Vegetation History and Archaeobotany (2025) 34:53–70
https://doi.org/10.1007/s00334-024-01001-y

ORIGINAL ARTICLE

Modern vegetation and its pollen spectra in the Cantabrian mountains, northern Iberian Peninsula, compared with fossil pollen records

Marc Sánchez-Morales[1] · Ramon Pérez-Obiol[2] · Virginia Carracedo[3] · Jordi Nadal[1] · Ana Ejarque[4] · Albert Pèlachs[1]

Received: 21 October 2023 / Accepted: 9 March 2024 / Published online: 7 June 2024
© The Author(s) 2024

Abstract

The study of the pollen rain from modern vegetation has greatly improved the interpretation of pollen diagrams and our understanding of ancient plant communities. In this study, 76 pollen samples were studied from various vegetation types in Cantabria, northern Iberian Peninsula. The pollen signals of the main taxa were compared to their estimated spatial coverage at various scales (100 m, 1 km and 5 km from the sampling point) using vegetation maps. Additionally, we investigated whether there were similar modern vegetation types to past ones interpreted from the pollen record from La Molina peatland, Cantabria. Our results revealed that the pollen rain from the laurel-evergreen oak community (Lauro nobilis-Quercetum ilicis) was mainly evergreen *Quercus* pollen (59–77%), with *Laurus nobilis* being very under-represented. The representation of *Fagus sylvatica* pollen varied according to its local presence. In the modern vegetation, two sample sites with over 95% cover of *Fagus* within a 100 m radius had a pollen content below 3%. Pine demonstrated high dispersal capability, with pollen values exceeding 20% even in samples with little or no pine cover within 1 and 5 km. Poaceae had limited representation, with up to 60% even in samples lacking tree cover within a 5 km radius. Mixed deciduous woodlands were dominated by deciduous *Quercus* and *Corylus*, and their resemblance to woods in the northern Iberian Peninsula during the mid Holocene is discussed. While a principal component analysis linked modern vegetation to the most recent part of the pollen diagram from La Molina, no clear parallels emerged between present-day and ancient vegetation. Finally, it was found that there were no differences in pollen concentrations trapped by acrocarpous and pleurocarpous mosses.

Keywords Pollen rain measurement · Mosses · Fossil pollen record · Landscape · Northern Iberian Peninsula

Introduction

The analysis of pollen records has become the main technique for studying the changes in vegetation and landscapes through time. The results are often presented in the form of pollen diagrams, in which the pollen percentages of each taxon vary through the sequences studied. However, interpreting these percentages can sometimes be complex because the amount of pollen that accumulates in sedimentary deposits and is reflected in the pollen diagrams depends on various factors, and if these are not considered, it can lead to the over- or under-representation of certain taxa.

For example, pollen production varies significantly between taxa (Piotrowska 2008). Anemophilous plants that disperse pollen by wind such as *Pinus* and *Abies* produce the most pollen and are generally the best represented in pollen spectra (Bresinsky et al. 2013). On the other hand,

Communicated by W. Tinner.

✉ Marc Sánchez-Morales
marc.sanchez.morales@uab.cat

[1] Department of Geography, Edifici B, Facultat de Filosofia Lletres, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, 08193 Bellaterra, Spain

[2] Department of Animal Biology, Plant Biology, and Ecology, Universitat Autònoma de Barcelona, Cerdanyola del Vallès, 08193 Bellaterra, Spain

[3] Department of Geography, Urban Studies and Land Planning, Avenida de Los Castros s/n, Universidad de Cantabria, 39005 Santander, Spain

[4] ISEM, CNRS, IRD, University of Montpellier, Montpellier, France

animals, particularly insects, disperse the pollen of many plants (zoophily). The pollen is produced in smaller quantities and it is not adapted for airborne transport, but rather for attachment to animals. Therefore, this group is much less represented in pollen records, for example Fabaceae, Rosaceae, Liliaceae, *Salix, Eucalyptus* and *Laurus* (Bresinsky et al. 2013; Lara-Ruiz 2019). Finally, a small number of angiosperms disperse pollen via water (hydrophily). These are mostly aquatic plants such as *Potamogeton* and may be represented in the pollen spectra if they are present in the bodies of water where the sedimentary deposits are found. However, they are generally not indicative of the vegetation of the regional landscape (Bresinsky et al. 2013).

In addition, pollen transport is also influenced by physical barriers, such as plant community structure and the geomorphology of the region. Some authors have observed that in dense woodlands, it is difficult for pollen to penetrate from surrounding plant communities. In contrast, open and less wooded areas allow for easier pollen dispersion (for example, Pérez-Obiol and Roure 1985; Sugita et al. 1999). Additionally, there are distinctions between coniferous or evergreen woods and deciduous ones. Deciduous woods have less canopy area for pollen interception during springtime before the leaves grow large, potentially leading to an increased contribution of pollen from vegetation growing elsewhere (Jackson and Lyford 1999).

All these factors therefore imply complex relationships between vegetation and its pollen rain. To introduce objective weightings into the interpretation of pollen records, the study of modern vegetation and its pollen output has proven to be a very valuable tool in Europe since the 1930s (for example, Pohl 1933, 1937; Heim 1963, 1970). This type of study is based on the fact that modern pollen deposition can be recorded in a similar way in modern surface samples of mosses as it is for ancient pollen in lakes and bogs (Wilmshurst and McGlone 2005). It allows for the determination of the output of pollen by different plant communities and an assessment of which taxa may be over- or under-represented. In the Iberian Peninsula, there is a considerable body of literature on the modern pollen rain, especially for mountainous areas such as the Pyrenees (Pérez-Obiol and Roure 1985; Mazier 2001; Mazier et al. 2006, 2009; Cañellas-Boltà et al. 2009; Cugny et al. 2010; Ejarque et al. 2011; López-Vila et al. 2014; Leunda Esnaola 2019; Pérez-Obiol et al. 2019, 2021), in the Iberian and central mountain systems (Vazquez-Gomez and Peinado-Lorca 1993; Sánchez-Goñi and Hannon 1999; López-Sáez et al. 2010, 2013; Aranbarri 2016; Broothaerts et al. 2018; Morales-Molino et al. 2020), in the Sierra Morena (Díaz-Fernández 1994) and in mountain ranges of the northwestern Iberian Peninsula (Catrufo-Ferreño and Aira-Rodríguez 1990; González-Porto et al. 1993). The modern pollen rain has also been studied in some coastal environments, such as the southeastern Iberian Peninsula (Carrión 2002), Galicia (García-Moreiras et al. 2015; Castro-Parada and Muñoz-Sobrino 2022) and the Balearic Islands (Servera-Vives et al. 2022). Some works have studied the pollen rain along altitudinal gradients of vegetation (such as Cañellas-Boltà et al. 2009; Ejarque et al. 2011), while others have explored the relationships between the current pollen signal and that found in fossil pollen records to interpret the development of the plant landscape (Broothaerts et al. 2018).

Overall, Cantabria, has received less attention, despite the numerous palaeoecological studies there (for example, Menéndez-Amor and Florschütz 1963; Mariscal 1983, 1986, 1987, 1989, 1993; Salas 1993; Peñalba 1994; Muñoz-Sobrino et al. 2005; García-Amorena et al. 2008; González-Pellejero et al. 2014; Pérez-Díaz et al. 2016; Pérez-Obiol et al. 2016; Carracedo et al. 2018; Sánchez-Morales et al. 2022). In the La Molina peatland in Cantabria, (484 m a.s.l.), the development of the vegetation and landscape has been recorded over the last ca. 17,500 years, showing the succession of various distinct landscape types (Pérez-Obiol et al. 2016; Sánchez-Morales et al. 2022). However, doubts persist about the interpretation of the pollen data, particularly the extent to which past plant communities can be considered analogous to those currently growing in this region. The lack of data on the modern pollen rain from Atlantic vegetation types, such as mixed deciduous woodlands, *Fagus sylvatica* woods, the Cantabrian laurel-evergreen oak woods (Lauro nobilis-Quercetum ilicis association) and open landscapes with grasslands restricts the interpretation of the pollen record. In particular, the laurel-evergreen oak woods can be considered a biogeographical speciality in the area (Amigo et al. 2017). It would be interesting to find out whether its pollen signal can be identified in fossil records, which could provide insights into its past presence. In accordance with Alessi et al. (2021), the observed recent expansion of *L. nobilis* in woodlands in Italy can be ascribed to a process of natural recovery of a potential ecological niche following a change in land use. In addition, the lack of attention given to the study of grazed grasslands, which have been heavily altered by human activity, raises questions regarding their origins and the extent to which they have developed in the past. The study of the pollen signal of the main types of vegetation in the area such as these could potentially help with the interpretation of the fossil data.

