *Pinus* as main contributors. *Pistacia* is the only shrub reaching >1-2% in all the samples (<2%). Poaceae undiff. dominates a diversified herbaceous spectrum, while *Avena/Triticum*-t and *Hordeum*-t are up to 6%. *Plantago lanceolata*-t, *Hornungia*-t, Cichorieae and Chenopodiaceae undiff., together with *Plantago* sp, *Polygonum, Rumex* and *Sinapis*-t are well represented. *Pinus, Olea, Hornungia*-t pollen clumps and *Parietaria*-t tetrads are observed.	*Ceratonia siliqua;* Poaceae undiff; *Avena/Triticum*-t; *Plantago lanceolata*-t; *P. major/media; Urtica dioica*-t; Rumex; *Polygonum*; Cichorieae; *Matricaria*-t
Coastal saltmarshes and saline	AP ranges from 5% to 48% with *Pinus* and *Juniperus*-t as main tree taxa. Amongst herbs, *Verbascum*, Chenopodiaceae undiff, *Plantago* cf *crassifolia, P. coronopus*-t and	*Tamarix; Plantago coronopus*-t; *Plantago* cf *crassifolia*; Chenopodiaceae

riverine scrubs (CSV)	Poaceae undiff. are the best represented. The presence of *Typha/Sparganium,* Plumbaginaceae undiff, Cyperaceae undiff and *Juncus* should be underlined.	undiff; *Limonium group*; *Juncus*
Mediterranean tall humid grassland + freshwater riverine scrubs (HFV)	AP ranges between 27-73%, with *Pinus* as main tree taxon (17-50%). *Juniperus* and *Olea* also reach noticeable values. *Pinus* and *Olea* clumps are also present. Among the shrubs, *Pistacia* dominates with values up to 21%; *Erica* cf. *multiflora, Cistus albidus*-t and *Rosmarinus*-t also are >1%. Poaceae undiff, *Plantago* sp., Cichorieae, Chenopodiaceae undiff. and *Senecio*-t prevail among herb taxa.	Poaceae undiff; Cichorieae; *Plantago coronopus*-t; Chenopodiaceae undiff; Cyperaceae undiff

Table 3- Pollen characterization of samples from the nine vegetation types studied. "Palynological features" refers to main palynological trends within the vegetation category, while "characteristic taxa" refers to taxa showing a preferential relationship to a specific vegetation type.

4.2. Davis and Fidelity-Dispersibility indices

Davis and Fidelity-Dispersibility indices represent the relationship between of pollen types and vegetation occurrence. Cluster analysis based on both complementary indices resulted in 5 groups (Figures 3 and 4; Table 4). Cluster classes and the corresponding association type category were calculated based on Fjordheim et al. (2018). **Cluster 1**: taxa with zero fidelity, low to moderate dispersibility, high overrepresented values (O), zero underrepresented (U) and associated values (A) and mainly anemophilous syndrome (e.g., *Taxus, Alnus, Vitis,* etc.). **Cluster 2**: taxa with high fidelity, moderate to high dispersibility, moderate to high values of O, A, and low values of U, including both anemophilous (*Pinus, Olea*), and entomophilous with exposed anthers taxa (e.g., Brassicaceae undiff., etc.). **Cluster 3**: taxa with moderate fidelity, low dispersibility, moderate values of U and low values of A and O; including mostly entomophilous taxa (e.g., *Asphodelus* group, *Hypericum, Myrtus*, etc.). **Cluster 4**: taxa with moderate fidelity and moderate dispersibility; low to moderate A, moderate U and O values, predominance of entomophilous taxa (e.g., Cichorieae, etc.) and low dispersal anemophilous (*Hordeum*-t, *Avena/Triticum*-t). **Cluster 5:** taxa with high fidelity and low dispersibility; moderate to high A, low U and low to moderate O values; only entomophilous taxa (e.g., *Matricaria*-t; *Buxus, Ceratonia siliqua*).

4.3. Clustering and ordination

The results of the PCA scatterplot showing the relationships between the retained 64 taxa and calculated Davis indices (1984) are shown in Figures 3 and 4, respectively. In the PCA, Group 1 correspond to overrepresented taxa; Group 2 includes weakly associated and overrepresented taxa; Group 3 and 4 include weakly associated and associated taxa; Group 5 mostly strongly associated taxa and some associated and overrepresented taxa. PC1 contrasts taxa with high association values (i.e., Poaceae, *Pistacia*, Cistaceae undiff., *Buxus*) with taxa with high overrepresented values (i.e., Chenopodiaceae, *Quercus*, *Plantago coronopus*-t, *Juniperus*). PC2 set up pollen types with high underrepresented values (i.e., Scrophulariaceae, Cichorieae, *Senecio*-t) against types with high associated values (i.e., *Globularia* cf. *alypum, Buxus, Ceratonia*).

Cluster analysis based on 54 pollen taxa (excluding rare taxa) show three distinct cluster groups, which are plotted together with RDA results in Figures 5A and B. The Forward/Backward method for stepwise model selection distinguish nine statistically significant ($p\text{-value} \leq 0.05$) explanatory variables (Table 5 and supplementary material) and a total of thirteen variables explain a 22% of the variation in the pollen dataset. RDA1 contrasts closed environments (with most of HOF, BUX, GAR and MAQ samples) in the negative values to open habitats, anthropogenic and wetland/dune formations habitats (mainly ANT, DUN, CSV and HFV samples). RDA2 presents locations with higher rainfall requirements, fire activity, trampling and slope in the positive values and thermic/drought-tolerance formations in the negative scores of the axis. Higher positive scores in RDA2 correspond to HOF, BUX and CSV (negative values) VS most of GAR and MAQ samples (negative values). Both cluster and RDA results show that group 1 is mostly comprised of holm oak and box formation samples; group 2 mainly corresponds to *maquis*, garrigues and some anthropogenic habitats nearby these formations; and group 3 is formed by crop fields, pastures and coastal saltmarshes and riverine scrubs.

5. Discussion

5.1. Pollen rain and present-day vegetation relationships

Five groups were obtained through cluster analysis based on Davis and fidelity-dispersibility indices scores (Figures 3 and 4, Table 4 and Supplemental Material). In the present study, overrepresented types (ORT) with zero fidelity and low to moderate dispersibility (Cluster 1) includes *Alnus*, *Betula*, *Castanea*, *Fraxinus, Saxifraga*, *Taxus, Typha*/*Sparganium*, *Vitis*, and *Isoetes*. Some of these taxa are absent from the present-day vegetation in the archipelago such as alder, birch, and chestnut, but they are commonly found in paleoenvironmental sequences from the Balearic Islands (Burjachs et al., 2017; Servera-Vives et al., 2018). *Alnus*, *Betula*, *Castanea* do not record values > 1%, thus indicating long-distance pollen transport of these anemophilous trees. Aerobiological data from the Balearic Islands also reported the current pollen presence of such absent or extremely rare species. Their presence has been interpreted as long-distance transport from Iberian Peninsula, France, or Italy (Boi and Llorens, 2008, 2013). Additionally, modern analogue studies pointed out that *Castanea* can be related to local presence when pollen values are higher than 5% (Miras et al., 2009), achieving values of ca. 90% in monospecific cultivars (Mercuri, 2015).

Cluster group 2 mainly aggregates weakly and over-represented types (WAT and ORT) with high fidelity and moderate/high dispersibility. This group includes common anemophilous taxa in the Balearic landscape such as *Pinus*, *Olea, Quercus, Juniperus,* and *Pistacia.* Moderated to high dispersibility values within this group confirm that these taxa are frequently found even if the plant is not present in the sampling point. This is consistent with the results obtained in previous studies carried out in Mediterranean island environments (Fall, 2012). Nevertheless, Davis indices indicates that *Pistacia* and Poaceae undiff. are strongly associated taxa (SAT) in our study.

High fidelity values of taxa within this group may be explained by their recurrence and ubiquity in the landscape, and their wide pollen dispersal. We have only observed two *Corylus* individuals in our study (both in sample MA-15) and today its cultivation is extremely rare in the Balearics. Hazelnut pollen has been a present during the middle Holocene in the Gymnesic islands, reaching maximal values of 10-20% (Burjachs et al., 2017). In this study, *Corylus* pollen was present in 19 samples out of 47 but was recorded with noticeable values (ca 40%) only in one location, where the hazelnut trees are planted. This suggests that moderate values may be interpreted as local formations, while low values should be interpreted as long-distance pollen transport. Apiaceae undiff. and Brassicaceae undiff., with entomophilous pollination strategy, present moderate values in fidelity and dispersibility, being both weakly associated taxa (WAT).

