


Seasonal patterns of pollen sedimentation in Lake Montcortès (Central Pyrenees) and potential applications to high-resolution paleoecology: a 2-year pilot study

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Abstract Lakes with varved sediments are especially well suited for paleoecological study, from annual to even seasonal resolution. The interpretative power of such high-resolution paleoenvironmental reconstructions relies on the availability of modern analogs with the same temporal resolution. We studied seasonal pollen sedimentation in varved Lake Montcortès, Central Pyrenees (Spain), as a modern analog for high-resolution reconstruction of Late Holocene vegetation and landscape dynamics. Seasonal samples were obtained from sediment traps that were submerged near the maximum water depth for a 2-year period (fall 2013 to fall 2015). Seasonal pollen sedimentation was compared with meteorological variables from a nearby

weather station. Bulk pollen sedimentation, dominated by *Pinus* (pine) and *Quercus* (oak), followed a clear seasonal pattern that peaked during the spring/summer, coinciding with maximum temperature and precipitation, minimum relative humidity and moderate winds from the SSE. Pollen sedimentation lags (PSL) were observed for most pollen types, as substantial amounts of pollen were found in the traps outside of their respective flowering seasons. Two pollen assemblages were clearly differentiated by their taxonomic composition, corresponding to spring/summer and fall/winter. This pattern is consistent with existing interpretation of the sediment varves, specifically, that varves are formed by two-layer couplets that represent the same seasonality as pollen. We concluded that pollen sedimentation in Lake Montcortès exhibits a strong seasonal signal in the quantity of pollen, the taxonomic composition of the pollen assemblages, and relationships between the pollen and meteorological variables. Thus, varved sediments provide a potentially powerful tool for paleoecological reconstruction at seasonal resolution. This method could be used not only to identify paleoenvironmental trends, but also to identify annual layers and therefore date sediments, even in the absence of evident sediment laminations. A satisfactory explanation of PSL will require further studies that examine internal lake dynamics and pollen production/dispersal patterns.

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Introduction

Varved lake sediments are useful not only for high-resolution paleoecological studies, but also for bridging the temporal gap between ecology and paleoecology. Indeed, the annual/seasonal domain is the ideal time frame to produce truly continuous long-term, high-resolution ecological time series, which successfully merge ecological and paleoecological data (Rull 2014). The combination of ecological data from varved lake sediments and modern observations may yield long, high-resolution ecological time series comparable to the continuous, long-term climate series obtained by linking paleoclimate data derived from tree rings and similar proxies, with instrumental climate measures at annual/seasonal resolution (Mann et al. 1999). Formation of annually laminated lake sediments requires a seasonal climate, and variable flux to the sediment of components from multiple autochthonous and allochthonous sources. The preservation of varves is favored in small, deep lakes with a permanent (meromictic) or seasonal (monomictic/dimictic), hypoxic or anoxic hypolimnion. Varves are especially well preserved in meromictic lakes with a clear chemical contrast between the epilimnion and hypolimnion, which differ in water density, thereby maintaining stratification and preventing water column circulation (O'Sullivan 1983; Ojala et al. 2012; Zolitschka et al. 2015). Lakes with varved sediments are more frequent in northern, temperate regions. In Europe, more than 60 lakes with annually laminated sediments have been studied, of which more than half have continuous varve chronologies for at least the last 100 years. Middle and late Holocene records are frequent, and in some cases varved sediments extend back to the late glacial and early Holocene (Ojala et al. 2012). These particular types of sediments have been used for a variety of paleoecological studies, most notably to calibrate radiometric (^{14}C , ^{210}Pb , ^{137}Cs , ^{32}Si) chronologies and to obtain high-resolution paleorecords of Earth's magnetic field, solar forcing, volcanic and seismic activity, climatic change, ecological shifts and human activities (Zolitschka et al. 2015).

In the Iberian Peninsula, four lakes with annually laminated sediments have been studied to date, a Pliocene paleolake (Muñoz et al. 2002) and three extant lakes with Holocene varves: La Cruz, with laminations that date from AD 1579 to the present

(Romero-Viana et al. 2008, 2011), Zóñar, with intermittent varved sections over the last 2500 years (Martín-Puertas et al. 2009) and Montcortès, the longest, continuous varved record retrieved thus far, representing the last ~1550 years (Corella et al. 2011, 2012) (Fig. 1). Preliminary paleoclimate, paleoecological and paleolimnological studies of the Montcortès record were conducted at multi-decadal to centennial resolution (Corella et al. 2011, 2012; Rull et al. 2011; Scussolini et al. 2011; Rull and Vegas-Vilarrúbia 2014, 2015). The only high-resolution study to date is an annual reconstruction of the extreme rainfall events that occurred since the mid-fourteenth century (Corella et al. 2014). The varve chronology of this lake (ca. AD 400 to the present) is ideal for studying the transition from the Medieval Warm Period (MWP) to the Little Ice Age (LIA) and ongoing Global Warming (GW), at annual resolution. A recent initiative was launched to increase the resolution of climatic and ecological reconstructions, which includes the study of present-day varve formation and preservation, so that they can be used as modern analogs of the past. Modern sedimentation was monitored using sediment traps in the lake to record seasonal variations in sediment flux and composition, a widely used method in studies of lakes with laminated sediments (Bloesch and Burns 1980; Mieszcankin 1997; Mieszcankin and Noryskiewicz 2000; Punning et al. 2003; Giesecke and Fontana 2008; St. Jacques et al. 2008; Hugué et al. 2012; Zolitschka et al. 2015).

In this paper, we present results of 2 years (fall 2013 to fall 2015) of pollen trapping, and investigate potential relationships between seasonal patterns of pollen sedimentation and relevant climate variables. The primary aim of this study was to identify seasonal pollen sedimentation patterns that would be useful for interpreting past records from the same lake. In this study, we concentrated our efforts on pollen sedimentation features; analysis of pollen–vegetation relationships, which is required to interpret past pollen records in terms of vegetation changes, is beyond the scope of this study, but will be addressed in the future. Pollen seasonality could be useful to resolve annual sediment layering, and therefore achieve high-resolution dating, even if physical sediment features are difficult to discern, e.g. when sublayers are absent, turbidites are present, or there are no laminations at all (Tippett 1964; Lotter 1986; St. Jacques et al. 2008). Sediment