In order to better interpret the pollen record of the Cantabrian mountain range, we studied the modern pollen rain of a number of vegetation types, using samples from mosses. The specific aims of this work were: 1, to study the pollen signal of the main landscape units in the Cantabrian range of mountains, and 2, to investigate the relationship between the pollen signal of the main plant taxa and their estimated vegetation cover. We also tried 3, to evaluate the extent to which the present landscape could be analogous to

past plant communities by comparing the pollen signals of the main landscape units in Cantabria with the pollen data of the La Molina fossil record. Finally 4, it was thought that morphological differences between the two main groups of mosses, acrocarpous and pleurocarpous, could affect their ability to store and preserve pollen. Due to their spongy morphology, acrocarpous mosses were thought to be better at trapping and preserving pollen than pleurocarpous mosses, whose morphology is like a creeping mat. Therefore, a methodological objective was to determine whether there are variations in the concentration of preserved pollen between these two moss types.

Materials and methods

Study area

The geographical scope of this research covers an area on the northern slopes of the Cantabrian mountain range (Fig. 1). The morphology of this mountain system, with peaks higher than 2,600 m, has important implications for the local climate. Moisture-laden oceanic winds usually condense into precipitation on the northern slopes leading to annual amounts ranging from 1,000 to 1,800 mm (climate Cfb, according to the Köppen-Geiger classification, Beck et al. 2018). Winter temperatures can be low in some deep inland valleys due to both thermal inversion and also the lack of direct sunlight (Ortega-Villazán and Morales-Rodríguez 2015). At the highest altitudes, the average minimum temperature can be lower than 0 °C during the coldest month (climate Dfc/Dsb/Dsc) and annual precipitation may exceed 2,200 mm (Ancell Trueba and Célis Díaz 2012). On the other hand, the continental slopes receive dry winds from the north and have inland Mediterranean traits, with colder winters due to a greater distance from the sea, water deficit in summer and less than 800 mm of annual precipitation (climate Csb).

The climate and geographical features of the area determine a clear differentiation in vegetation cover between the northern and southern slopes of the Cantabrian range. On the oceanic slope, there are mixed eutrophic deciduous woods along the low valleys and mid-mountain areas. In particular, there are mainly woods with *Fagus sylvatica, Quercus robur* and *Q. petraea,* all of them with a Eurosiberian distribution. Woods of *Fagus sylvatica* typically grow between 800 and 1,600 m, in areas with frequent fog and high rainfall between 1,400 and 2,000 mm. In Cantabria, there are three types of beech woods according to the soil characteristics where they grow. Firstly, oligotrophic beech woods grow on acidic soils. Secondly, in terms of abundance, sciophilous and basophilic beech forests grow in areas where water is abundant despite the limestone soil. Lastly, the rarest type, known as xerophilous beech forests, are situated on limestone terrain with steep slopes and sunny positions, with 700 to 800 mm precipitation. These are found at the distribution limits of *Fagus* in the south of the region. Oak woods with *Quercus robur* grow in Cantabria up to 1,000 m usually on well drained, acidic to neutral soils, with 900–1,400 mm precipitation. *Q. petraea* (sessile oak) replaces *Q. robur* in woodlands higher up, in more inland places that are far from the sea and with a more continental climate, although they sometimes hybridize with the *Q. robur* and grow up to approximately 1,700 m. These woods are tolerant of any soils and usually grow on sunny slopes with 1,400 to 2,000 mm precipitation. Accompanying these dominant taxa are also *Fagus sylvatica* (beech). *Fagus sylvatica*, *Q. robur* and *Q. petraea* can be found as part of mixed deciduous woods as well as in beech and oak woods. When found as part of mixed deciduous woods, they are accompanied by other trees such as *Fraxinus excelsior, F. angustifolia, Corylus avellana, Acer pseudoplatanus, A. campestre*, *Alnus glutinosa* and *Ulmus minor*, while small woods of *Ilex aquifolium* and *Taxus baccata* can develop in the surrounding areas (Amigo et al. 2017).

On the other hand, although there are no natural pine woods on the northern slopes, but recent plantations of *Pinus radiata*, *P. sylvestris, P. pinaster* and *P. nigra* (and other taxa such as *Eucalyptus* spp.) form important components of the current wooded landscape. Particularly noteworthy are also the Mediterranean thermophilous taxa that, either favoured by the local climate or soils, grow on the Cantabrian northern slopes. Some evergreen taxa are found as part of the mixed woodlands, and they form significant pure communities in the drier areas of the region too. *Quercus ilex* ssp. *ilex* (holm oak) is distributed from sea level up to 500–600 m on rocky outcrops of limestone and generally on calcareous rocks, without preferred orientation of slope. This woodland requires a fairly dry soil, which is why it grows on such highly permeable base rocks. In particular, Lauro nobilis-Quercetum ilicis, woods of *Quercus ilex* ssp. *ilex* and *Laurus nobilis*, are common on the coast of Cantabria (Blanco et al. 1997; Sainz-Ollero et al. 2010; Amigo et al. 2017). *Quercus ilex* ssp. *rotundifolia* (= *Q. rotundifolia*) grows in higher places, up to 600 m on poorly developed mountain soils as it is also resistant to windy conditions. It grows in a Mediterranean climate, semi-moist or moist (700 to 1,400 mm), on limestone and siliceous soils, generally on sunny slopes.

Scrub vegetation also grows over large areas in mid-mountain areas and is the result of openings of the woodland by human-related activities such as grazing or recurring fires over centuries or millennia (Carracedo et al. 2018).

In montane and subalpine environments, where precipitation may exceed 2,000 mm and above the altitudinal limit of the other deciduous trees, woods of *Betula*

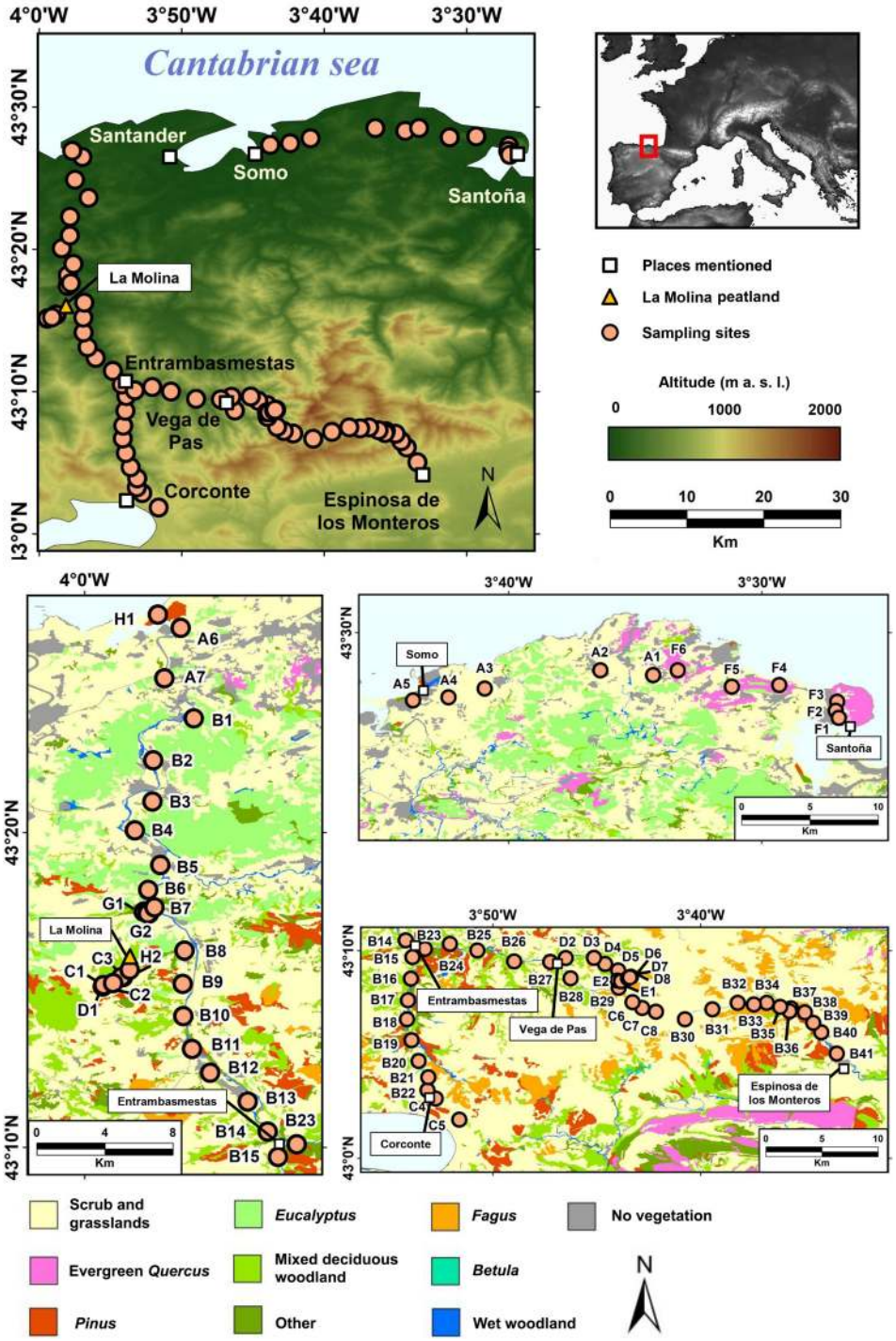


Fig. 1 Top, map of the study area showing the location of modern pollen samples and of the La Molina peatland. Bottom, vegetation types coloured according to the reclassification of the Mapa forestal de España 1:25,000 (MFE25). The letter in the code of each sample indicates the plant community from which it was sampled; **A** grazed grasslands and *Quercus ilex* woodland stands; **B** grazed grasslands, mixed deciduous woods and *Pinus* plantations; **C** grazed grasslands and shrubs; **D** mixed deciduous woods; **E** *Fagus sylvatica* woods; **F** *Quercus ilex* woods with *Laurus nobilis*; **G** open *Quercus ilex* woods; **H** *Pinus* plantations

pubescens (= *B. alba*) grow up to 2,100 m, on nutrient-poor siliceous soils and steep slopes in western Cantabria. Also, there is a great variety of grasslands above or beyond areas characterized by temperate conditions at high elevations, most of them dominated by *Festuca eskia, Nardus stricta* and *Brachypodium rupestre*, and accompanied by herbs from several families, such as *Carex brevicollis, Potentilla tabernaemontani, Helianthemum nummularium* and *Plantago media* (Díaz-González and Penas 2017).