Groups 3 and 4 mostly include entomophilous taxa, but group 3 records lower dispersibility values. Both groups include most of the WAT taxa and some associated types (AT). The AT taxa are Ranunculaceae undiff., *Teucrium, Mentha*-t and *Hypericum*. Group 3 includes some shrubby and arboreal taxa such as *Phillyrea, Genista*-t, *Ephedra, Tamarix* and *Myrtus*; and herbaceous taxa such as *Limonium, Asphodelus*-group, Fabaceae, Lamiaceae undiff. and Urticaceae undiff. This low dispersibility values indicate that pollen is hardly found when vegetation is absent, despite its WAT classification. Meanwhile, main taxa included in Group 4 are Cichorieae, *Avena/Tricum*-t, *Hordeum*-t, *Senecio*-t, *Euphorbia* and Asteroideae. This cluster group of WAT types record a moderate fidelity and dispersibility values. This means that the pollen is not recorded in ca. 37-73% of sites where the plant is present, while in ca. 20-57% of the sites the pollen was present when the plant was absent. Even though former research has categorized Cichorieae, Cerealia-t and Poaceae undiff. as SAT (Brun et al., 2007), in our research Cichorieae and *Avena/Triticum*-t (WAT) record moderate fidelity and dispersibility values in this study, while Poaceae undiff. (SAT) gets 100% fidelity and dispersibility values.

Cluster Group 5 includes most of the strongly associated types (SAT) with high fidelity and low dispersibility, such as *Buxus, Ceratonia siliqua,* Cistaceae undiff. and *Globularia* cf. *alypum.* Moreover, some AT (*Erica* and *Stachys*) and ORT (*Matricaria*-t and *Polygonum*-t) are also recorded within this group. Obtained data indicate that taxa included into this group are reliable local indicators. The low dispersibility values displayed by Group 5, as in Group 3, indicate that they may not contribute significatively to the regional pollen rain far away from the plant source.

5.2. Palynological characterization of the Balearic landscape

Modern pollen assemblages and ordination show strong differentiation between the studied samples. This is especially clear among three groups of vegetation types (Fig. 3 and 4): a) HOF-Holm oak and BUX-box formations; b) MAQ-*maquis* and GAR-garrigues; and c) anthropogenic and open habitats (mainly HFV, CSV, DUN and ANT samples). While pollen rain provides an adequate representation of vegetation types, it should be considered that land-use changes in mosaic landscapes implies parallel, recurrent changes in vegetation communities. This process can influence pollen assemblages and may result in a mixture of multiple types of surrounding vegetation. The heterogeneous transformation of the landscape is particularly relevant in the Balearic Islands, where the rural owner structure is traditionally based on small and medium-sized properties, therefore resulting in a wide range of land-use combinations and vegetation communities in a specific area (Lucas-Vidal, 2002). The main features of palynological assemblages are discussed below:

a) HOF - Holm-oak forests are characterized by moderate and high AP values (70-95%), with *Quercus* pollen prevailing in HOF samples. Holm-oak formations usually records values higher than ca. 50% and minimum values of ca. 20% of *Quercus ilex*-t pollen, while below this threshold they should be interpreted cautiously as they may be the result of distance transport. Moderate values of *Pinus* are also recorded in HOF samples, which is explained by the fact that Aleppo pine is a companion in degraded holm-oak formations. Another characteristic taxon from holm oak forests is *Arbutus unedo,* a Mediterranean shrub which generally inhabits clearings and fringes of holm oaks forests and wet garrigues related to holm oak succession dynamics. Despite the low occurrence in our study, the zero dispersibility values, the low fidelity, and the insect-pollination strategy of this species, the presence of *Arbutus* pollen implies the local presence of the strawberry tree. *Taxus* is considered a relict species in the Balearic Islands being located only in some locations 800 and 1415 m asl of the Serra de Tramuntana range (Moragues et al., 2017; Pérez-Obiol et al., 2003). In this study, *Taxus* pollen has only been identified in sample 14 which corresponds to holm-oak formation nearby an area with some yew trees.

b) BUX - Box formations record variable abundances of *Buxus* cf. *balearica* pollen, which primarily depends on the specific location of the sample and the type of formation. In this sense, sample 42 recording the highest *Buxus* values (69%) was obtained from a small box woodland formed by tall individuals up to 6m-height in the northern slope of Puig de Galatzó. Also, high pollen values have been recorded in sample 44, in the upper part of the same mountain, where a *Buxus* formations of medium-sized individuals occupies the rock fissures. Box formations with isolated individuals record *Buxus* values lower than 5%. This is the case of xero-thermophilus box formations in rocky slopes, such as those reported in Cabrera Island, where heathers, junipers and mastic are widely represented. RDA results highlight the importance of *Quercus*, *Hypericum* and *Buxus* in characterizing pollen assemblages from HOF and BUX formations (Figure 5). *Buxus* and *Hypericum* are SAT and AT respectively, both with zero dispersibility and high fidelity scores (Figure 4 and Table 4). This highlights the correlation between box pollen and its parent plant, demonstrating their value as a local vegetation indicator. In this sense, it should be emphasized that we did not find *Buxus* pollen in samples located outside box formations. *Buxus* was a key taxon during the mid-Holocene in the Gymnesics, as attested in other palynological records (e.g., Burjachs et al., 2017; Pérez-Obiol et al., 2000). Although well-formed forest communities are currently absent in the Balearic landscape, studying these communities offer new insights into further interpreting box formations in the past.

c) MAQ, GAR - Maquis and garrigues present overall similar pollen assemblages characterized by moderate to high values of *Pinus*, *Olea, Pistacia* and *Juniperus* constituting the main arboreal taxa. RDA results point out that it is not statistically possible to discern between *maquis* and garrigues based on studied modern pollen assemblages. The cultivated olive tree *Olea europaea* and its wild form (*Olea europaea* L. var *sylvestris* (Mill) Lehr) are major arboreal taxa in the Balearic landscape, the former as part of olive orchards and the later mainly associated with macchia formations (Llorens and Gil, 2017). Even though the high airborne dispersibility of *Olea* pollen (Osborne et al., 2000), some modern analogue studies showed drastic decreases in pollen percentages (ca. 85% on average) when comparing inside and outside of this arboreal formation (Florenzano et al., 2017). In our study area, the higher *Olea* pollen values were found in maquis and garrigue samples, with better representation in closed and semi-open environments. For instance, samples inside and from macchia edge formations (23 and 24) from the Parc de Llevant in Mallorca record a 68% and 30% respectively, confirming that olive-tree pollen values tend to decrease with distance from the source area. Another common feature of MAQ-GAR is that pollen values >1% of *Ceratonia siliqua* have only been found in these vegetation types. *Ceratonia siliqua* is a SAT taxon with high fidelity and near-to-zero dispersibility, suggesting that the occurrence of its pollen, especially with values higher than 4%, may be associated to the presence of this plant. Despite this, we do not have enough data to assess the wild role of this tree in Balearic Islands, as its presence in the shrublands may be a consequence of the abandonment of cultivated areas.