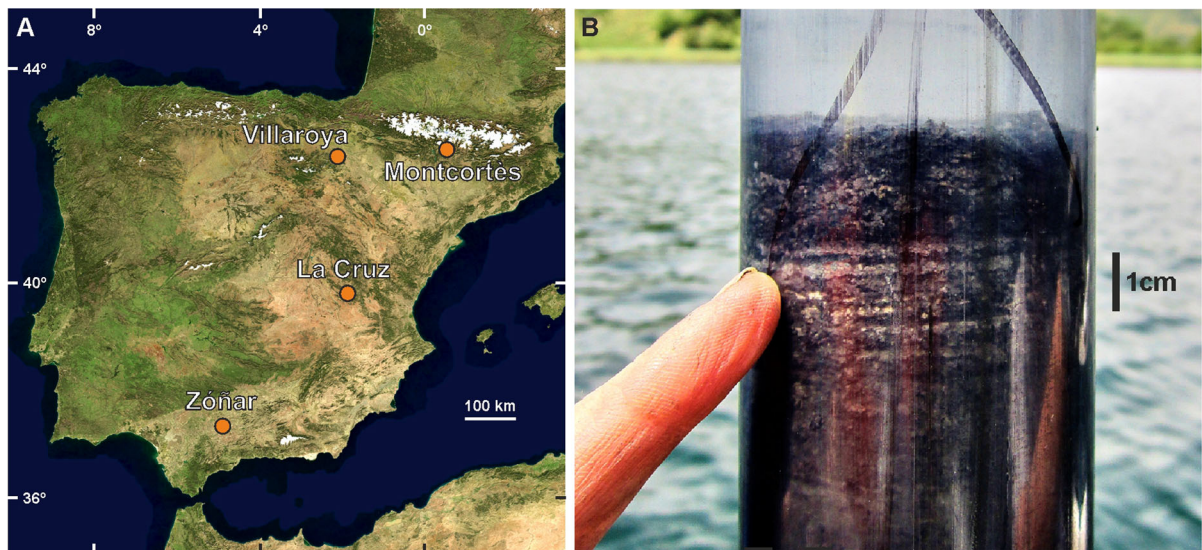


Fig. 1 **a** Map of the Iberian Peninsula showing lakes with varved sediments that have been studied to date. **b** Close-up of the top of a gravity sediment core retrieved from Lake

Montcortès in 2013 that shows the varves of the previous years, with a clear alternation of *white* and *brownish* layers (see text). (Color figure online)

trap studies have been used to monitor pollen sedimentation in many parts of Europe, across a wide array of environments and vegetation types, and have provided insights into the importance of intra-annual weather conditions and pollination patterns (Mieszcankin 1997; Mieszcankin and Noryskiewicz 2000; Punning et al. 2003; Giesecke and Fontana 2008; Giesecke et al. 2010; van der Knaap et al. 2010; Pidek et al. 2015). To our knowledge, however, this is the first study to use submerged pollen traps in varved lakes on the Iberian Peninsula. Previous studies of this type were carried out in non-varved, high-mountain Pyrenean lakes to examine plankton sedimentation and its relationship to climate seasonality (Pla-Rabes and Catalan 2011). Our aim is to maintain the traps in Lake Montcortès to study pollen sedimentation over the medium to long term.

Study site

Lake Montcortès is situated on the southern flank of the Central Pyrenees, in the Pallars Sobirà region of Catalonia (Spain), at 42°19'N, 0°59'E and 1027 m altitude, with a surface of 12.36 ha. The lake lies in karst terrain that is primarily characterized by Triassic limestones, marls and evaporites, and Oligocene carbonate conglomerates. Triassic ophyte outcrops primarily occur in the southern Quaternary lacustrine

sediments that surround present-day water bodies (Corella et al. 2011). The catchment is small, and the lake is fed primarily by groundwater, with intermittent small creeks and scattered springs. Most water is lost to evaporation and a small seasonal outlet at the north end of the lake. The lake is roughly kidney-shaped, with a diameter between 400 and 500 m and a maximum water depth of 30 m near the center (Corella et al. 2014) (Fig. 2). Climate data from a nearby weather station (La Pobla de Segur), which is situated ~9 km to the south (Fig. 2) at 513 m elevation, show the annual average air temperature of the area is 12.8 °C, which ranges from 2.9 °C in January to 23.2 °C in July. Total annual precipitation is 669 mm. February is the driest month (33.4 mm) and May is the wettest month (88.4 mm). Maximum and minimum temperatures recorded at this location were 41 and −20 °C, respectively. The maximum daily precipitation recorded was 138 mm.

The lake lies near the altitudinal boundary of the Sub-Montane belt, which is located in the Pyrenees at 800–1000 m elevation, depending on local features (Vigo and Ninot 1987). Four major forest formations occur in the lake region (Fig. 3): (1) Mediterranean sclerophyllous forests represented by *Quercus rotundifolia* woods; (2) Sub-Montane deciduous oak forests, which experience higher levels of precipitation and are dominated by *Quercus pubescens* and *Q.*

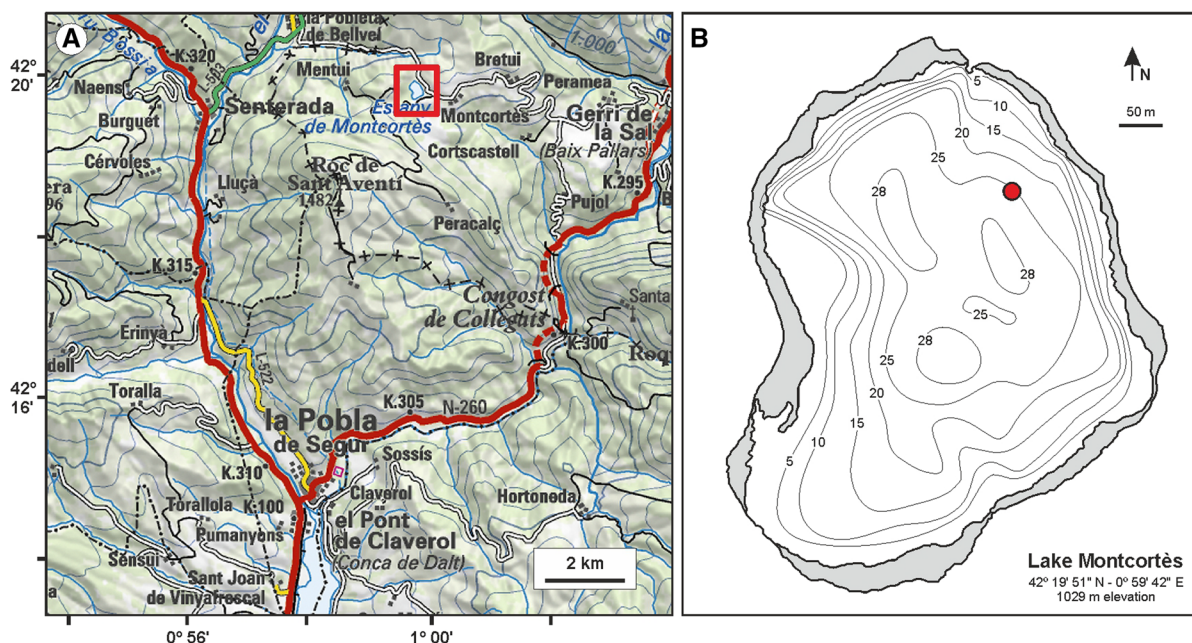


Fig. 2 **a** Map of the region around Lake Montcortès, indicating the location of the lake (red box) and the meteorological station used in this study (La Pobla de Segur). Base map:

Institut Cartogràfic I Geològic de Catalunya (www.icc.cat). **b** Bathymetry of Lake Montcortès with the location of sediment traps (red dot). (Color figure online)

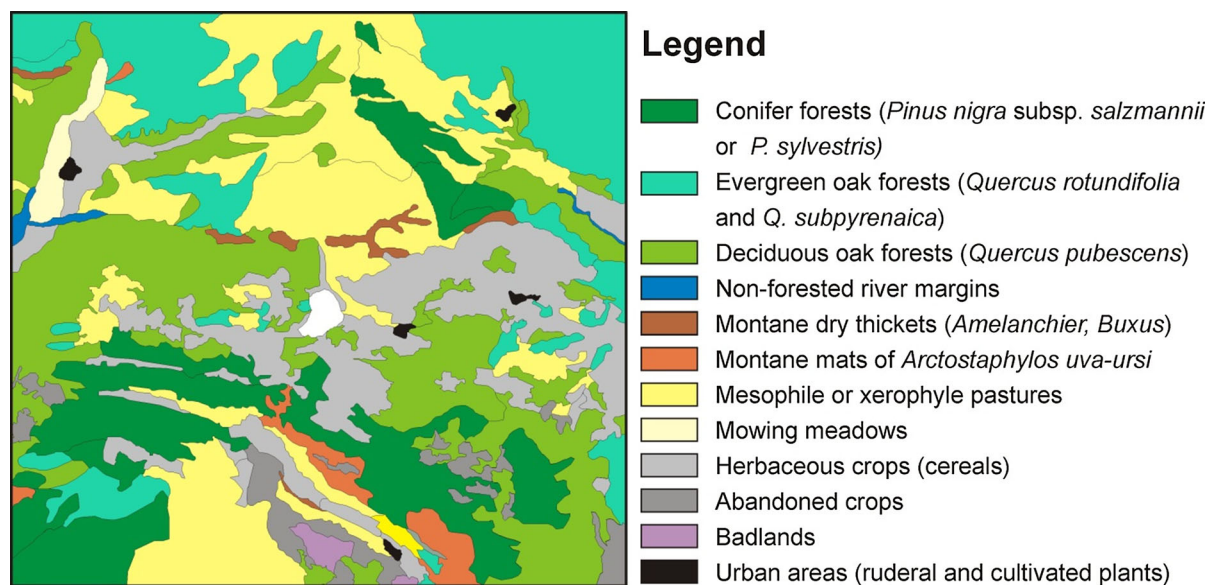


Fig. 3 Regional vegetation map of Montcortès using the CORINE system (CEC 1991). The lake is represented as a white area in the center. Modified from Ninot (2006) and Ferré and Carrillo (2007). (Color figure online)

subpyrenaica; (3) conifer forests of *Pinus nigra* subsp. *salzmannii*, which are usually secondary and replace the deciduous oak forests in the lower and southern regions, but are probably natural here (Bolòs et al.

2004); and (4) higher-elevation forests of *Pinus sylvestris*, which mark the transition between Sub-Montane and Montane belts. Portions of these conifer woods were likely planted. *Pinus* forests are

monospecific with a poorly developed understory, whereas oak woodlands are more taxonomically diverse.

The evergreen *Q. rotundifolia* communities have a well-developed understory with several shrubs (*Q. coccifera*, *Rhamnus* spp., *Prunus spinosa*, *Buxus sempervirens* and *Lonicera japonica*) and an herbaceous stratum with nemoral (shade-adapted) species such as *Rubia peregrina*, *Teucrium chamaedris*, *Asparagus acutifolius* and *Brachypodium retusum*. The *Q. pubescens*-*Q. subpyrenaica* deciduous forests include a variety of other trees in the arboreal stratum, notably *Pinus sylvestris*, *Fagus sylvatica*, *Tilia cordata* and some *Acer* species. The understory is dominated by *Buxus sempervirens*, *Coronilla emerus*, *Amelanchier ovalis*, *Colutea arborescens*, *Cytisophilum sessilifolium* and *Viburnum lantana*. In the herbaceous stratum, the most common species are *Primula veris*, *Hepatica nobilis*, *Brachypodium phoenicoides* and *Campanula persicifolia*. There are two main types of regional shrubland: one dominated by *Amelanchier ovalis*, *Buxus sempervirens* and *Rhamnus saxatilis*, and another dominated by *Arctostaphylos uva-ursi* with *Buxus sempervirens*. Herbaceous communities primarily consist of meadows and pastures of *Aphyllanthes monspelliensis* and *Arrhenatherum elatius*, herbaceous cereal crops (*Hordeum* sp., *Avena sativa*, *Triticum* sp., *Secale cereale*) and some forage plants (*Medicago sativa*), with several weeds (*Lolium rigidum*, *Papaver rhoeas*, *Polygonum aiculare*, *Bromus* sp.). Abandoned croplands, colonized by shrubs and ruderal species, and badlands devoid of vegetation or with scattered shrubs and herbs from other communities, also occur in some areas (Carreras et al. 2005–2006) (Fig. 2).

The local vegetation around the lake is closely tied to microclimate conditions and is fairly diverse in comparison to surrounding regional patterns. A recent detailed study by Mercadé et al. (2013) recognized 534 species of vascular plants distributed across 52 vegetation units of the European CORINE biotope classification (Vigo et al. 2005–2008). Aquatic and semi-aquatic habitats are represented by submerged vegetation, sometimes with floating leaves (*Potamogeton*, *Myriophyllum*, *Chara*, *Utricularia*, *Ranunculus*), and a macrophyte fringe surrounding the lake that is dominated by the grass *Phragmites*, with *Cladium* and *Typha*. Hygrophilous vegetation grows on wet or inundated soils. The most common

vegetation consists of sedges, such as *Carex*, *Eleocharis* and *Scirpus*. *Juncus* species, together with *Cyperus* and *Plantago*, dominate the plant communities on temporarily flooded soils. Several types of meadows and pastures around the lake are characterized by *Arrhenatherum* (hay meadows), *Trifolium* (calcicolous grasslands), *Filipendula* (mesophilous grasslands), *Festuca* and *Aphyllanthes* (xerophilous grasslands) and *Poa* (dwarf grasslands). Shrubby vegetation is primarily represented by communities dominated by *Buxus*, *Genista* and *Thymus*. Forest formations around the lake are dominated by various *Quercus* species and small stands of *Fraxinus*, *Populus* and *Salix*. Anthropogenic habitats consist of intensive pastures, crop fields (*Hordeum*, *Medicago*, *Chenopodium*), fruit-tree orchards (*Malus*, *Prunus*, *Pyrus*) and ruderal communities (*Arctium*, *Artemisia*, *Galium*, *Pastinaca*, *Urtica*, *Melilotus*, *Polygonum*). A very detailed description of the vegetation around the lake can be found in Mercadé et al. (2013).