In contrast to the slopes facing the Atlantic, the tree layer of the continental-facing slopes is mainly composed of marcescent taxa which keep their dead leaves in winter, and evergreen trees. *Quercus pyrenaica* grows at 600 to 1,000 m as part of various associations on siliceous soils, generally sandy with low water retention and preferably on sunny

slopes, especially in the driest areas of the valleys, where woods of *Fagus sylvatica* and *Quercus petraea* cannot grow due to their higher water dependence. On the carbonaceous soils, *Q. faginea* and *Q. ilex* ssp. *rotundifolia* are the most frequent trees, in some cases together with *Juniperus thurifera* and other calcicolous taxa (Penas et al. 2017). There is also a large area devoted to agriculture.

Sampling

The sampling campaign was designed to characterise the composition of the modern pollen rain from different types of vegetation. In April 2019, a total of 76 surface pollen samples of mosses were collected (Fig. 1). The sampling strategy was based on transect sampling to cover the variation of the landscape from sea level to the Cantabrian mountains. Most of the fieldwork was carried out on the north-facing slopes of the Cantabrian mountain range, mainly in the province of Cantabria, although some samples were also collected on the south-facing slopes too, reaching as far as Espinosa de los Monteros, in the province of Castilla y León. The set of samples was collected between 3 and 1,154 m altitude. At each sampling point, a field sheet was filled in, indicating the plant species observed within a 10 m radius and describing the main vegetation types of the surrounding area (ESM 1). Geographical coordinates, altitude and the moss growth habit (acrocarpous or pleurocarpous) were also recorded. With regard to the latter, it was thought that morphological differences between the two main groups of mosses, acrocarpous which are unbranched and erect, and pleurocarpous, with creeping branched shoots, could affect their ability to retain and preserve pollen. Therefore, acrocarpous mosses were sampled at some sites (n = 35) and pleurocarpous mosses at others (n = 29). At least two mosses were collected and mixed to obtain averages. A combination of acrocarpous and pleurocarpous mosses was sampled if there were not enough mosses of a single type at the sampling site (n = 12). In all cases, mosses located on a rocky and horizontal surface were chosen to avoid possible contamination from ancient pollen in the soil and also to reduce pollen loss by leaching.

The most common plant communities in Cantabria and therefore the most sampled were mosaics of grazed grasslands with stands of various trees and shrubs (Fig. 1). These grazing areas are often used by herders, who usually light fires to create and maintain them. On the coastal plain, the mosaics were composed of grazed grasslands, stands of *Quercus ilex* ssp. *ilex* and plantations of *Eucalyptus* spp. (n = 7; from A1 to A7). It should be noted that the planted woods are used when the trees are young, before they are sexually mature, and therefore the pollen representation of *Eucalyptus* spp. was expected to be poor. Further inland, the composition of the trees changed and a range of mosses was sampled in a landscape consisting of grazed grasslands, plantations of *Pinus* spp. and mixed deciduous woods consisting of *Quercus robur, Q. petraea* and *Corylus avellana,* with increasing presence of *Fagus sylvatica* in the higher parts (n = 41; from B1 to B41). Other deciduous trees, such as *Fraxinus excelsior*, *Acer* spp. and *Castanea sativa*, were also present. Mosaics of grazed grasslands with various shrubs were sampled in three different areas. The first, located near the La Molina peatland, was an open field which had been frequently burnt to improve grazing, and was composed of grazed grasslands with patches of *Ulex europaeus*, *Rubus* sp., *Vaccinium myrtillus* and *Erica* spp. (n = 3; from C1 to C3). There were also scattered individuals of *Ilex aquifolium*, *Betula* sp. and *Crataegus monogyna* nearby. In the second area, close to Corconte, Campoo de Yuso, the vegetation was composed of grazed grasslands and areas of *Pteridium aquilinum*, *Rubus* sp., *Ulex* sp. and *Erica* sp., reaching a maximum altitude of 1,003 m (n = 2; C4 and C5). Finally, on the mountain pass between Vega de Pas and Espinosa de los Monteros at 1,166 m, a mosaic landscape with grazed grasslands dominated by Poaceae (mainly *Festuca*), *Ulex europaeus, Erica* spp., *Daboecia cantabrica* and scattered individuals of *Corylus avellana* and *Betula pubescens* was sampled (n = 3; from C6 to C8). Mixed deciduous woodlands were also studied in two different areas. The first one was located close to the La Molina peatland, and was dominated by *Quercus robur* and *Q. petraea,* with secondary presence of *Fagus sylvatica* and an understorey of *Pteridium aquilinum* (n = 1; D1). The second mixed deciduous wood ran for about 7 km along the Pas valley near Vega de Pas and was composed of *Quercus robur, Q. petraea* and *Corylus avellana* (n = 7; from D2 to D8). Along the transect there was also riverside vegetation, with trees such as *Fraxinus excelsior, Alnus glutinosa*, *Salix* spp. and *Corylus avellana*, and with more *Fagus sylvatica* with increasing altitude. In the upper part of the valley from 700 to 850 m, there was a woodland dominated by *F. sylvatica*, with an understorey of *Erica* sp., *Hedera helix* and *Polypodium* sp. One sample was collected within the beech wood and another at its upper limit, where there were grazed grasslands (n = 2; samples E1 and E2, respectively). In the coastal area, the Lauro nobilis-Quercetum ilicis was sampled, close to Santoña (n = 6; from F1 to F6). This laurel-evergreen oak community was dominated by *Quercus ilex* ssp. *ilex* and *Laurus nobilis*, along with *Crataegus monogyna*, *Arbutus unedo*, *Phillyrea latifolia*, *Erica arborea*, *Hedera helix*, *Lithospermum* sp., *Helianthemum* sp., Poaceae and *Polypodium* sp. Further inland, an open woodland of *Quercus ilex* ssp. *ilex* with a scattered presence of *Laurus nobilis* was also sampled (n = 2; G1 and G2). Finally, two plantations of *Pinus* spp. were sampled. One was located on a coastal dune (n = 1; H1), consisting of *P.*

pinaster and *P. pinea*, and the other was near the La Molina peatland, consisting of *P. sylvestris* (n = 1; H2).

Pollen preparation

The 76 samples were prepared for pollen analysis following standard chemical procedures. Moss samples of 3 g each were weighed out and sieved on a 300 µm mesh. One tablet of *Lycopodium* spores was added to each sample to estimate the pollen concentration (Stockmarr 1971). The chemical procedure included HCl (10%), HF (70%), KOH (10%) and acetolysis, followed by mounting in glycerol (Fægri and Iversen 1989; Moore et al. 1991; Bennett and Willis 2001).

Counting and identification were carried out with a microscope using the reference collections of the Universitat Autònoma de Barcelona and the Université Clermont Auvergne, photographic atlases including Reille (1992, 1998) and van Geel and Aptroot (2006) and morphological identification keys such as Fægri and Iversen (1989) and Moore et al. (1991). A minimum of 400 terrestrial pollen grains were counted in each sample. After counting, a general check was carried out on the pollen slides to detect the presence of less common taxa. The pollen diagrams were calculated and drawn using Tilia and TiliaGraph (Grimm 1991).