Overall high pollen values of *Olea* and *Pinus* in Balearic maquis and garrigue samples may contribute to the difficulty of discerning them by ordination analysis. Also, there is a moderate specificity of species between this vegetation types, which may be related to the mosaic landscape structure where maquis and garrigues appears in contact. While pine pollen values are quite regular with moderate values within garrigue samples (45-69%), they are more irregular within macchia where they reach high values (up to 87%). This is also the case of *Juniperus*-t, which records higher pollen percentages in macchia samples (up to 54%). Notwithstanding *Pistacia* pollen, which is also recorded in garrigue samples, seems to be better represented in macchia communities, suggesting that moderate values of mastic pollen may be a good pollen indicator of this formation. Furthermore, some taxa such as *Erica* cf. *multiflora, Myrtus, Senecio*-t and Apiaceae undiff. are better recorded in macchia, whereas *Cistus monspeliensis, Salvia/Rosmarinus*-t and *Globularia* cf. *alypum* in garrigue samples. Regarding *Globularia* cf. *alypum*, it is only recorded in the GAR sample 21, and in BUX samples 50 and 51 from xero-thermophilous formations in Cabrera and located near a garrigue formation. Moreover, this is a SAT taxon with 100% fidelity and 0% dispersibility values, attesting its role as local pollen indicator.

d) ANT, HFV - Amongst the taxa which are statistically correlated with ANT and HFV vegetation types in the RDA, Chenopodiaceae undiff., Cichorieae, Poaceae undiff., *Plantago* sp, Apiaceae undiff., and Cerealia-t are reliable pollen indicators of such environments. Nevertheless, apart from Poaceae undiff., which is SAT type, other taxa are WAT (Cichorieae, *Plantago* sp, Apiaceae undiff. and Cerealia-t) or ORT (Chenopodiaceae undiff.) with moderate fidelity and dispersibility, suggesting that they may reflect a regional pollen rain and not only the local vegetation. Moderate pollen values of Cichorieae may be related to both the occurrence of dry-resistant communities on natural open areas or secondary open-habitats with pastures (Cremaschi et al., 2016; Florenzano, 2019; Florenzano et al., 2015). In off-site pollen records, Cichoriae pollen, when accompanied with Poaceae increases, usually reflects the extension of dry grassland during climate aridity episodes and human impact during the late-Holocene (Mercuri et al., 2013; Servera-Vives et al., 2018). Cerealia-t pollen is an important anthropogenic taxon as values >5% have mainly been recorded in ANT samples. It has been proved that the amount of Cerealia-t depends on agricultural practices and cereal processing techniques (Hall, 1988; Portillo et al., 2017). Cerealia-t pollen has been classified as SAT taxon in other modern pollen analog studies (e.g., Brun et al., 2007), while in this study it appears as a WAT taxon with moderate dispersibility and fidelity. This highlights that Cerealia-t pollen occurrences, as other synanthropic taxa, need to be correlated to other paleoenvironmental indicators to be interpreted as evidences of local human impact (Deza-Araujo et al., 2020; Mercuri et al., 2013).

e) CSV - Coastal saltmarshes/saline riverine scrubs (CSV) and DUN- coastal stable dune grassland samples are associated in the RDA (Figure 5) to Chenopodiaceae undiff., *Plantago coronopus*-t (including *Plantago crassifolia* in the ordination analysis), and Scrophulariaceae undiff. *Plantago* pollen types and Scrophulariaceae undiff. are WAT taxa, while Chenopodiaceae undiff. is ORT, with moderate to high dispersibility scores. *P. crassifolia* pollen is included within the *P. coronopus*-t (Ubera et al., 1988). This taxon mainly develops as a halophyte on coastal marshes (Llorens et al., 2007; Vicente et al., 2004) suggesting that *P. coronopus* should be interpreted prudently as an anthropogenic pollen indicator in littoral sequences from the past (Servera-Vives et al., 2018). In this sense, higher morphological levels are preferable to define past anthropogenic activities (Deza-Araujo et al., 2021; Mercuri et al., 2013). Chenopodiaceae undiff. appears in most of the samples in this study (44 out of 47), attesting its role as over-represented taxon with high dispersibility capability. Most Chenopodiaceae species are salt-tolerant well represented in littoral environments from the Balearic Islands such lagoons and associated habitats. However, they are common as a companion species in ruderal and nitrophilous environments. While there is a good match between the concomitant presence of both parent plant and pollen, there is no unambiguous correlation in our study.

5.3. Environmental triggers influencing pollen composition

Redundancy analysis (Figure 5) shows that a set of variables such as landscape form, mean decadal rainfall, mean decadal temperature, fire activity (EFFIS, 2018), trampling, slope percentage, wet/flooded soil, salty soil, distance to agropastoral areas, gHM (Global Human Modification) index (Kennedy et al., 2019), domestic herbivory presence, agropastoral use and soil type explain the variability of modern pollen assemblage. At the regional scale, climate variables such as rainfall and temperature are likely major agents in constraining Mediterranean environments distribution (Fall, 2012; López-Sáez et al., 2018). Axis 1 of the RDA shows an openness gradient starting from forest formations (mainly HOF and BUX), followed by semi-open environments (mainly MAQ, GAR, SPH and HFV) and open lands from anthropogenic and wetland environments (mainly HFV, CSV, ANT and DUN samples). Landscape openness plays an important role in the pollen assemblage composition, as is shown in former studies (Ejarque et al., 2011; Mazier et al., 2006). In this sense, pollen assemblages seem to give a consistent image of an openness gradient and can give insight of the mosaic landscape formation in the Balearic landscape. Despite that MAQ and GAR may develop mature closed formations, they are frequently found as semi-open formations, as shown by the site scores on axis 1 of the RDA. Salty and flooded soils seem to be correlated to CSV and DUN sites. Pollen types linked to such formations are *Plantago coronopus*-t, Scrophulariaceae undiff., Asteraceae, *Euphorbia*, *Matricaria*-t, Cyperaceae undiff. and *Hordeum*-t. In this study, *Matricaria*-t includes *Anthemis* species, *Chrysanthemum segetum* L., *Glebionis coronaria* and *Santolina chamaecyparissus.* Most of these species are found in coastal and anthropogenic habitats such as cultivated fields, paths, and roadsides. In the RDA this pollen type is mainly associated to CSV sites due to high

Matricaria-t pollen values in sample ME-30, but it should be also considered that values higher than 1% are just recorded in ANT sites.

In Axis 1, despite most of pollen types with positive scores are correlated to direct human pressure, some show a more evident correlation to gHM index, agropastoral use, land openness and herbivory pressure variables. This is the case of the following taxa: Chenopodiaceae, Poaceae undiff., *Plantago* sp., Apiaceae undiff., Cerealia-t and Cichorieae. In this sense, most of samples with agropastoral use correspond to ANT, HFV and MAQ communities, located in open and semi-opened environments (see supplemental Material). *Plantago lanceolata*-t is a common anthropogenic pollen indicator associated to regional dynamics (Ejarque et al., 2011; Mazier et al., 2006). While the relationship between herbivory pressure and *P. lanceolata*-t is also confirmed in this study, it is reported that this pollen type is also correlated to warmer locations. In this regard, Chenopodiaceae (ORT), Poaceae undiff. (SAT), *Plantago* sp. (WAT), Apiaceae undiff. (WAT), Cerealia-t (WAT) and Cichorieae (WAT) record moderate to high dispersibility, suggesting that point notations, low or isolated evidence of this pollen requires a careful interpretation in terms of human disturbance dynamics.

Axis 2 of the RDA is mainly related to climate trends, but human-induced disturbances may also play an important role. More specifically, positive values in the axis are correlated to rainfall, fire activity, slope percentages and, to a less extent, trampling. Most of HOF and BUX sites are in the positive side of the axis (Cluster group 1). Main taxa associated to these environmental variables are *Quercus* pollen types (mainly including *Quercus ilex*-t in this work, which also includes *Q. coccifera*), *Hypericum* and *Buxus*. Evergreen oak is one of the main arborescent components of the Balearic landscape, broadly spreading in mesic locations such as hillsides and humid valleys between 500-800 m asl of the Serra de Tramuntana in Mallorca, in inland and deep soil locations of Minorca. Furthermore, very restricted areas of *Quercus coccifera* also exist in Mallorca and Eivissa, while both *Q.* ilex and *Q. coccifera* are absent from Formentera and Cabrera (Llorens and Gil, 2017). Regarding fire activity, between the period of 2006-2016 ca. 80% of the fires occurred in forest areas of Mallorca. Most of large fires occurred in the Serra de Tramuntana, where the largest forest of the archipelago is located, which likely explains the correlation of HOF and BUX sites with fire activity in the RDA. The correlation of trampling with cluster group 1 may be related to understory disturbance caused by historical grazing of domestic and feral livestock, such as pigs, sheep and goats (Bolòs et al., 1970). Negative values of axis 2 in the RDA correspond to cluster group 2 including most of MAQ and GAR sites, being positively correlated to mean decadal temperature and negatively correlated to rainfall. In this sense, most of the *maquis* and garrigues are clearly associated to high mean temperatures and to closed and semi-opened environments in the RDA. This fact underlines the dryness-adapted character of most taxa associated to both environmental types. Additionally, distance to agropastoral areas, gHM index and herbivory are correlated to cluster group 2. Main taxa linked to negative scores in axis 2 of the RDA are *Pistacia, Pinus, Juniperus*-t and *Olea.*

6. Conclusion

Modern pollen assemblages obtained from the Balearic mosaic landscape furnishes novel and key information to understand pollen-vegetation relationships, as well as the correlation of

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pollen assemblages with environmental and anthropogenic variables. This information will open new opportunities to better interpret fossil pollen records from the Balearic Islands and other Mediterranean landscapes. The main conclusions of this research are:

- Major vegetation types can be distinguished through pollen analysis. Ordination and pollen results show three major groups HOF/BUX, MAQ/GAR and open/anthropized environments (DUN, HFV, ANT, CSV). Although ordination results present limitations in discerning between some pollen assemblages (i.e., MAQ vs GAR), overall the pollen highlights the main features of each vegetation type.