The region is rather densely populated and the lake has historically been an important water source for the numerous surrounding villages and farmhouses. An artificial pond was recently built to use the water from the lake for fire-fighting purposes. Cultivation (wheat, oat, barely, olives, rye, hemp and legumes) and livestock husbandry (cattle and sheep) have also increased in the area during the last millennium and possibly longer (Rull and Vegas-Vilarrúbia 2015). Currently, cereal and alfalfa fields, intermingled with pastures for cattle and horses, and hay meadows, are common and heavily exploited. The lake and its catchment area are part of the European Natura 2000 network for the protection of species and habitats (http://ec.europa.eu/environment/nature/natura2000/index_en.htm).

In Lake Montcortès, varved sediments extend down to a depth of 543 cm, which encompass the last 1548 years. Varves are thin (1.16 mm average thickness) and are composed of two (three) layers, intermingled with occasional turbidites (6.8 mm average thickness). The basic varve unit is a biogenic couplet of two layers, a white calcite layer and a brownish organic layer (Fig. 1). A third, grayish detrital layer may be present between the calcite and organic layers. According to Corella et al. (2012), the white layer corresponds to spring/summer and is characterized by rhombohedral calcite crystals, whereas sediments of the brownish layer correspond to fall/winter and are

primarily composed of amorphous organic matter, diatoms, detrital carbonate and quartz grains within a clayey matrix. The grayish detrital layer is deposited during phases of increased runoff and consists of irregularly shaped detrital calcite, quartz and feldspar grains, terrestrial plant remains and clay minerals (Corella et al. 2012). Detailed limnological study of the lake dynamics in relation to varve formation and preservation is in progress.

Materials and methods

A set of sediment traps was suspended from a floating platform located above the deepest part of the lake, where the sediment cores were collected for paleoecological study. Each trap consisted of an opaque cylindrical plastic tube (8.5 cm diameter and 80 cm long), with the top open and the base sealed, and was suspended by a plastic line at a water depth of 20 m, i.e. ~5 m above the bottom. The content of the pollen traps was collected quarterly at the end of each season: March (winter), June (spring), September (summer) and December (fall). Sediments were allowed to settle in the laboratory for a minimum of 48 h. The supernatant was decanted and filtered through a glass-fiber filter and was added to the sediment to minimize losses. A tablet of exotic *Lycopodium* spores (batch no. 1031, 20,848 spores/tablet, on average) was added to the sediment prior to chemical processing, which included acid digestion (HCl and HF), acetolysis and storage in glycerine (Bennett and Willis 2002). Microscope slides were prepared with glycerine, without sealing. Pollen identification was made following previous, lower-resolution studies (Rull and Vegas-Vilarrúbia 2014, 2015; Rull et al. 2011). Pollen was counted until a minimum of 300 pollen grains per sample had been enumerated—excluding *Pinus* and *Quercus*, which were super-abundant (~40–90% of the total counts)—and the diversity of the sample was saturated (Rull 1987). Total pollen counts averaged 729 (range 305–1118) and exotic *Lycopodium* counts averaged 70 (range 23–171). Taxonomic classification of plants and the grouping of pollen into vegetation types followed Mercadé et al. (2013). Diagram plotting and statistical analyses were performed with Psimpoll 2.7 and MVSP 3.22, respectively.

The meteorological variables used in this study were obtained from the nearest weather station, La

Pobla de Segur, which is located ~9 km to the south (Fig. 2) at 513 m elevation. The meteorological variables considered were average, maximum and minimum temperature (T_m , T_x , T_n , respectively, in °C); average, maximum and minimum relative humidity (H_m , H_x , H_n , respectively, in %); average, maximum and minimum pressure (P_m , P_x , P_n , respectively, in hPa); total precipitation (PPT; in mm); wind velocity (W ; in m s^{-1}) and wind direction (W_d ; in °) at 10 m above the ground. Seasonal values for these variables were obtained by averaging daily values for each season, using raw meteorological measures from the reference station.

Cluster analysis was used to identify seasonal pollen assemblages. In this case, we used the Gower similarity coefficient and the centroid clustering method, which have proven to be suitable for similar purposes using pollen data (Rull 2001, 2003). Spearman rank correlation coefficient was used to study relationships between pollen and meteorological variables. This non-parametric correlation method is recommended when the requirements for using the parametric Pearson product-moment correlation coefficient are not met (Siegel and Castellan 1988). In our case, we used the Spearman index because of the low sample size ($n = 9$). Canonical correspondence analysis (CCA) was used to define new multi-dimensional variables that account for maximum variance in the dataset, and to graphically display pollen and meteorological data simultaneously in the space of these new variables (Jongman et al. 1995). All statistical analyses were carried out on percentage data using MVSP version 3.22.

Results

Total pollen sedimentation displays a clear seasonal pattern, with maxima during the spring/summer and minima during the fall and winter (Fig. 4). The 2 years studied had similar patterns except for the dramatic maximum recorded in the spring of 2015, with values more than three times higher than in the spring of 2014. The major components of the pollen assemblages were *Pinus* and *Quercus*, with their percentages oscillating between 15 and 35%, respectively, throughout the year, except during the spring, which is the flowering season of both taxa, when *Pinus* increased to 50–65%. In the case of *Quercus*, the

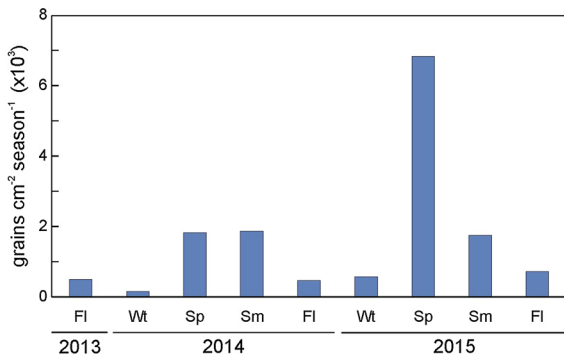


Fig. 4 Seasonal trends of total pollen sedimentation expressed as influx units (number of grains per cm² per season). *Sp* spring, *Sm* summer, *Fl* fall, *Wt* winter. (Color figure online)

seasonal pattern is less apparent, and the spring percentages were below 30% (Fig. 5). In both cases, the supply of pollen to the sediment traps was continuous throughout the year, although parent plants were no longer in bloom. This phenomenon, called pollen sedimentation lag (PSL), is better assessed using influx values (Fig. 6). A large fraction of *Pinus* and *Quercus* pollen settled onto the sediments during the spring, but a significant portion of pollen settled later, particularly between summer and winter. This negative exponential trend occurred in both years, with lower decreasing rates in 2014 than in 2015. In both cases, however, summer to winter values were very similar, indicating that, no matter the intensity of the spring peak, the background signal for the rest of the year was almost the same.