Estimated vegetation cover

A vegetation map (Mapa forestal de España, 1:25,000, MITECO 2023) was used to extract information on estimated vegetation cover to be compared with the pollen percentages from modern surface samples. The vegetation map has several categories, which were reclassified as follows: *Pinus, Fagus,* mixed deciduous woodlands, evergreen *Quercus,* scrub and grasslands, *Betula* and wet woods (Table 1, Fig. 1). The information of the reclassified categories was extracted within circular areas of 100 m, 1 km and 5 km radius around each sample site (Fig. 2). These dimensions were used in a similar study (Li et al. 2015) and they were also considered appropriate for the present work, to characterise the pollen percentages in terms of the estimated vegetation cover from a local to a more regional

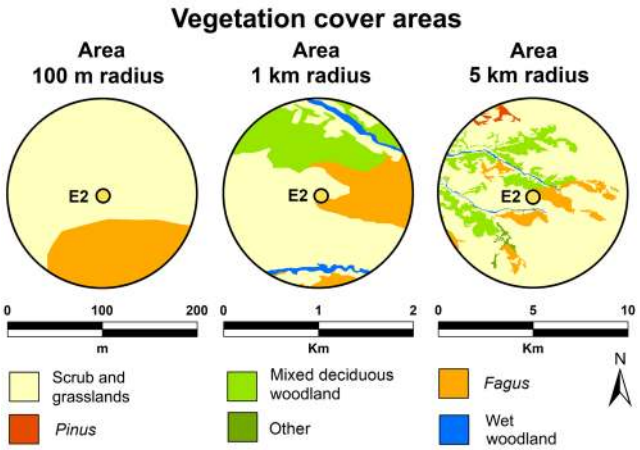


Fig. 2 Example of the three areas (100 m, 1 km and 5 km radius) used to obtain information about the vegetation cover around the modern pollen sampling sites; the moss sample is indicated as a yellow dot in the centre of each circle

Table 1 Reclassification of vegetation types in the Mapa forestal de España, 1:25,000 vegetation maps (MITECO 2023)

Mapa Forestal de España 1:25,000 vegetation types (MITECO 2023)	Vegetation types reclassification used in this work
Woodlands of (1) *Pinus sylvestris*; (2) *P. halepensis*; (3) *P. uncinata*; (4) *P. pinea*; (5) *P. nigra*; (6) *P. radiata*; (7) Mediterranean *P. pinaster* woodland; (8) atlantic *P. pinaster* woodland; (9) mixture of naturally growing and planted conifers, mainly *Pinus* spp.	*Pinus*
(1) *Fagus sylvatica* woodland; (2) mixed native broadleaved woodlands in the Atlantic biogeographical region, with *F. sylvatica* as the dominant species	*Fagus*
Woodlands of (1) *Quercus pyrenaica*; (2) *Q. faginea*; (3) *Q. rubra*; (4) *Q. robur*/*Q. petraea*; (5) mixed native broadleaved woodlands in the Atlantic biogeographic region, with oak dominant; (6) naturally growing and planted broadleaved trees and conifers, mainly oak; (7) coniferous and broadleaved natural and planted woods, mainly oak	Mixed deciduous woodlands
(1) *Quercus ilex* woodland; (2) mixed native broadleaved woodland in the Atlantic biogeographical region, with *Q. ilex* or *Laurus nobilis* as the dominant species, in the latter case with *Q. ilex* as the second main species; (3) naturally growing and planted broadleaved and other trees, with *Quercus ilex* as the dominant species	Evergreen *Quercus*
(1) Non-wooded, including the following sub-categories: crops, crops with sparse woodland, agricultural mosaic with artificial, mosaic of cultivation with scrub and/or grassland, treeless, bushes, grasslands, grassland and scrub, marshes, beaches, dunes and sandbanks, grasslands, hedged grasslands, residual woodland area, woodland clearances and burnt wooded and non-wooded areas	Scrub and grasslands
(1) Birch woodland	*Betula*
(1) Wet woodland	Wet woods

level. In order to explore the relationships between pollen and estimated vegetation cover of the reclassified categories and, taking into account the information from the three sizes of circles, scatter plots were created. The data for the mixed deciduous woodlands was compared to the pollen percentages of deciduous *Quercus.* Similarly, the area covered by scrub and grasslands was compared to the Poaceae pollen records. The limited representation of *Betula* and wet woodlands in the vegetation maps prevented any comparison between their estimated vegetation cover and pollen percentages.

Statistical analyses

To test whether there were differences in the ability of different mosses to trap and preserve pollen, the pollen concentrations were compared for acrocarpous (n = 35) and pleurocarpous (n = 27) mosses. Two pollen concentration values from pleurocarpous mosses were excluded because very few *Lycopodium* spores were counted in the pollen samples (samples F3 and F5). Pollen concentration data were transformed for normality assumptions and normality was tested using the Shapiro-Wilk test ($p > 0.05$). Fisher's F-test confirmed that the variables had equal variances ($p = 0.45$). Accordingly, an unpaired Student's *t*-test was done, giving a significance level of $p \leq 0.05$.

Principal component analysis (PCA) was done to compare the distribution of the modern (n = 76) and the fossil pollen records (n = 395) from the La Molina MOL2/MOL6 sedimentary sequence, Cantabria (Sánchez-Morales et al. 2022). The pollen assemblage zones (PAZs) of the pollen record were used to better identify chronological periods. The pollen data were log (x + 1) transformed to fulfil normality assumptions. All statistical analyses and the PCA plot were done with GraphPad Prism v. 9.

Results and discussion

Modern pollen representation of Cantabrian vegetation types

The pollen rain of several types of vegetation in Cantabria has been measured to provide a better understanding of the relationships between the presence of plants in the current vegetation and how they are represented in pollen samples (Fig. 3). In addition to the pollen representation for each vegetation type, relationships between the pollen signals of the main plant taxa and their estimated vegetation cover were explored to better understand the quantitative representation of pollen. In particular, the pollen percentages of *Pinus, Fagus,* evergreen and deciduous *Quercus*, and Poaceae were compared with the estimated vegetation cover of *Pinus, Fagus,* evergreen *Quercus*, mixed deciduous woodlands, and scrub and grasslands, respectively, within circles of 100 m, 1 km and 5 km radius around the sampling points (Fig. 4).

Scrub and grasslands was the most widespread category of vegetation cover recorded around the study sites. In some samples, this vegetation reached cover values up to 100% within a 1 km circle around the samples. However, arboreal pollen was always above 20% and Poaceae, which was the main non-arboreal pollen type in almost all the samples, never exceeded 60%. These results can be explained by many factors. First of all, open unwooded landscapes facilitate the transport of arboreal pollen from distant wooded areas due to the lack of physical barriers such as a tree canopy. Previous research has shown the importance of the plant community structure for its pollen dispersion (Sugita et al. 1999; Cañellas-Boltà et al. 2009). The presence of arboreal pollen is to be expected since the tree and shrub taxa detected in samples from open areas are mainly wind pollinated, such as *Pinus*, deciduous *Quercus* and *Corylus*, which explains their great pollen dispersal capacity. As regards pollen production by grasses, most of the open areas were grazed, which may have limited the flowering and subsequent release of pollen by herbs. Apart from the direct effects on the plants themselves, some plants reduce their flowering when grazed (Strauss et al. 1996; Hambäck 2001; Hladun and Adler 2009) and their phenology, sex ratio and pollen production may also be affected (Strauss et al. 1996; Mothershead and Marquis 2000; Avila-Sakar et al. 2003; Arceo-Gómez et al. 2009). Besides, some species change to self-pollination strategies (Garcia and Eubanks 2019) as is the case for some species of *Festuca,* which can produce flowers which do not open and self pollinate under certain environmental conditions (Connor 1998). In fact, the representation of Poaceae was particularly low in open mountain areas where *Festuca* sp. was dominant together with other grasses, as in samples C6 to C8, with pollen values ranging from 13 to 28%. On the other hand, all the samples had at least a minimal signal of Poaceae even where the presence of grasses was lower. Accordingly, many authors have found that there is a high degree of association between the presence of grasses in the field and the amounts of Poaceae pollen (Bunting 2003; Mazier et al. 2006; Ejarque et al. 2011).

Various shrubs were also present as mosaics in the grazed grasslands, such as *Erica* spp., *Daboecia cantabrica, Vaccinium myrtillus*, *Ulex* spp. and *Rubus* sp. Although all of them are usually insect pollinated, some *Erica* species can also disperse pollen efficiently by wind (Rebelo et al. 1985). Consequently, the Ericaceae pollen signal from open areas with shrubs stood out with a maximum value of 33%. By contrast, the Fabaceae and *Rubus* pollen signals were poor. The presence of Ericaceae in the pollen spectra is not surprising as it is