- Landscape openness, rainfall, slope, salty soil, flooded soil, and fire activity are the major environmental variables constraining RDA results, whereas agropastoral use, distance to agropastoral cells, soil type, herbivory pressure and gHM index are also important variables. Therefore, this approach offers new and robust information regarding pollen-vegetation relationships, as well as the main natural and cultural factors influencing mosaic landscape composition.

- Key taxa arise as reliable indicators of most vegetation types from the Balearic Islands. Our work suggests that low pollen percentages of anemophilous and high pollen producing taxa should be interpreted with caution as they likely reflect regional dynamics. This is the case of some taxa typically considered as anthropogenic pollen indicators such as *Plantago lanceolata*-t or Chenopodiaceae undiff.

In conclusion, this research emphasizes the importance of developing modern analogues in Mediterranean regions to improve our interpretations of paleoenvironmental records. Further research on anthropogenic pollen indicators and non-pollen palynomorphs will offer new insights on anthropogenic and climate triggers inducing environmental changes in the past and will contribute to characterize agropastoral practices and local landscape transformation of mosaic landscapes.

Author's contribution

GSV, MMA and AMM designed the research. MMA and GSV carried out fieldwork, sample, and data collection. Palynological analysis was carried out by GSV with morphological supervision by AMM, PT and AF. GS and GSV performed all data wrangling and statistical procedures. JEB obtained and analyzed modern climate data and elaborated maps. GSV and MMA wrote the main text. All authors wrote important sections, revised, and approved the manuscript. GS also revised English language grammar and readability.

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Declaration of competing interest

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

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CAPTIONS

Figures

Fig. 1- Map of the study area, topography and mean annual rainfall in the Balearic Islands (upper figure). Map showing sampling locations of modern pollen and vegetation relevés. Vegetation categories are based on Corine Land Cover classes (bottom figure).

Fig. 2- Percentage pollen diagrams of selected taxa of the surface samples from the Balearics Islands.

Fig. 3- Principal Component Analysis (PCA) showing the relationship between the calculated Davis indices and different taxa. Arrow labels correspond to abbreviations for each index: association index (A), over-representation index (O) and under-representation index (U). Colours refer to cluster groups derived from the Davis and Fidelity-Dispersibility indices for each taxon.

Fig. 4- Fidelity and dispersibility indices plotted for each pollen taxa. The shape, size and colour of each observation corresponds to the cluster group, taxa height, and pollination syndrome for each taxa, respectively.

Fig. 5- Redundancy analysis (RDA) biplots indicating the relationships between modern pollen samples and selected environmental variables (a) and selected pollen types and environmental variables (b).

Tables

Table 1- Description of all environmental variables included in the analysis. Variables in bold correspond to those selected after ANOVA permutation test.

Table 2- Main vegetation taxa and phytosociological communities associated with vegetation types.

Table 3- Pollen characterization of samples from the nine vegetation types studied. “Palynological features” refers to main palynological trends within the vegetation category, while “characteristic taxa” refers to taxa showing a preferential relationship to a specific vegetation type.

Table 4- ANOVA permutation test results for the 13 environmental variables selected for the RDA using the Forward/Backward method for stepwise model selection. Significant p-values (≤0.05) are in **bold**.

Table 5- Results of the Davis and Fidelity/Dispersibility indices, with pollination syndrome and taxa height.