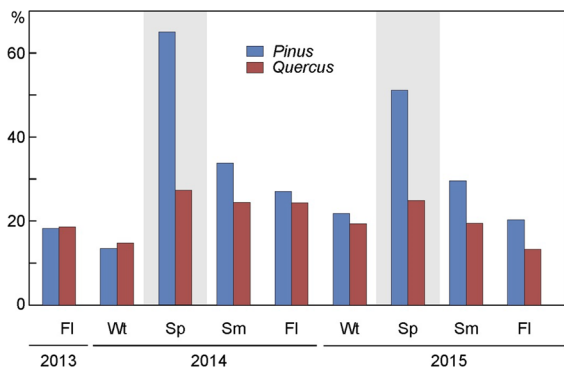


Fig. 5 Pollen percentages of *Pinus* and *Quercus*, the two major components of the pollen assemblages, throughout the year. Grey bands represent the flowering season of *Pinus* and *Quercus* species present in the Montcortès region, according to Bolòs et al. (2000). *Sp* spring, *Sm* summer, *Fl* fall, *Wt* winter. (Color figure online)

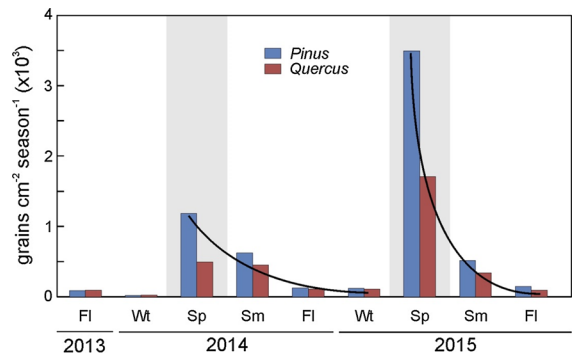


Fig. 6 Pollen influx values for *Pinus* and *Quercus* during the study period. *Sp* spring, *Sm* summer, *Fl* fall, *Wt* winter. (Color figure online)

The most important pollen taxa, in terms of abundance and seasonality (Fig. 7) illustrate that trees tend to bloom before (winter/spring) herbs (spring/fall), a trend that is also reflected in patterns of pollen sedimentation. In general, percentage pollen peaks coincide with the flowering season of each taxon, but almost all plant species exhibited PSL, expressed by the presence of pollen outside the flowering season. Taxa with a lower PSL, that is, with pollen sedimentation patterns that are very similar to flowering patterns, such as *Corylus*, *Fraxinus*, and *Artemisia*, are all represented by a single species in the lake (Mercadé et al. 2013). The genus *Olea* had the highest PSL. On the other hand, *Plantago* and *Chenopodium* had an intermediate PSL. Possible presence of several species from the adjacent flora with similar pollen morphology, but with different flowering seasons, might also explain these patterns. In families such as Poaceae and Cyperaceae, which include many genera and species, this is certainly the case. In general, aside from *Pinus* and *Quercus*, the most abundant pollen type belongs to *Cannabis*, especially during the fall, when it reaches values of 40% or more. Cluster analysis yielded two groups that represent two distinct pollen assemblages, the spring/summer assemblage and the fall/winter assemblage (Fig. 8). The only exception was the sample from fall 2014, which was more similar to the spring/summer samples.

Regarding the relationship between pollen and meteorological variables, a preliminary visual inspection showed that the influx of total pollen and of pollen from major types (i.e. *Pinus* and *Quercus*) roughly matched seasonal trends in temperature and precipitation (Fig. 9). Pollen maxima occurred during

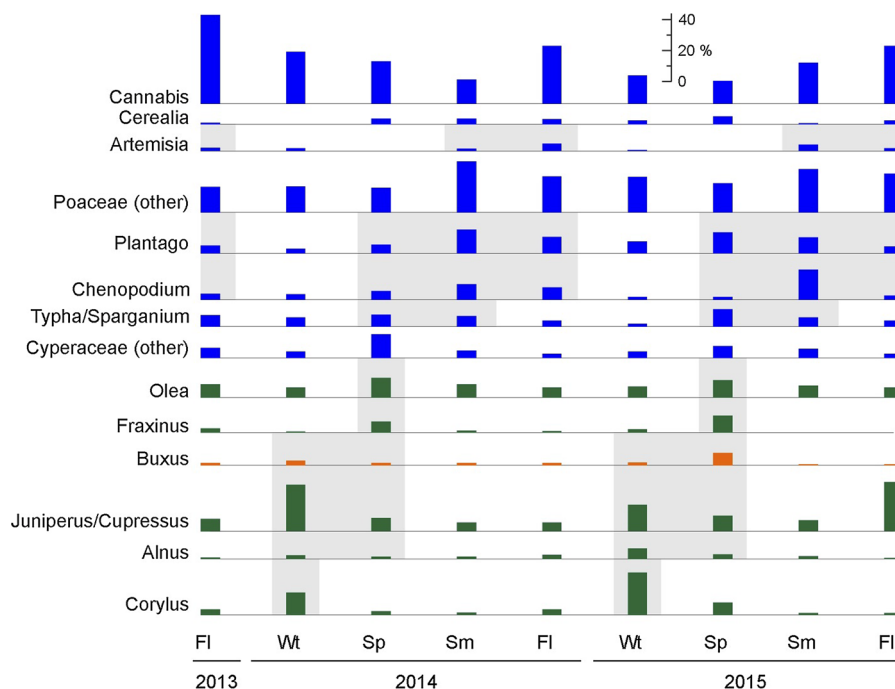


Fig. 7 Percentage diagram of the most relevant pollen taxa during the study period. Percentages were calculated, excluding the super-abundant *Pinus* and *Quercus* (Fig. 5). Taxa are ordered by their respective flowering seasons (grey bands) (Bolòs et al. 2000), from bottom to top and from left to right. The flowering season of all species of the different genera present in

the Montcortès region (Mercadé et al. 2013) was considered. Cultivated plants, such as *Cerealia* and *Cannabis*, and families including many genera (*Poaceae*, *Cyperaceae*) are located based on their pollen patterns because of the difficulty of establishing a definite flowering season. *Sp* spring, *Sm* summer, *FI* fall, *Wt* winter. (Color figure online)

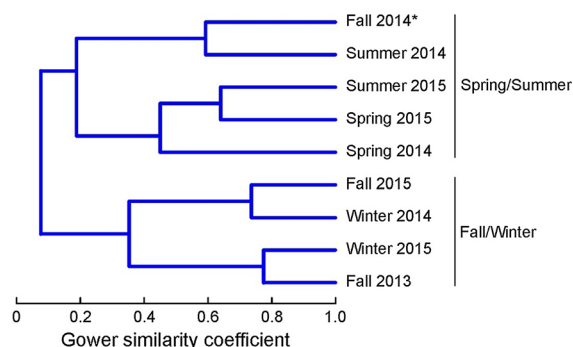


Fig. 8 Cluster analysis using the Gower (1971) similarity coefficient and the centroid clustering method. The asterisk indicates the only sample that does not follow the spring/summer versus fall/winter pattern. (Color figure online)

the flowering season of the involved taxa (spring), one season before temperature and precipitation maxima (summer). The relationship between pollen and relative humidity was inverse. Moreover, maxima of pollen influx coincided with moderate wind velocities

with a predominant SSE ($\sim 150^\circ$) direction, whereas pollen minima coincided with slower winds with a WSW ($\sim 250^\circ$) direction.