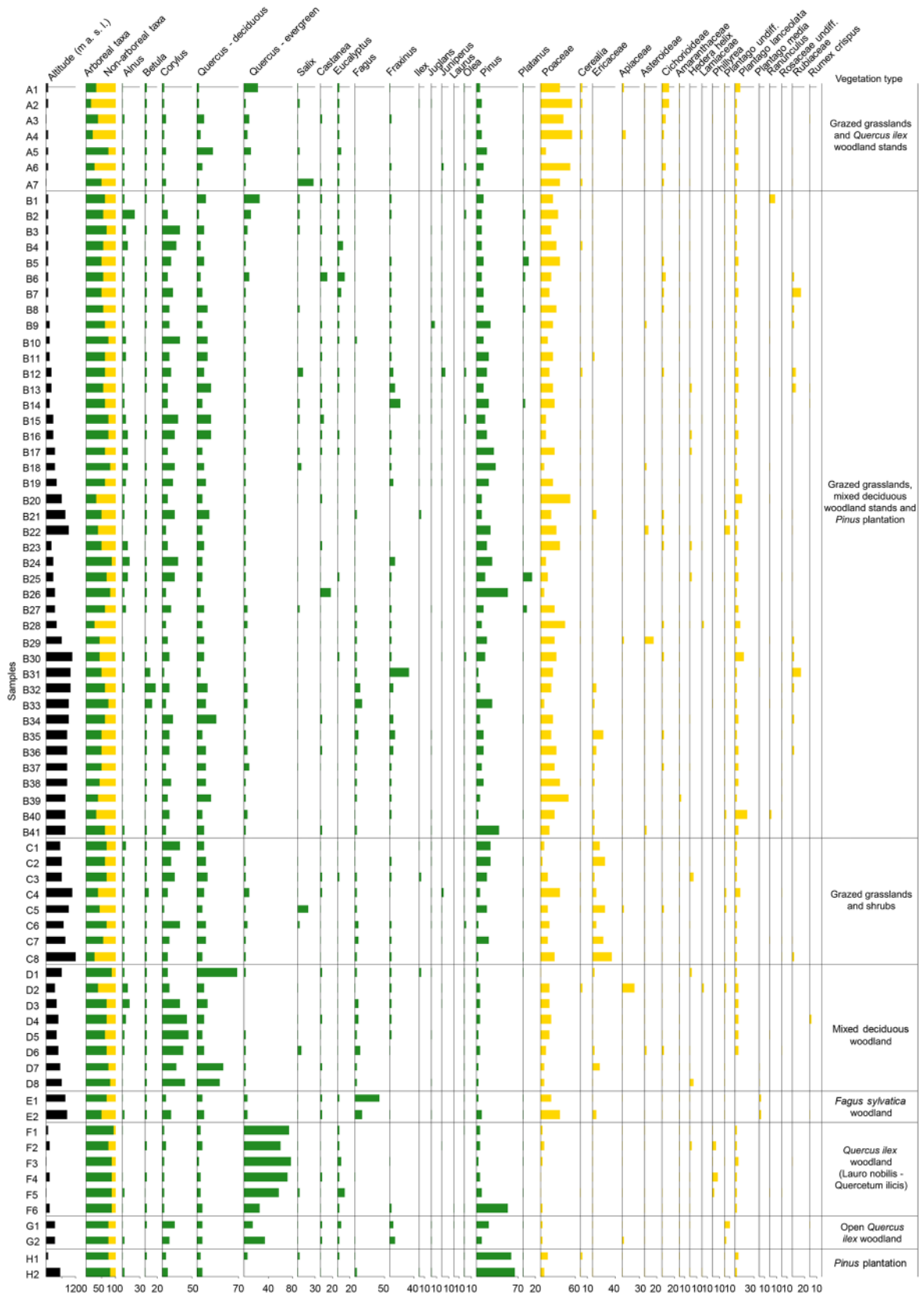


Fig. 3 Percentage pollen spectra of the modern moss samples showing selected taxa

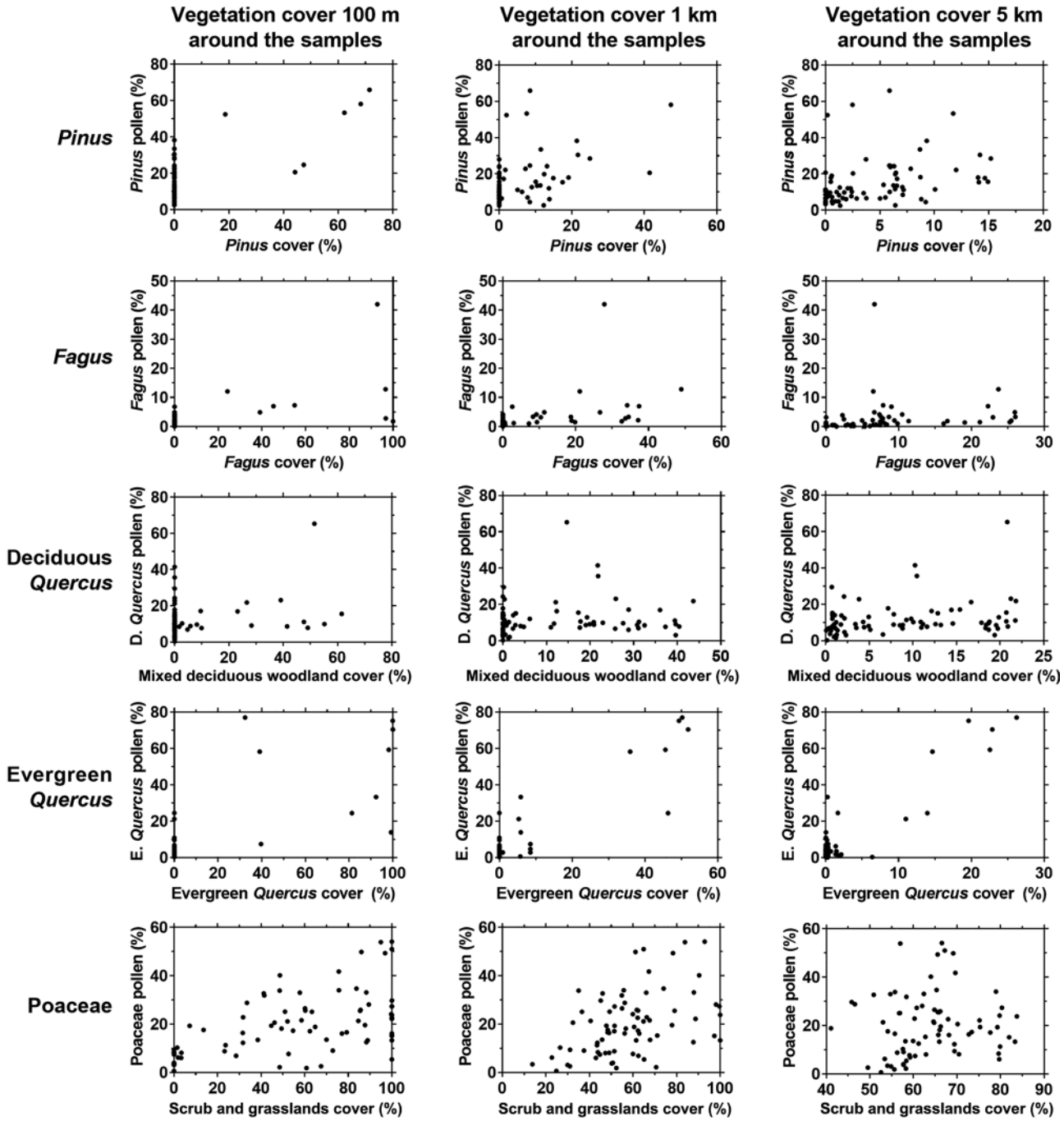
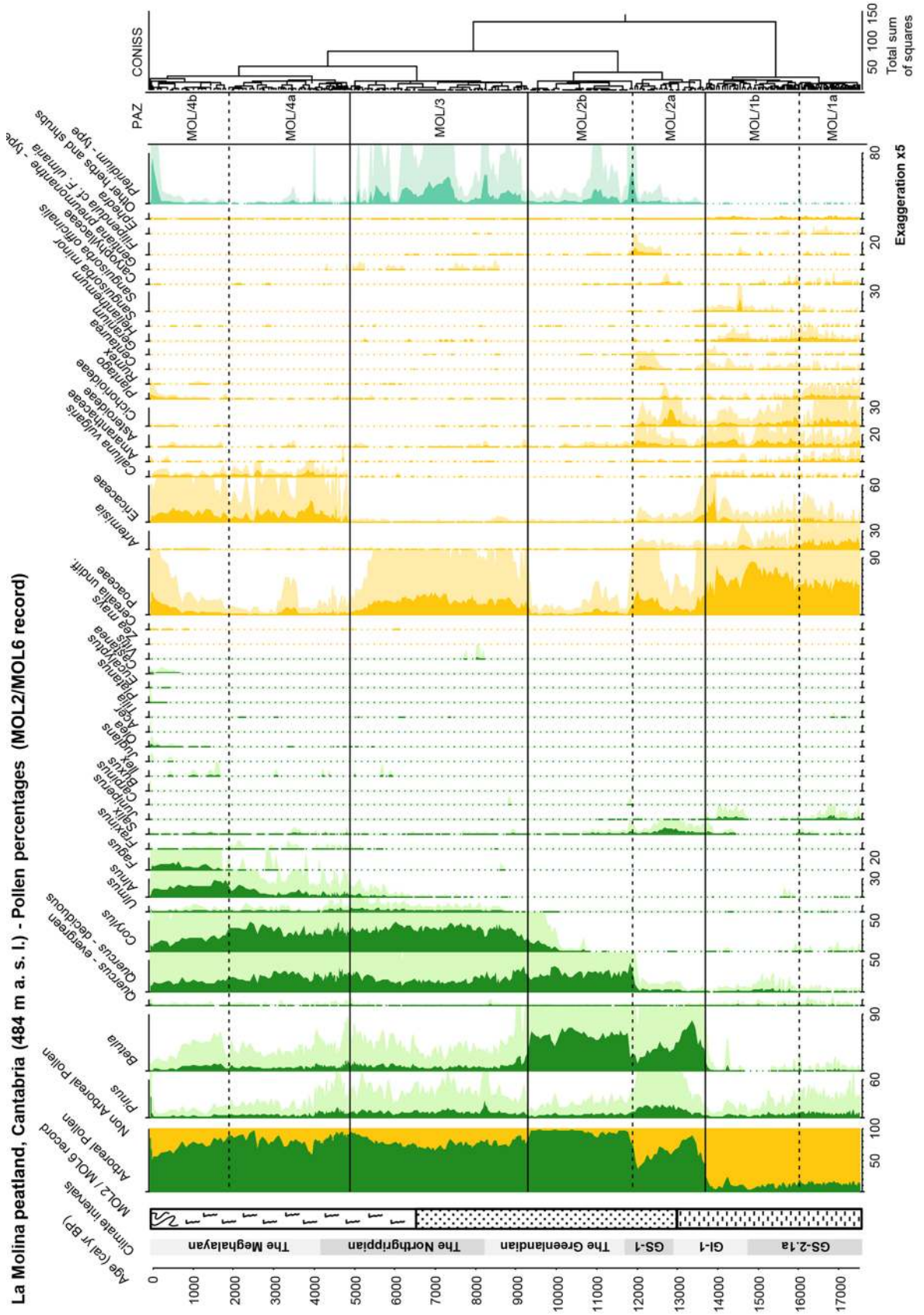