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Fig. 1

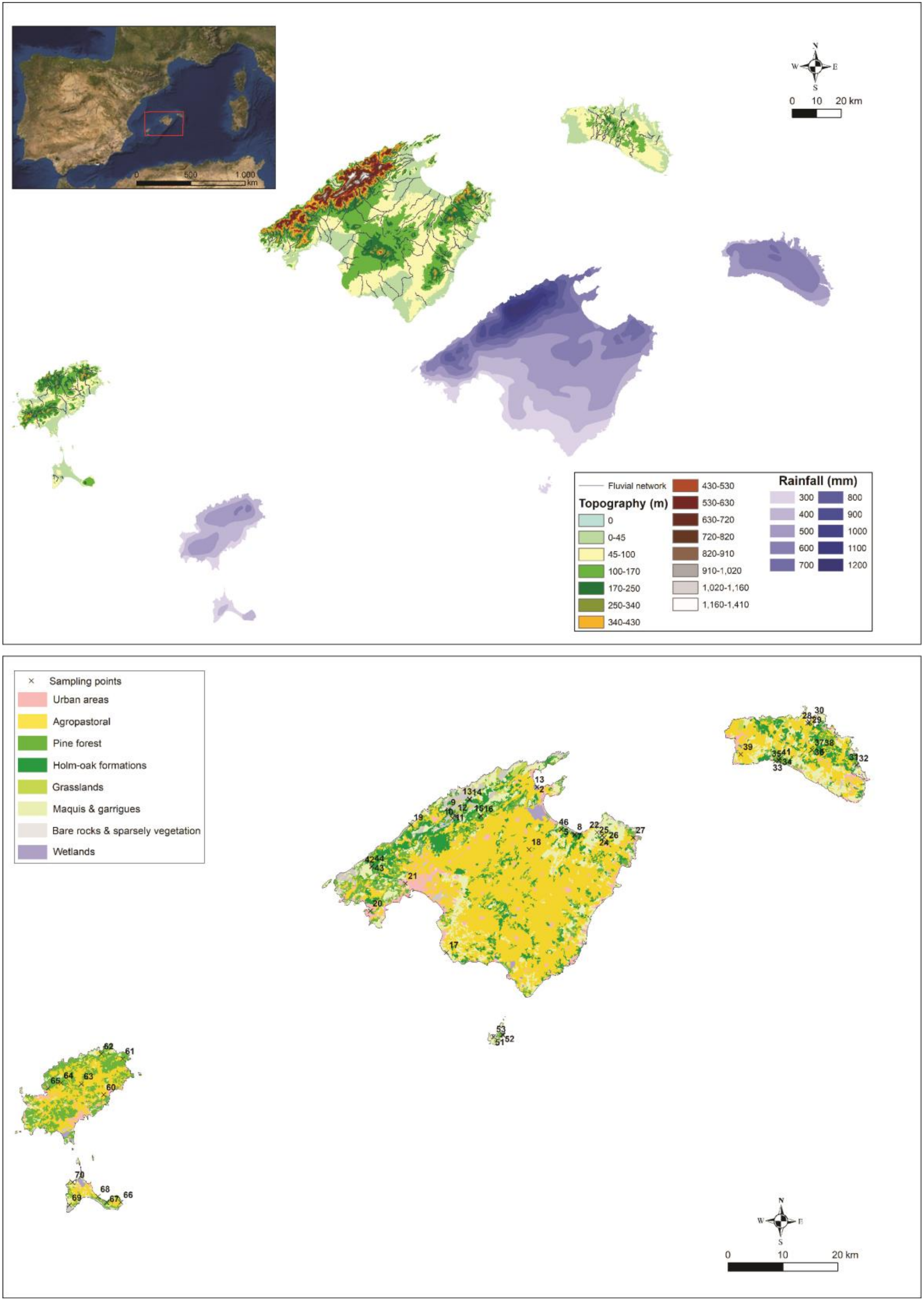

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Fig. 2

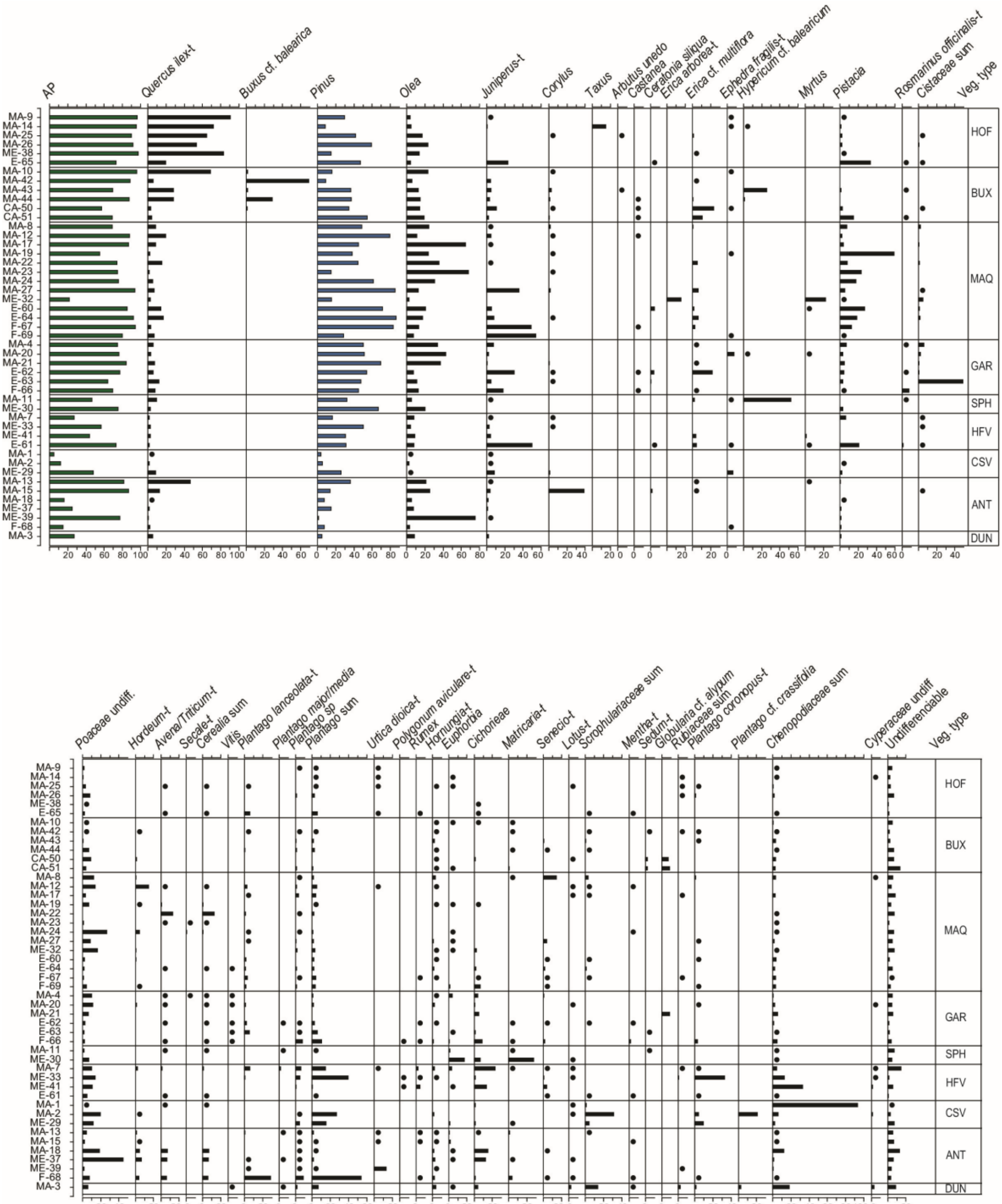

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Fig. 3

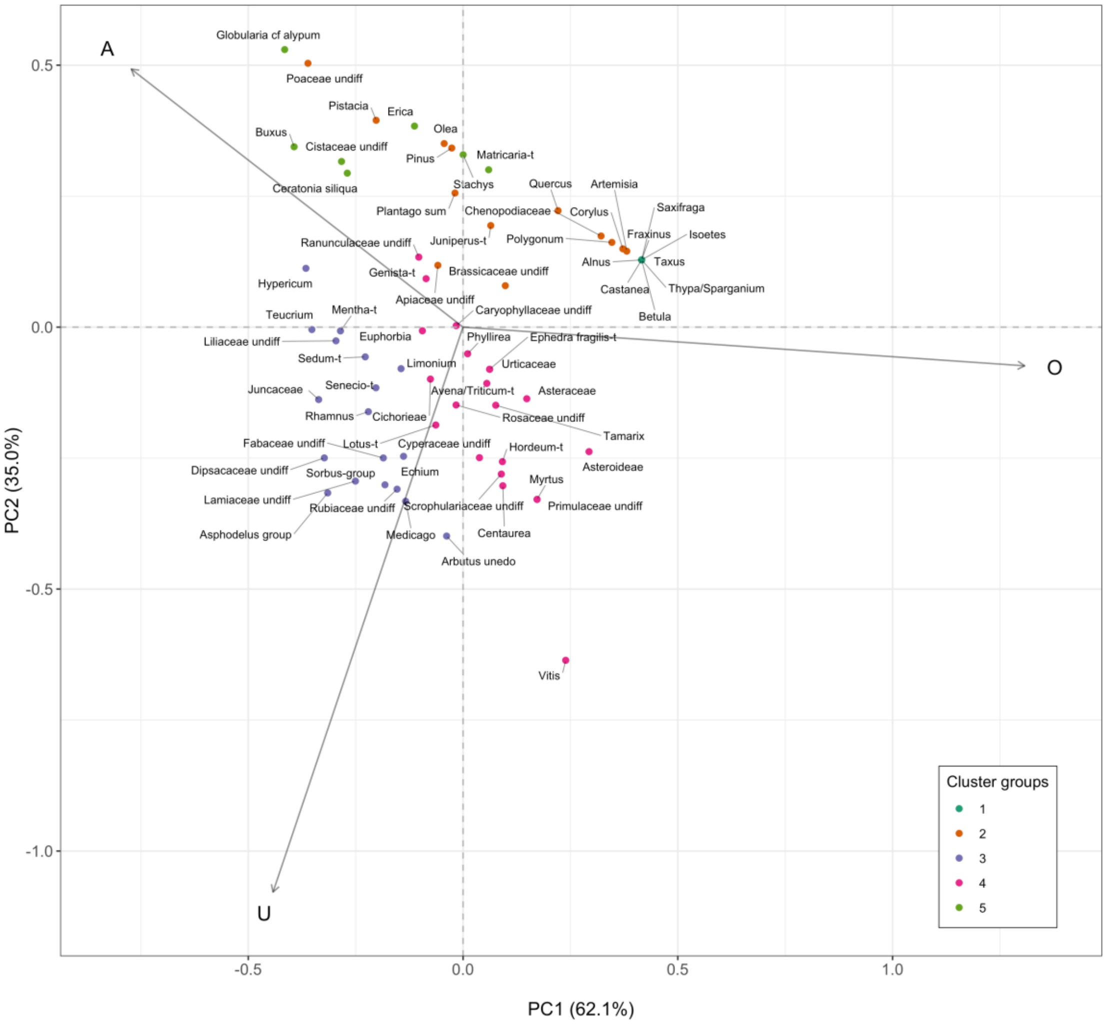

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Fig. 4

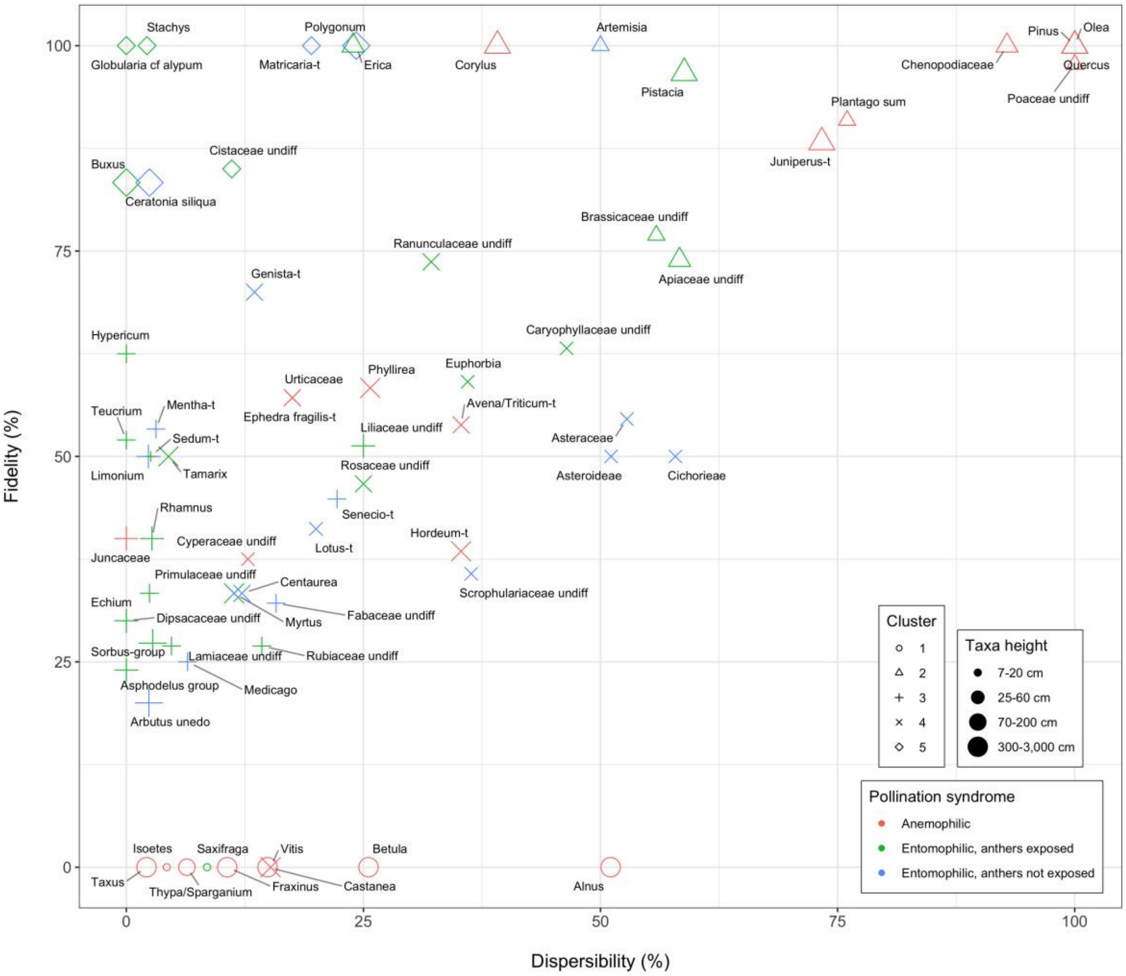

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Fig. 5

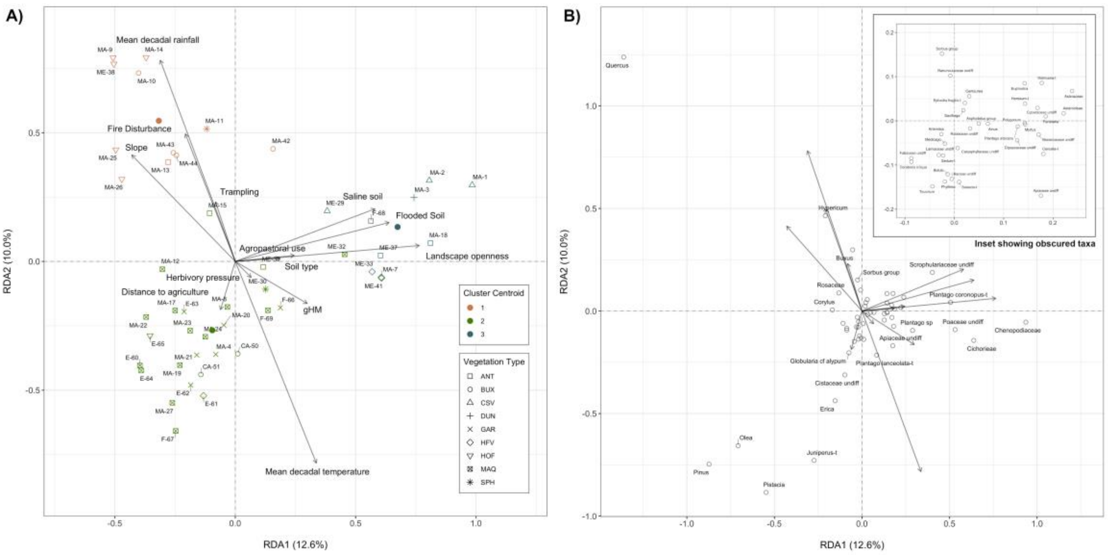

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Table 1-

Environmental variable	Scale	Source of data	Description
Herbivory pressure	0-2	direct observation	Degree of herbivory pressure: absence of herbivores (0); wild herbivores (1); domestic herbivores (2)
Agropastoral use	0-1	direct observation	Absence (0) or presence (1) of agricultural and/or pastoral activities in the sampling point
Trampling	0-1	direct observation	Evidence of trampling (human or animal): absent (0) and present (1)
Landscape openness	0-2	direct observation	Closed environment (0); semi-open (1); closed (2)
Soil type	0-1	IGN	0= non calcareous soil; 1= calcareous soil
Mean decadal rainfall	mm	AEMET stations	Mean rainfall for the period 2008-2018 recorded in the nearest meteorological station
Mean decadal temperature	degrees (°C)	AEMET stations	Mean temperature for the period 2008-2018 recorded in the nearest meteorological station