Individually, a number of pollen taxa exhibited significant correlations with meteorological variables, whereas others did not (Table 1). Some of the relationships are worthy of mention. The variables with greatest significant correlations were wind velocity, wind direction and relative humidity, whereas pressure did not show a significant correlation. Pollen taxa that lacked significant correlations with meteorological variables were *Alnus*, *Artemisia*, *Buxus*, *Cerealia*, *Corylus*, *Plantago* and *Poaceae* (others). *Olea*, *Pinus*, *Quercus* and *Cyperaceae* (others) were negatively associated with relative humidity and wind direction and positively correlated with wind velocity. *Chenopodium* and *Juniperus/Cupressus* were correlated with temperature (together with *Pinus*) and total precipitation. *Cannabis* was correlated only with wind velocity.

Fig. 9 Relationships between pollen influx and the most relevant meteorological variables. Average temperature (T_m), relative humidity (H_m) and wind velocity (W) are represented by *lines*. Total precipitation (PPT) is represented by *bars*. The predominant direction of the wind (W_d) is shown in *circles*. (Color figure online)

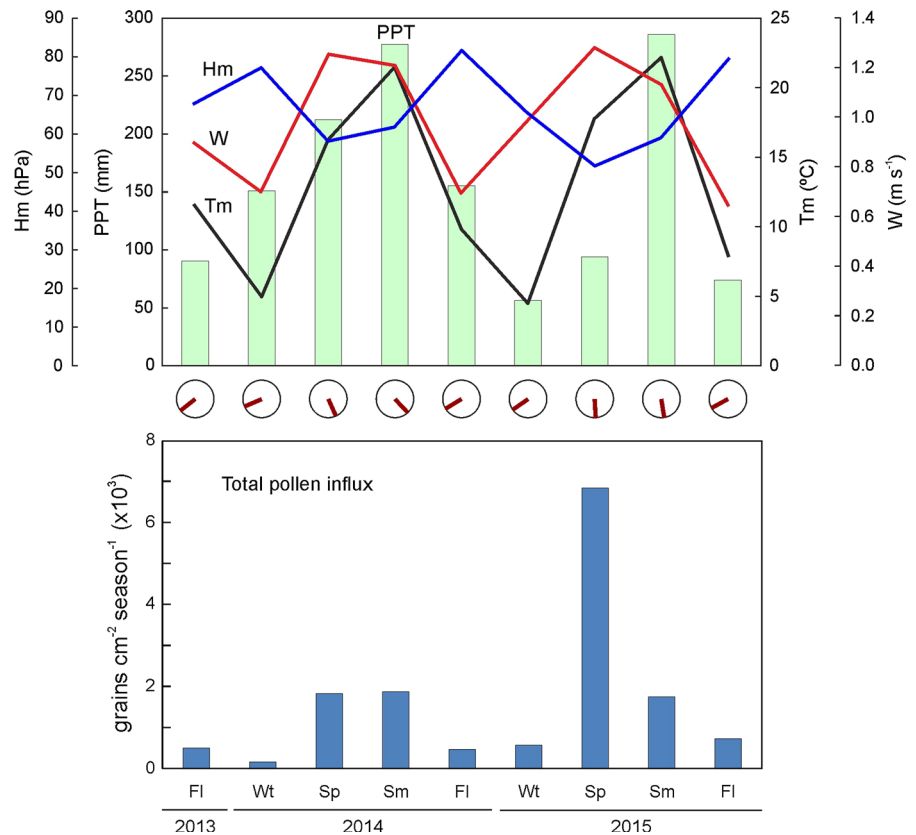


Table 1 Spearman-rank correlation coefficients between the most relevant pollen taxa and meteorological variables

See “[Materials and methods](#)” section for abbreviations
 T_m , average temperature;
 H_m , average relative humidity; P_m , average pressure; PPT, total precipitation; W , average wind velocity; W_d , predominant wind direction
 Significant correlations (* $\alpha = 0.05$; ** $\alpha = 0.01$) are in bold

Pollen taxa	T_m	H_m	P_m	PPT	W	W_d
<i>Alnus</i>	-0.200	-0.167	-0.217	-0.100	0.250	0.117
<i>Artemisia</i>	-0.008	0.661	0.025	0.226	-0.661	0.368
<i>Buxus</i>	-0.150	-0.383	-0.417	-0.100	0.500	-0.033
<i>Cannabis</i>	-0.383	0.750	0.150	-0.200	-0.767*	0.533
Cerealia	0.300	-0.500	0.000	0.067	0.617	-0.533
<i>Chenopodium</i>	0.683*	-0.033	-0.417	0.900**	0.083	-0.500
<i>Corylus</i>	-0.533	-0.033	-0.167	-0.467	0.117	0.317
Cyperaceae (others)	0.567	-0.883**	-0.017	0.233	0.850**	-0.717*
<i>Fraxinus</i>	0.117	-0.577	0.017	-0.176	0.678*	-0.427
<i>Juniperus/Cupressus</i>	-0.667*	0.150	0.267	-0.700*	-0.300	0.650
<i>Olea</i>	0.650	-0.850**	0.050	0.267	0.867**	-0.867**
<i>Pinus</i>	0.667*	-0.750*	-0.200	0.517	0.800**	-0.800**
<i>Plantago</i>	0.617	-0.433	-0.050	0.433	0.567	-0.650
Poaceae (others)	0.317	0.150	0.133	0.300	-0.150	-0.150
<i>Quercus</i>	0.600	-0.700*	-0.367	0.533	0.817**	-0.767*
<i>Typha/Sparganium</i>	0.567	-0.650	-0.183	0.333	0.700*	-0.533

A synthetic analysis was conducted using Canonical Correspondence Analysis (CCA). Figure 10 shows the scatter plot with the first two axes, which

accounted for 70.74% of the total variance. The strongest gradient corresponds to axis 1 (56.80% of the total variance), which was highly correlated with