Fig. 4 Scatter plots of modern pollen percentages of selected taxa and estimated vegetation cover within 100 m, 1 km and 5 km radius of the sampling sites, according to the Mapa Forestal de España 1:25,000 vegetation maps. Various different scales are used on the axes of the plots

very commonly found there. Cañellas-Boltà et al. (2009) described it as a good indicator for the montane/subalpine boundary as it is mainly detected above it. Now it is possible to add that Ericaceae can also be indicative of vegetation altered by human activities including the use of fire to manage land, which is the case in the areas studied. This vegetation is frequently burned to generate and maintain fresh growth in grazing areas, and several *Erica* species benefit from this since they can quickly sprout again after burning (Iglesia-Rodríguez 2010). In any case, Ericaceae pollen dispersal has a strong local component since values above 20% were only reached when they were growing very close to the sampling point.


La Molina peatland, Cantabria (484 m a. s. l.) - Pollen percentages (MOL2/MOL6 record)
CONISS
Total sum of squares
PAZ
MOL/4b
MOL/4a
MOL/3
MOL/2b
MOL/2a
MOL/1b
MOL/1a
Exaggeration x5
Other herbs and shrubs
Pteridium - type
Ephedra
Filipendula cf. F. ulmaria
Gentiana pneumonanthe
Caryophyllaceae
Sanguisorba minor
Helianthemum
Geranium
Centaurea
Rumex
Plantago
Chenopodiaceae
Asteraceae
Artemisia
Ericaceae
Calluna vulgaris
Poaceae undif.
Cerealia undif.
Zea mays
Vitis
Castanea
Eucalyptus
Platanus
Alnus
Juglans
Olea
Acer
Buxus
Ilex
Carpinus
Ulmus
Salix
Fraxinus
Fagus
Alnus
Ulmus
Corylus
Quercus - deciduous
Quercus - evergreen
Betula
Non Arboreal pollen
Pinus
Arboreal pollen
MOL2 / MOL6 record
Climate intervals
Age (cal yr BP)
The Meghalayan
The Northgrippian
The Greenlandian
GS-1
GI-1
GS-2.1a
0
1000
2000
3000
4000
5000
6000
7000
8000
9000
10000
11000
12000
13000
14000
15000
16000
17000

◂**Fig. 5** Pollen diagram of La Molina peatland (MOL2/MOL6 sedimentary record) showing selected pollen taxa. Light silhouettes indicate × 5 exaggeration. Pollen assemblage zones (PAZ) MOL 1a to 4b are also shown. *GS* Greenland Stadials; *GI* Greenland Interstadials. Modified from Sánchez-Morales et al. (2022)

In the woodlands, the most abundant trees in the mixed deciduous woods were *Quercus robur, Q. petraea* and *Corylus avellana* followed by *Fagus sylvatica, Fraxinus excelsior* and to a lesser extent other deciduous taxa such as *Acer* spp. and *Castanea sativa.* The pollen spectra of these communities were dominated by deciduous *Quercus* (7.7 to 65.3%) and *Corylus* (7.9 to 43%), accounting for between 46 and 73% of the total. In mosaics with grazed grasslands, mixed deciduous woodlands and *Pinus* plantations, the pollen signal of deciduous *Quercus* reached 29.5% in some samples (Fig. 3). In particular, there were some studied sites with 0% of mixed deciduous woodland cover at the local scale within the 100 m and 1 km circles, but there were significant pollen values from deciduous *Quercus* with maxima around 25%. These results show that deciduous oaks have a high pollen dispersal capability. The pollen representation of *Corylus* was also important in grazed grasslands with mixed deciduous woods. However, this could be due to the presence of hazel in the wet woodlands.

As regards *Fagus sylvatica,* its pollen signal depended to a large extent on its local presence. Within the beech woods, the *Fagus* pollen signal reached 42% (sample E1), although it was significantly lower at the woodland edge (sample E2, 12%), where there was more Poaceae pollen than from beech. The scatter plots showed that even when beech cover was high at the local scale (> 90% of *F. sylvatica* cover within 100 m around the samples), its pollen signature remained modest. In particular, there were two samples from mixed deciduous woods (D7 and D8) with more than 95% *Fagus* cover within a 100 m radius, but the pollen signal was below 3% (Fig. 4). It can be seen how the pollen signals of other taxa growing close to the studied sites, such as *Corylus* and deciduous *Quercus*, but less abundant than beech in the woods within a 100 m radius, were greater than those of *Fagus*. In the other samples from the mixed deciduous woods, where beech was found together with other deciduous trees in a similar proportion, its pollen signal did not reach more than 8% (Fig. 3). A similar pollen representation (5 to 12%) was recorded from grazed grasslands with shrubs and from mixed deciduous woodlands (samples B32 to B35), with *Fagus* covering more than 30% of the estimated area within a 1 km radius around the samples. The fact that the samples were not collected from within the beech woods seems to have significantly influenced the pollen representation of *Fagus*.

In the Lauro nobilis-Quercetum ilicis, *Q. ilex* ssp. *ilex* and *Laurus nobilis* were the dominant species. Arboreal pollen ranged from 80 to 93% and evergreen *Quercus* dominated the pollen spectra, with most values between 59 and 77% (Fig. 3). At both local and regional scales, a positive correlation is observed between evergreen *Quercus* pollen and the abundance of holm oak woods (Fig. 4). Its positive representation can be explained by the fact that both *Q. ilex* ssp. *ilex* and *L. nobilis* are evergreen trees that form a very dense tree canopy, which may have limited the penetration of regional pollen from elsewhere. By contrast, the evergreen *Quercus* pollen signal was lower in open *Q. ilex* woods (14 to 33%). The pollen composition of the laurel-evergreen oak community resembles that of communities from the central Iberian Peninsula dominated by *Q. ilex* ssp. *rotundifolia,* such as warm Mediterranean (Köppen Csb) evergreen oak woods on acid soils at altitude, warm Mediterranean woody scrub and hot Mediterranean (Csa) scrub (supra-mesomediterranean silicicolous evergreen oak forests, mesomediterranean woody scrub and thermomediterranean scrublands) (López-Sáez et al. 2010). Equally, the pollen signal of open woods dominated by *Q. ilex* ssp. *ilex* is comparable to that of managed landscapes of grasslands with *Q. ilex* ssp. *rotundifolia* in the central Iberian Peninsula (*dehesas*) (López-Sáez et al. 2010). If *Laurus nobilis* pollen had been detected, it could have helped to distinguish between the Lauro nobilis-Quercetum ilicis and other communities. However, its pollen signal was only identified in one sample and that was below 1% although there was more *L. nobilis* than *Q. ilex* ssp. *ilex* at some study sites. Bay laurel is dioecious, but both male and female individuals were found at the sampling points. The lack of *L. nobilis* pollen is probably explained by its low pollen dispersal as it is insect pollinated. Besides, it has also been reported that its pollen is poorly preserved in sediments and tends to disintegrate during chemical treatments (Connor et al. 2012), so its pollen is clearly under-represented.