Slope	percentage (%)	DTM	Slope percentage based on DTM
Saline soil	0-1	direct observation	0= not saline soil; 1= saline soil
Flooded soil	0-1	direct observation	0= not wet soils; 1= Wet soils (stagnant water)
Fire disturbance	n	EFFIS Database	Number of fire episodes within a 10km radius of each sampling point during the period 2008-2018 based on European Forest Fire Information System dataset (EFFIS 2018)
Distance to agriculture	km	CORINE Land Cover	Distance to agropastoral cells
gHM	0-1	Google Earth Engine Data Catalog	The global Human Modification database provides a cumulative measure of anthropogenic modification of terrestrial lands globally at 1 square-kilometer resolution (Kennedy et al., 2019)
Altitude	m asl	DTM	Altitude in meters above sea level, based on DTM
Aspect	cardinal points	DTM	Z aspect based on raster cells of 25m. downslope direction of the maximum rate of change in value from each cell to its neighbors.
Sea distance	meters	DTM	Linear distance from sampling point to the sea
Direct human pressure	0-1	direct observation	Presence/absence of evidence for human pressure (grazing, cultivation, buildings, paths, forestry, etc)
Nitrophily index	1-3	direct observation	3 categories based on vegetation relevés:1= <20% of taxa are nitrophilous; 2= 20-40% of taxa are nitrophilous; 3= >40% of taxa are nitrophilous
Crop index	0-2	direct observation	3 categories based on vegetation relevés: Absent (0); 0,1-4,9% (1); 5-9,9% (2); ≥ 10% (3)