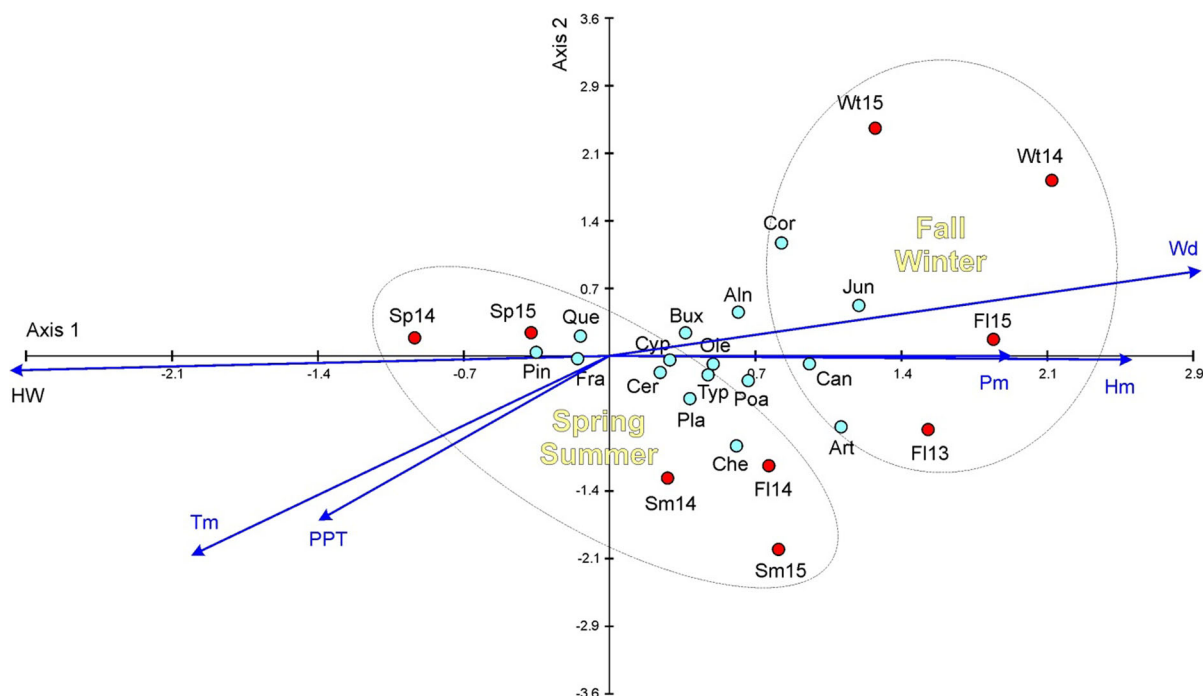


Fig. 10 CCA biplot using the scores of the first two axes accounting for 70.74% of the variance. Samples are represented by red dots and pollen taxa are represented by blue dots. (Color figure online)

relative humidity and pressure with its positive values, and with wind velocity with its negative values. Along this gradient, samples were ordered according to a seasonal gradient from spring (left) to winter (right), with summer and fall occupying intermediate positions. Pollen taxa were also ordered according to the same gradient: *Pinus*, *Quercus* and *Fraxinus* were close to spring samples and *Juniperus/Cupressus*, *Corylus*, *Cannabis* and *Artemisia* were located in the fall/winter cluster. The remaining taxa occupied an intermediate position. The spring group was highly correlated with temperature, precipitation and wind velocity. The fall group was also highly correlated with wind direction, which in this season comes from the WSW. This wind direction contrasts with the winds during the spring/summer, which blow from the SSE. Taxa most associated with WSW winds were *Juniperus* and *Cannabis*, which are typically fall taxa.

Discussion

In general, our results show a distinct seasonal pattern in pollen sedimentation that is reflected in

both total influx and taxonomic composition. In the spring/summer assemblage, *Pinus* had values of 50–65% of the total counts and *Quercus* had approximately 25%, whereas in the fall/winter, *Pinus* was below 30% and *Quercus* was lower than 20% (Fig. 5). Regarding the other plant species, the most significant differences were in *Plantago*, *Chenopodium*, *Typha/Sparganium*, *Cyperaceae*, *Fraxinus* and *Juniperus/Cupressus*, which were more abundant in the spring/summer assemblage, and *Cannabis* and *Corylus*, which were more abundant in the fall/winter assemblage (Table 2). This seasonal pattern appears to coincide with the varved pattern of the sediments, which are formed by two-layered couplets that correspond to the same seasons, as interpreted by Corella et al. (2012). Such a correspondence should be demonstrated by analyzing individual sediment layers, which may show that the spring/summer pollen assemblage coincides with the white layer and that the fall/winter assemblage coincides with the dark layer. Physico-chemical analyses of the bulk material collected in the other traps used in this study are in progress and can provide additional evidence for this correlation

Table 2 Composition of the pollen assemblages obtained in the cluster analysis (Fig. 7), using the average percentages of major pollen types (Fig. 6), excluding *Pinus* and *Quercus*

Pollen taxa	Spring/summer	Fall/winter
<i>Cannabis</i>	16.02	27.95
Cerealia	2.36	1.05
<i>Artemisia</i>	1.06	1.19
Poaceae	18.39	15.53
<i>Plantago</i>	8.66	3.92
<i>Chenopodium</i>	7.08	2.31
<i>Typha/Sparganium</i>	6.03	3.64
Cyperaceae	6.48	3.38
<i>Olea</i>	7.67	5.58
<i>Fraxinus</i>	3.57	0.95
<i>Buxus</i>	2.14	1.27
<i>Juniperus/Cupressus</i>	5.83	1.65
<i>Alnus</i>	1.44	2.00
<i>Corylus</i>	2.39	8.82

between pollen seasonality and the formation of white and dark seasonal sediment layers.

Specific aspects of the pollen sedimentation require further discussion. For example, there is a lag in pollen sedimentation (PSL), i.e. between production and deposition, throughout the year. The cause of this lag might be manifold. First, such lags may be explained by water dynamics in the lake (Punning et al. 2003). Second, PSL may arise because of re-suspension of sediments from the uppermost layers (Mieszcankin 1997; Mieszcankin and Noryskiewicz 2000). Third, PSL may stem from the fact that pollen deposited on catchment soils during the flowering season can be washed into the lake for several months (St. Jacques et al. 2008). The first potential explanation (internal water dynamics) is currently under study. This additional study should shed some light on the potential mechanics of PSL via thermal and other density stratification. Resuspension can be identified and measured using sediment traps at different depths, in combination with aerobiological samplers at the lake surface (Bloesch 1994; Mieszcankin and Noryskiewicz 2000; Giesecke and Fontana 2008). The same combination of techniques, along with aerobiological samplers distributed across the catchment soils, might be useful for distinguishing the different processes that participate in pollen dispersal and could provide

insights into the potential role of pollen washing into the lake.