Finally, the role of pine as a major pollen disperser is shown in this study. Its pollen signal was detected in all the samples and it even penetrated significantly into dense woodland of Lauro nobilis-Quercetum ilicis with a pine plantation nearby, as was the case of sample F6 (*Pinus* values of 52%). The high level of pollen dispersal was such that there were samples with little or no pine cover within 1 and 5 km radii of the surrounding area, but the *Pinus* pollen values exceeded 20% (Fig. 4). Here it should be stressed that these are not likely to be errors in the vegetation maps since the presence of pines in Cantabria is restricted to well-delimited plantations, while isolated pine trees are not abundant. Therefore, it was considered that the maps correctly reflected the coverage of pine. Inside the plantations, pine values were around 60%, which are

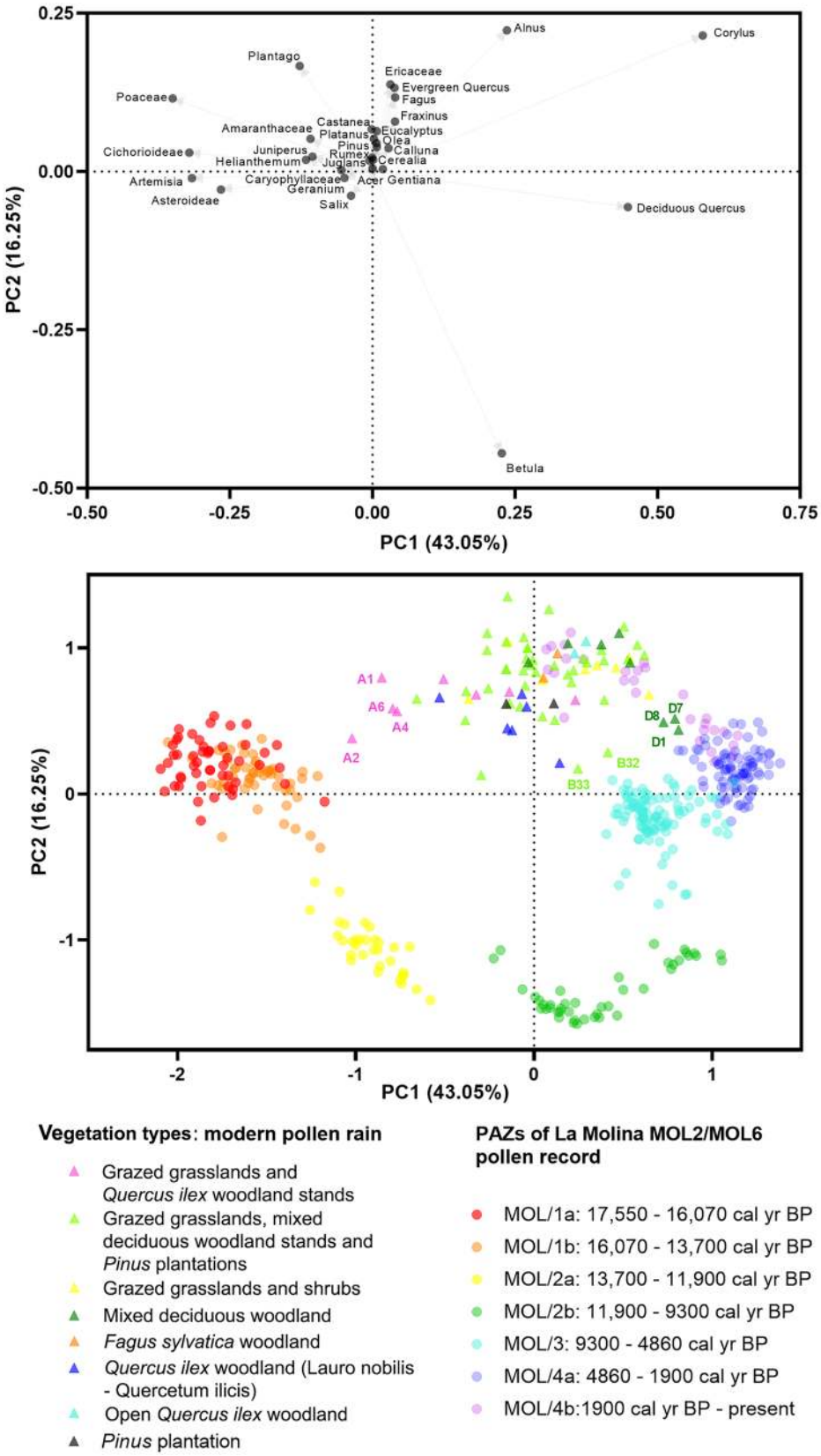


Fig. 6 Principal component analysis of the most abundant taxa in the modern surface samples and in the pollen record MOL2/MOL6 of the La Molina peatland. Explained variance is 59.3%. Top, the first axis contrasts the main taxa of mixed deciduous woodlands with those that are representative of open vegetation. The second axis is positively correlated with some taxa that are indicative of human activities and negatively correlated with *Betula*. Bottom; triangles, distribution of the analysed vegetation types according to the modern pollen rain; circles, pollen assemblage zones of the La Molina pollen record. There is a lack of overlap between the modern vegetation and the fossil records from La Molina, except for the most recent period from ca. 1,900 cal BP to the present

generally similar to those from woods of *P. sylvestris* var. *iberica* in the central Iberian Peninsula (López-Sáez et al. 2013).

Relationships between the modern pollen samples and the fossil record of the La Molina peatland

According to the principal component analysis (PCA), which analysed data from the modern surface samples and the fossil record from the La Molina peatland (Fig. 5; Sánchez-Morales et al. 2022), 59.3% of the total variation was explained by the first two components (Fig. 6). The first axis (PC1: 43.05%) contrasts the main taxa of mixed deciduous woods, *Corylus* and deciduous *Quercus*, with those that are representative of open vegetation with Poaceae, Cichorioideae, Asteroideae, *Artemisia, Plantago,* Amaranthaceae, *Juniperus, Helianthemum,* Caryophyllaceae and *Geranium.* The second axis (PC2: 16.25%) was positively correlated with *Alnus,* Ericaceae, evergreen *Quercus, Fagus, Fraxinus, Castanea, Platanus, Olea, Pinus, Calluna, Rumex* and Cerealia, some of which are indicators of human activities, and negatively correlated with *Betula.* The ordination shows a strong differentiation between the different pollen assemblage zones of the fossil record and a positive correlation between PC2 and the modern surface samples. The only overlap between the modern surface samples and the La Molina record is for the samples of the last ca. 1,900 years (PAZ MOL/4b). This study did not find past vegetation types in Cantabria that are similar to modern ones, but suggests that they may potentially exist in other regions. There is plenty of evidence that biomes across Europe have undergone substantial transformations over the past 6,000 years (Prentice et al. 1996).

From ca. 17,550 to 13,700 cal BP (MOL/1a and MOL/1b), the pollen record revealed an open vegetation at La Molina (Fig. 5). No modern surface samples recorded such low levels of arboreal pollen, even at sites with no tree cover for 5 km around them (Figs. 3, 4). This would indicate that there was little or no tree cover throughout the region during this glacial period. The vegetation bears some resemblance to some modern pollen samples from grazed grasslands with *Quercus ilex* stands (samples A1, A2, A4 and A6; Fig. 6), although the pollen composition is more similar to that of other European regions. For example, the glacial landscape could be analogous to present-day alpine grasslands above the treeline of the Alps (Furlanetto et al. 2019) or to the steppes of southeastern Turkey, where *Artemisia* is dominant and mean annual precipitation is around 250 mm (van Zeist et al. 1970). That this is likely is shown by the study of a speleothem (mineral cave deposit) record from Cantabria which indicated cold and dry conditions from 18,200 to 15,400 yrs BP (Moreno et al. 2010), suggesting that the potential vegetation could be similar to these alpine and steppe examples.

From ca. 13,700 to 9,300 cal BP (MOL/2a and MOL/2b), *Betula* was the best represented taxon and its percentages came to more than 80% in some places within these subzones (Fig. 5). According to the PCA, these would represent the vegetation with the lowest degree of association with the current plant cover (Fig. 6). The highest pollen values of *Betula* (8–16%) in the modern landscape were from mountain environments close to the upper limit of the treeline on the southern slopes of the Cantabrian mountains, where there were scattered trees of *B. pubescens* (samples B31 to B33). Birch woods were not sampled in this research because there are no large ones in our area, although other studies have shown that the *Betula* signal can exceed 80% in northern European birch woods (Räsänen 2001), suggesting a high degree of similarity.