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Table 2-

Sample number	Phytosociological adscription	Main vegetation taxa	Pollen type equivalences used in this work
14, 38	*Cyclamini balearicae-Quercetum ilicis* (O. Bolòs & Molinier 1958) O. Bolòs 1965	*Quercus ilex* L., *Ruscus aculeatus* L. , *Carex halleriana* Asso, *Arbutus unedo* L., *Euphorbia characias* L., *Cyclamen balearicum* Willk., *Pinus halepensis* Mill.	*Quercus ilex* -t, Liliaceae undif., Cyperaceae undiff., *Arbutus unedo, Euphorbia* , *Cyclamen* , *Pinus*
9, 25, 26, 63, 65	*Clematido cirrhosae-Quercetum rotundifoliae* (O. Bolòs & Molinier 1958) Rivas-Martínez & Costa 1987		
10	*Buxo balearicae-Genistetum majoricae* Rivas-Martínez in Rivas-Martínez, Costa, P. Soriano, Pérez-Badia, Llorens & Roselló 1992	*Buxus balearica* Lam., *Genista majorica* Cantó & Mj. Sánchez, *Ephedra fragilis* Desf-, *Primula acaulis* (L.) L. subsp. *balearica* (Willk.) Greut. & Burdet, *Smilax aspera* L. var. *balearica* Willk.	*Buxus* cf. *balearica, Genista* -t, *Ephedra fragilis* -t, Primulaceae, *Rhamnus*
50+51	*Cneoro tricocci-Ceratonietum siliquae* O. Bolòs in O. Bolòs & Molinier 1958 subass. *Rhamnetosum ludovici-salvatoris* O. Bolòs et Vigo 1976		
42, 43+44	*Primulo balearicae-Aceretum granatensis* Rivas-Martínez, Costa & Loidi 1992		
8, 27	*Clematido balearicae-Juniperetum lyciae* (O. Bolòs, Molinier & P. Montserrat 1970) Rivas-Martínez 1975	*Cneorum tricoccon* L., *Euphorbia dendroides* L., *Rhamnus alaternus* L., *Phillyrea* spp., *Olea europaea* L., *Arum italicum* Mill., *Cistus* spp., *Chamaerops humilis* L., *Juniperus phoenicea* L. subsp. *turbinata* (Guss.) Parl., *Quercus coccifera* L., *Pinus halepensis*	*Cneorum tricocon, Euphorbia, Rhamnus* , *Phillyrea, Olea, Arum, Cistus, Chamaerops humilis, Juniperus* -t, *Quercurs ilex* -t, *Pinus*
17, 22, 23+24	*Cneoro tricocci-Ceratonietum siliquae O. Bolòs in O. Bolòs & Molinier 1958*		
64, 67, 69	*Cneoro tricocci-Pistacietum lentisci* O. Bolòs & Molinier (1969) 1984		
31	*Prasio majoris-Oleetum sylvestris* O. Bolòs & Molinier 1969		
53	*Rhamno ludovici-salvatoris-Juniperetum turbinatae* (Camarasa, Cardona, Masalles, Terradas, E. Velasco & Vigo 1976) Gil, Llorens, Tébar & Costa 1995		
60	*Cisto albidi-Genistetum hirsutae* Rivas-Martínez, Costa & Loidi 1992		
19	*Euphorbietum dendroidis* Guinochet in Guinochet & Drouineau 1944		
12	*Smilaco balearicae-Ampelodesmetum mauritanicae* Rivas-Martínez in Rivas-Martínez, Costa, P. Soriano, Pérez-Badia, Llorens & Roselló 1992		
32	*Ampelodesmo mauritanicae-Ericetum scopariae O. Bolòs, Molinier & P. Montserrat 1970*	*Smilax aspera* L. var. *balearica* Willk., *Ampelodesmos mauritanica* (Poiret) T. Duran& Schinz, *Erica* spp., *Teucrium capitatum* L., *Lotus cytisoides* L., *Pistacia lentiscus* L., *Rosmarinus officinalis* L., *Thymbra capitata* (L.) Cav, *Pinus halepensis*	*Smilax* , *Poaceae undiff.* , *Erica* , *Teucrium, Anthyllis, Pistacia, Rosmarinus* (=*Salvia pratensi* s group), *Mentha* -t, *Pinus*
4, 21, 52	*Anthyllido cytisoidis-Teucrietum majorici* O. Bolòs & Molinier 1958		
62	*Cytiso fontanesii-Genistetum dorycnifoliae* Rivas-Martínez, Costa & Loidi 1992		
35	*Loto tetraphylli-Ericetum multiflorae* O. Bolòs & Molinier 1958		
66	*Teucrio piifonti-Corydothymetum capitati* Rivas-Martínez, Costa & Loidi 199		
20	*Ephedro fragilis-Withanietum frutescentis Rita & Bibiloni 1993*		
30	*Santolino magonicae-Anthyllidetum hystricis* (O. Bolòs, Molinier & P. Montserrat 1970) Gil & Llorens 1995	*Launaea cervicornis (* Boiss.) Font Quer & Rothm., *Santolina chamaecyparissus* L., *Teucrium marum* L., *Astragalus balearicus* Chater, *Carduncellus balearicus* (J.J. Rodr.) G. López,	Cichorieae, *Matricaria* -t, *Teucrium, Astragalus, Carthamus* -t, *Hypericum* cf. *balearicum, Euphrobia*
11	*Teucrietum subspinosi O. Bolòs & Molinier 1958*		
7	*Typho-Schoenoplectetum glauci* Br.-Bl. & O. Bolòs 1958	*Ranunculus macrophyllus* Desf., *Scirpus lacustris* L., *Leucojum aestivum* L. subsp. *pulchellum* (Salisb.)Briq., *Eleocharis palustris* (L.) Roem. & Schultes	*Ranunculua acris-t,* Cyperaceae undiff., *Galanthus-t* , Cyperaceae undiff.
33, 41	*Geranio dissecti-Ranunculetum macrophylli* O. Bolòs & Molinier 1958		
61	*Rubo ulmifolii-Nerietum oleandri* O. Bolòs 1956		
2	*Schoeno nigricantis-Plantaginetum maritimae* Rivas-Martínez 1984	*Tamarix* spp., *Schoenus nigricans* L., *Limonium* spp., *Atriplex portulacoides* L., *Juncus maritimus* Lam., *Arthrocnemum fruticosum* (L.) Moq., *Inula crithmoides* L.	*Tamarix,* Cyperaceae undiff., *Limonium,* Chenopodiaceae undiff., Juncaceae undiff., Chenopodiaceae undiff., *Senecio* -t
1	*Statico bellidifoliae-Salicornietum fruticosae* Br.-Bl. 1933		
28	*Scirpetum compacto-litoralis* (Br.-Bl. in Br.-Bl., Roussine & Nègre 1952) O. Bolòs 1962 corr. Rivas-Martínez, Costa, Castroviejo & E. Valdés 1980		
70	*Limonietum retuso-biflori* Llorens 1986		
29	*Tamaricetum gallicae* Br.-Bl. & O. Bolòs 1958		
39	*Silybo-Urticetum Br.-Bl. in Br.-Bl., Gajewski, Wraber & Walas 1936*	Cerealia, *Carduus* spp., *Silybum marianum* (L.) Gaertn, *Urtica dioica* L., *Gladiolus* spp., *Galactites tomentosa* Moench, *Plantago afra* L., *Diplotaxis*	Cerealia-t, *Carduus* -t, *Carduus* -t, *Urtica* -t, *Gladiolus* -t
13, 15, 18, 34, 36, 37, 68	-		
3	*Loto cretici-Crucianelletum maritimae* Alcaraz, T.E. Díaz, Rivas-Martínez & P. Sánchez 1989	*Crucianella maritima L., Helichrysum stoechas (L.) Moench, Lotus creticus L., Teucrium dunense Sennen*	Crucianella cf. (Rubiaceae), *Senecio* -t, *Lotus* -t, *Teucrium*

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Table 4-

Environmental variable	*Df*	Variance	F	p-value
Herbivory pressure	1	1,56	1,97	**0,01**
Agropastoral use	1	1,37	1,73	**0,04**
Trampling	1	1,16	1,46	0,08
Landscape openness	1	2,06	2,60	**<0.01**
Soil type	1	1,58	1,99	**0,03**
Mean decadal rainfall	1	1,82	2,29	**0,01**
Mean decadal temperature	1	1,42	1,79	**0,03**
Slope	1	1,37	1,72	**0,04**
Saline soil	1	1,36	1,71	**0,04**
Flooded soil	1	2,11	2,65	**<0.01**
Fire disturbance	1	1,19	1,50	0,09
Distance to agriculture	1	1,18	1,49	0,09
gHM	1	1,25	1,57	0,06
Residual	33	26,23	--	--