The similarity in the sedimentation patterns between *Pinus* and *Quercus* pollen is also striking because the pollen grains of these two genera are different morphologically. *Pinus* pollen is inaperturate and bears two large empty sacchi, which confer unique “buoyancy” to this pollen in air. On the other hand, *Quercus* pollen is tricolporate/tricolporoidate (Erdtman 1952) and has no distinct morphological traits or ornamentation. In spite of these differences with respect to air suspension, once the pollen is in the waters of Lake Montcortès, the sedimentation of the pollen of *Pinus* and *Quercus* was quite similar, even during summer when the lake thermal stratification is very stable. This finding could suggest that internal lake dynamics are not as important for pollen sedimentation as resuspension or catchment runoff. Aerobiological studies, however, are needed to assess this hypothesis.

Pollen of *Cannabis* (hemp) was the most abundant during the fall; however, the parent plant was not reported in an intensive floristic study of the lake catchment (Mercadé et al. 2013), or in regional surveys (Carreras et al. 2005–2006). The pollen of *Cannabis* is similar to *Humulus*; however, the criteria that distinguish them in the Montcortès sediments have already been established (Rull and Vegas-Vilarrúbia 2014). *Cannabis* is a cultivated plant whose pollen has been present and fairly abundant around Montcortès for the last 1200 years. The exact source of the pollen, however, has been impossible to locate (Rull and Vegas-Vilarrúbia 2015; Rull et al. 2011). This plant is known to have been cultivated in the adjacent lowlands (Gerri de la Sal, La Pobla de Segur and La Pobleta de Bellveí; Fig. 2) during the nineteenth century. In addition, Lake Montcortès may have been used for hemp retting, especially between the fifteenth and eighteenth centuries, but no historical documents have been found to support this hypothesis. Currently, the source for the pollen of *Cannabis* is unknown. More studies will be required to identify the source of *Cannabis* pollen. The same is true for *Humulus*, which is very scarce in the wild and has only been observed near Gerri de la Sal (A. Mercadé, pers. commun. 28 April 2016).

The overall pollen influx patterns are consistent with the fact that, in anemophilous species, high temperature, low humidity and moderate winds favor

passive flower dehydration, thereby facilitating the opening and release of pollen from the anthers (Helbig et al. 2004). These meteorological variables, however, do not provide a clear explanation for the difference in intensity of the spring pollen peaks of 2014 and 2015. Although temperature and wind velocity show almost identical patterns across 2014 and 2015, precipitation and relative humidity do not. Indeed, precipitation was significantly higher before the spring of 2014 than in 2015, whereas relative humidity was lower in the spring of 2015. These differences might have affected the release of pollen, but this hypothesis remains speculative until more local aerobiological studies are conducted. Slight differences in the location of the pollen sources cannot be dismissed, as there was a slight variation in the direction of the predominant winds between the springs of 2014 and 2015.

Individual correlations also deserve further comment, especially in the case of relative humidity, wind direction and velocity, which primarily affected *Olea*, *Pinus* and *Quercus*. Cyperaceae will not be discussed here as it may contain several species with different flowering periods and pollen dispersion/sedimentation features. *Olea* is a lowland taxon that is not common around Montcortès, which is located near the boundary of lowland and montane biomes (Rull et al. 2011; Mercadé et al. 2013). In a previous study in the Central Pyrenees, Cañellas-Boltà et al. (2009) found that *Olea* pollen occurred consistently from the lowlands to the alpine zone above 2500 m elevation. The authors attributed this distribution of pollen to the effect of upward winds. This explanation is supported by our results from Montcortès, which show that dry and windy conditions favor the sedimentation of this pollen type in lake sediments. In addition, the significant negative correlation with wind direction, expressed in degrees, indicates that the source for this pollen should be from the SW ($\sim 225^\circ$), that is, in the southern lowlands, where the species grows. The same is true for the pollen of *Pinus* and *Quercus* forests, which are better represented in the southern part of the area under study (Fig. 2).

The CCA plot (Fig. 10) yielded the same groups as the cluster analysis, which strengthened the seasonal character of the pollen succession throughout the year and showed the clear separation of the spring/summer and the fall/winter assemblages. This analysis also provided the more relevant meteorological variables linked to seasonal pollen sedimentation as a whole.

The main environmental gradient resulted from the windy, rainy and warmer character of the spring/summer seasons, with winds from the SSE, and the high pressure and high relative humidity of the fall/winter seasons, with winds from the WSW. This gradient was strongly associated with the abundance of the main pollen taxa that are characteristic of each seasonal assemblage.

Conclusions

General patterns of pollen sedimentation in Lake Montcortès during the two study years were consistent with there being a strong seasonal signal. This signal permitted the spring/summer and fall/winter assemblages to be distinguished. These seasonal differences were expressed in terms of the amount of pollen sedimentation and also in the taxonomic composition of the pollen assemblages. In addition, the main meteorological variables that influence these seasonal features of pollen were identified. Pollen seasonality coincided with the same seasonal patterns previously identified in sedimentological (varve) studies. Therefore, seasonal pollen patterns described in this study appear to adhere to a pollen-varve model that is constrained by meteorology, and which can be extrapolated down-core to be used in high-resolution paleoecological investigations. This finding needs to be corroborated with a detailed palynological analysis of the assumed seasonal sediment layers and with physico-chemical analyses of the bulk content of sediment traps. By analogy, differences in the pollen content of past varves could be explained in terms of meteorological variability, which makes pollen a potentially powerful paleoenvironmental proxy in this particular lake. In addition, pollen analysis of down-core sediments can be used to identify intra-annual seasonal patterns and to date the sediments, even in the absence of varves or at depths where the varve record has been partially disturbed. The seasonal pollen model obtained here can be applied, at least, to the last 1200 years, as all pollen types have been present with reasonably similar abundances (Rull et al. 2011). The seasonal patterns described here are sufficiently well established for use in Lake Montcortès paleoenvironmental studies. Pollen analysis of trap sediments should continue in efforts to account for potential inter-annual variability. As a general observation, the

trends and relationships established in this paper should be considered empirical, with some causal relationships yet to be demonstrated. The present study can account for processes that occur after pollen has reached the lake surface. Therefore, our study can account only for factors such as the flowering season of each pollen type and internal lake processes involved in pollen sedimentation. Other factors such as pollen production, dispersal, diagenesis or other post-depositional phenomena should be addressed with further aerobiological and sedimentological studies. In summary, our data suggest that phenological traits (i.e. flowering season) of the plant taxa involved exert a dominant control on the seasonal patterns of pollen sedimentation and inter-annual meteorological variations cause minor quantitative shifts. Sedimentological processes linked to internal lake dynamics, mainly the mixing–stratification regime and sediment reworking/resuspension, may, however, modify the original expression of biological and meteorological seasonality, and should be taken into account to explain the final pollen sedimentation patterns.

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