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Table 5

Taxa	A	U	O	Fid	Dis	Taxa Height	Pollination Syndrome	Cluster Group	Classical Indices Categories
Alnus	0	0	1	0	51,06382979	300-3000cm	Anemophilic	1	**ORT**
Betula	0	0	1	0	25,53191489	300-3000cm	Anemophilic	1	**ORT**
Castanea	0	0	1	0	14,89361702	300-3000cm	Anemophilic	1	**ORT**
Fraxinus	0	0	1	0	10,63829787	300-3000cm	Anemophilic	1	**ORT**
Isoetes	0	0	1	0	4,255319149	7-20cm	Anemophilic	1	**ORT**
Saxifraga	0	0	1	0	8,510638298	7-20cm	Entomophilic, anthers exposed	1	**ORT**
Taxus	0	0	1	0	2,127659574	300-3000cm	Anemophilic	1	**ORT**
Typha/Spa	0	0	1	0	6,382978723	70-200cm	Anemophilic	1	**ORT**
Vitis	0	1	1	0	15,2173913	300-3000cm	Anemophilic	1	**UT**
Apiaceae	0,459459	0,26087	0,451613	73,91304	58,33333333	70-200cm	Entomophilic, anthers exposed	2	**WAT**
Artemisia	0,041667	0	0,958333	100	50	25-60cm	ntomophilic, anthers not expose	2	**ORT**
Brassicace	0,3125	0,230769	0,655172	76,92308	55,88235294	25-60cm	Entomophilic, anthers exposed	2	**WAT**
Chenopod	0,113636	0	0,886364	100	92,85714286	70-200cm	Anemophilic	2	**ORT**
Corylus	0,052632	0	0,947368	100	39,13043478	300-3000cm	Anemophilic	2	**ORT**
Juniperus-	0,384615	0,117647	0,594595	88,23529	73,33333333	300-3000cm	Anemophilic	2	**WAT**
Olea	0,553191	0	0,446809	100	100	300-3000cm	Anemophilic	2	**AT**
Pinus	0,531915	0	0,468085	100	100	300-3000cm	Anemophilic	2	**AT**
Pistacia	0,725	0,033333	0,25641	96,66667	58,82352941	300-3000cm	Entomophilic, anthers exposed	2	**SAT**
Plantago s	0,487805	0,090909	0,487179	90,90909	76	25-60cm	Anemophilic	2	**WAT**
Poaceae u	0,934783	0	0,065217	97,72727	100	25-60cm	Anemophilic	2	**SAT**
Quercus	0,234043	0	0,765957	100	100	300-3000cm	Anemophilic	2	**ORT**
Arbutus u	0,166667	0,8	0,5	20	2,380952381	300-3000cm	ntomophilic, anthers not expose	3	**WAT**
Asphodelu	0,24	0,76	0	24	0	70-200cm	Entomophilic, anthers exposed	3	**WAT**
Centaurea	0,181818	0,666667	0,714286	33,33333	12,19512195	70-200cm	ntomophilic, anthers not expose	3	**WAT**
Cyperacea	0,230769	0,625	0,625	37,5	12,82051282	25-60cm	Anemophilic	3	**WAT**
Dipsacace	0,3	0,7	0	30	0	70-200cm	Entomophilic, anthers exposed	3	**WAT**
Echium	0,285714	0,666667	0,333333	33,33333	2,43902439	25-60cm	Entomophilic, anthers exposed	3	**WAT**
Ephedra f	0,285714	0,428571	0,636364	57,14286	17,5	70-200cm	Anemophilic	3	**WAT**
Fabaceae	0,290323	0,678571	0,25	32,14286	15,78947368	25-60cm	ntomophilic, anthers not expose	3	**WAT**
Genista-t	0,466667	0,3	0,416667	70	13,51351351	70-200cm	ntomophilic, anthers not expose	3	**WAT**
Hypericum	0,625	0,375	0	62,5	0	25-60cm	Entomophilic, anthers exposed	3	**AT**
Juncaceae	0,4	0,6	0	40	0	70-200cm	Anemophilic	3	**WAT**
Lamiaceae	0,259259	0,730769	0,125	26,92308	4,761904762	25-60cm	Entomophilic, anthers exposed	3	**WAT**
Limonium	0,4	0,5	0,333333	50	2,325581395	70-200cm	ntomophilic, anthers not expose	3	**WAT**
Medicago	0,222222	0,75	0,333333	25	6,451612903	25-60cm	ntomophilic, anthers not expose	3	**WAT**
Mentha-t	0,5	0,466667	0,111111	53,33333	3,125	25-60cm	ntomophilic, anthers not expose	3	**AT**
Myrtus	0,125	0,666667	0,833333	33,33333	11,36363636	300-3000cm	Entomophilic, anthers exposed	3	**WAT**
Phyllirea	0,333333	0,416667	0,5625	58,33333	25,71428571	300-3000cm	Anemophilic	3	**WAT**
Primulace	0,125	0,666667	0,833333	33,33333	11,36363636	7-20cm	ntomophilic, anthers not expose	3	**WAT**
Rhamnus	0,363636	0,6	0,2	40	2,702702703	70-200cm	Entomophilic, anthers exposed	3	**WAT**
Rubiaceae	0,241379	0,730769	0,3	26,92308	14,28571429	25-60cm	Entomophilic, anthers exposed	3	**WAT**
Sedum-t	0,444444	0,5	0,2	50	2,564102564	7-20cm	Entomophilic, anthers exposed	3	**WAT**
Sorbus-gr	0,25	0,727273	0,25	27,27273	2,777777778	300-3000cm	Entomophilic, anthers exposed	3	**WAT**
Tamarix	0,25	0,5	0,666667	50	4,444444444	300-3000cm	Entomophilic, anthers exposed	3	**WAT**
Teucrium	0,52	0,48	0	52	0	25-60cm	Entomophilic, anthers exposed	3	**AT**
Urticaceae	0,285714	0,428571	0,636364	57,14286	17,5	70-200cm	Anemophilic	3	**WAT**
Asteracea	0,2	0,454545	0,76	54,54545	52,77777778	25-60cm	ntomophilic, anthers not expose	4	**WAT**
Asteroidea	0,04	0,5	0,958333	50	51,11111111	25-60cm	ntomophilic, anthers not expose	4	**WAT**
Avena/Tri	0,28	0,461538	0,631579	53,84615	35,29411765	70-200cm	Anemophilic	4	**WAT**
Caryophyl	0,375	0,368421	0,52	63,15789	46,42857143	25-60cm	Entomophilic, anthers exposed	4	**WAT**
Cichorieae	0,358974	0,5	0,44	50	57,89473684	25-60cm	ntomophilic, anthers not expose	4	**WAT**
Euphorbia	0,419355	0,409091	0,409091	59,09091	36	25-60cm	Entomophilic, anthers exposed	4	**WAT**
Hordeum-	0,2	0,615385	0,705882	38,46154	35,29411765	300-3000cm	Anemophilic	4	**WAT**
Liliaceae u	0,487805	0,487179	0,090909	51,28205	25	70-200cm	Entomophilic, anthers exposed	4	**WAT**
Lotus-t	0,304348	0,588235	0,461538	41,17647	20	25-60cm	ntomophilic, anthers not expose	4	**WAT**
Ranuncula	0,5	0,263158	0,391304	73,68421	32,14285714	70-200cm	Entomophilic, anthers exposed	4	**AT**
Rosaceae	0,304348	0,533333	0,533333	46,66667	25	70-200cm	Entomophilic, anthers exposed	4	**WAT**
Scrophula	0,192308	0,642857	0,705882	35,71429	36,36363636	25-60cm	ntomophilic, anthers not expose	4	**WAT**
Senecio-t	0,393939	0,551724	0,235294	44,82759	22,22222222	25-60cm	ntomophilic, anthers not expose	4	**WAT**
Buxus	0,833333	0,166667	0	83,33333	0	300-3000cm	Entomophilic, anthers exposed	5	**SAT**
Ceratonia	0,714286	0,166667	0,166667	83,33333	2,43902439	300-3000cm	ntomophilic, anthers not expose	5	**SAT**
Cistaceae	0,73913	0,15	0,15	85	11,11111111	25-60cm	Entomophilic, anthers exposed	5	**SAT**
Erica	0,636364	0	0,363636	100	24,24242424	300-3000cm	ntomophilic, anthers not expose	5	**AT**
Globularia	1	0	0	100	0	25-60cm	Entomophilic, anthers exposed	5	**SAT**
Matricaria	0,428571	0	0,571429	100	19,51219512	25-60cm	ntomophilic, anthers not expose	5	**ORT**
Polygonu	0,083333	0	0,916667	100	23,91304348	70-200cm	Entomophilic, anthers exposed	5	**ORT**
Stachys	0,5	0	0,5	100	2,173913043	25-60cm	Entomophilic, anthers exposed	5	**AT**

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