From ca. 9,300 to 1,900 cal BP (MOL/3 and MOL/4a), the fossil pollen spectra showed a certain degree of similarity with the modern pollen composition of mixed deciduous woods and grazed grasslands together with mixed deciduous woodland stands and *Pinus* plantations (Fig. 6). Although these modern pollen spectra cannot be considered to represent similar vegetation in the past, they are of great palaeoecological interest, since a similar pollen composition to PAZ 3 and 4a at La Molina is also found in other records from Cantabria, such as El Alto de la Espina (López-Merino 2009), La Molina mire (López-Merino et al. 2014), Villaviciosa estuary (García-Antón et al. 2006), lago Enol (López-Merino 2009), Pico Sertal (Mariscal 1986), Los Tornos (Peñalba 1994; Muñoz-Sobrino et al. 2005), Zalama (Pérez-Díaz et al. 2016), Saldropo (García-Antón et al. 1989), Belate and Atxuri (Peñalba 1994), which cover an altitudinal range from sea level to 1,330 m. The main differences between the present day deciduous woodlands and those of the mid Holocene interpreted from the La Molina record may be due to the greater representation of some trees in the modern landscape that have colonised the area relatively recently, such as *Fagus sylvatica*, or that were introduced in a still more recently, such as *Pinus* spp., *Eucalyptus* spp., *Platanus* sp., *Olea europaea* and *Castanea sativa*. In fact, the pollen spectra from 1,900 cal BP to the present (MOL/4b) show a strong similarity to current pollen rain samples. Besides, the role of *Pteridium* during the mid Holocene should also be considered. Its spores were significant from ca. 9,300 to 4,860 cal BP (MOL/3), but could not be included in the PCA because they were virtually absent from the spectra from modern vegetation.

As a final point, the pollen rain results also support the view that there were no pine woods on the northern slopes of the Cantabrian mountains during the last ca. 17,500 cal BP. In the La Molina pollen diagram, *Pinus* never exceeds

20%, with similar values obtained from other pollen sites on the Cantabrian coast (such as Mariscal 1993; Peñalba 1994; García-Antón et al. 2006; Iriarte-Chiapusso et al. 2006; López-Merino et al. 2006, 2010; López-Merino 2009; González-Pellejero et al. 2014). Similar pollen values were found from the present-day landscape, even in samples with no pine plantations within a 5 km radius. Therefore, although the pollen record shows a continuous presence of pine, it cannot be concluded that significant pine woods existed in the past. The long distance transport of *Pinus* pollen from southern regions where there are more extensive pine woods (Peñalba 1994; Gómez-Lobo et al. 1996; Peñalba et al. 1997; Ramil-Rego et al. 1998; von Engelbrechten 1998; Sánchez-Goñi and Hannon 1999; Iriarte-Chiapusso et al. 2001; Gil-García et al. 2002; Morales-Molino et al. 2022) could explain the pollen records of *Pinus* from the northern Cantabrian mountain range.

Pollen concentrations in acrocarpous and pleurocarpous mosses compared

The maximum concentration values recorded for acrocarpous mosses were 531,079 pollen g^{-1} and for pleurocarpous mosses 984,746 pollen g^{-1}, with average concentrations of 175,074 and 183,900 pollen g^{-1}, respectively. The pollen concentration was not significantly different between either type of moss (Student's *t*-test, $p = 0.94$). Therefore, it is not necessary to prioritise the sampling of either type in pollen rain studies.

Conclusions

This investigation adds to a growing amount of research that examines the modern pollen rain of various plant communities so as to better understand ancient pollen records. It fills an information gap by investigating the modern pollen rain from various types of vegetation in Cantabria that have been previously little studied, such as the Lauro nobilis-Quercetum ilicis (laurel-evergreen oak community), open woods of *Quercus ilex* ssp. *ilex*, mixed deciduous woods, *Fagus sylvatica* woods and mosaics of grazed grasslands and other vegetation. The main conclusions of this work are:

This study has acquired the pollen data for grazing areas, a subject that has received limited research attention until now. The representation of Poaceae has proved to be limited, as it never exceeded 60% of the total pollen, even when there was a lack of trees and shrubs within a 1 km radius around the sample sites. Their greater or lesser representation depends on many factors, such as the amount of grazing, the presence of cleistogamous plants and the composition of the surrounding vegetation. Also, in grasslands with shrubs, some insect pollinated taxa such as *Rubus* spp. and *Ulex* spp. were clearly under-represented. On the contrary, Ericaceae pollen was better represented but only when vegetation with Ericaceae was growing close to the sampling sites, and never reaching more than 33% of total pollen.

Lauro nobilis-Quercetum ilicis (laurel-evergreen oak community) showed a significant representation of evergreen *Quercus*, with pollen values ranging between 60 and 77%, whereas *Laurus nobilis* was almost absent because of the poor preservation of its pollen grains, even when there was more bay laurel than holm oak in the woodland.

The well-known high pollen dispersal of *Pinus* was also found in our study, as it accounted for more than 20% of the pollen representation in samples with few or no pine trees within a 5 km radius.

Fagus sylvatica showed a very strong local component. Within beech woods its pollen reached 42%, but outside them it decreased significantly, even when there were beech stands close to the sampling site with more than 30% of the cover within 1 km radius.

The pollen spectra of the mixed deciduous woods reflected the surrounding vegetation, as they were dominated by deciduous *Quercus* and *Corylus avellana*. The study shows that deciduous *Quercus* has a good pollen dispersal, so that some sample sites with a complete absence of mixed deciduous woodland within a 1 km radius still produced deciduous *Quercus* pollen values of up to 25%.

The pollen record from La Molina has not revealed any past vegetation types analogous to the present day ones in Cantabria, except in the most recent period from ca. 1,900 cal BP to the present. A certain relationship has been found between the pollen signal of the modern mixed deciduous woods and the vegetation of the mid Holocene, from ca. 9,300 to 1,900 cal BP.

As a methodological conclusion, it has been found that there are no differences in pollen concentration between acrocarpous and pleurocarpous mosses.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00334-024-01001-y.

Acknowledgements The authors appreciate the English language review by Stephen Smith. The authors would like to thank Juan Carlos García-Codron, Sara Rodríguez-Coterón, Joan Manuel Soriano, Ana Vera Martín, Cèlia Pérez Novo and Lucrezia Masci for their help during the fieldwork. Likewise, we gratefully acknowledge the invaluable contributions of J.S. Carrión and the other reviewer whose insightful comments and constructive feedback greatly improved the quality and clarity of this manuscript.

Funding Open Access Funding provided by Universitat Autonoma de Barcelona. This work has been supported by coordinated project grants from the Ministerio de Economia y Competitividad (Spanish Ministry of Economics and Competitiveness), "Calibración de indicadores de influencia humana y climática para la (re)interpretación de

la expansión postglacial y de las dinámicas forestales en los últimos 18.000 años" (PID2019108282GB-I00/AEI/10.13039/501100011033); "Geohistoria ambiental del fuego en el Holoceno. Patrones culturales y gestión territorial desde el inicio de la ganadería y la agricultura en la montaña Cantábrica y Pirineo" (CSO2012-39680-C02-02); "Estudio biogeográfico histórico comparado (Montaña Cantabrica, Sistema Central y Pirineos): 18000 años de cambios climáticos y antrópicos sobre especies forestales indicadoras" (CSO2015-65216-C2-1-P), awarded to the Department of Geography, Universitat Autònoma de Barcelona, which also awarded an FPI Doctoral grant (BES-2016-076641) within the project. In addition, the project was funded by the Catalan government's applied geography programme, "Grup de Geografia Aplicada" (Agència de Gestió d'Ajuts Universitaris i de Recerca, Generalitat de Catalunya, 2017 SGR-00343 and 2021 SGR-00522).

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Alessi N, Wellstein C, Spada F, Zerbe S (2021) Population structure of *Laurus nobilis* L. in Central Italian forests: evidence for its ongoing expansion. Rend Lincei Sci Fis Nat 32:365–376. https://doi.org/10.1007/s12210-021-00981-7

Amigo J, Rodríguez-Guitián MA, Honrado JJP, Alves P (2017) The lowlands and midlands of Northwestern Atlantic Iberia. In: Loidi J (ed) The vegetation of the Iberian Peninsula. Springer, Cham, pp 191–250

Ancell Trueba R, Célis Díaz R (2012) Termopluviometría de Cantabria durante el periodo 1981–2010. (Nota técnica 10) Agencia Estatal de Meteorología (AEMET), Madrid

Aranbarri J (2016) Impactos de la variabilidad climática rápida en el paisaje vegetal del noreste peninsular durante el Holoceno a partir de datos palinológicos. Universidad del País Vasco/Euskal Herriko Unibertsitatea, Leioa, Tesis Doctoral

Arceo-Gómez G, Parra-Tabla V, Navarro J (2009) Changes in sexual expression as result of defoliation and environment in a monoecious shrub in Mexico: implications for pollination. Biotropica 41:435–441. https://doi.org/10.1111/j.1744-7429.2009.00502.x

Avila-Sakar G, Simmers SM, Stephenson AG (2003) The interrelationships among leaf damage, anther development, and pollen production in *Cucurbita pepo* ssp. *texana* (Cucurbitaceae). Int J Plant Sci 164:395–404. https://doi.org/10.1086/374196

Beck HE, Zimmermann NE, McVicar TR, Vergopolan N, Berg A, Wood EF (2018) Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci Data 5:180214. https://doi.org/10.1038/sdata.2018.214

Bennett KD, Willis KJ (2001) Pollen. In: Smol JP, Birks HJB, Last WM (eds) Tracking environmental change using lake sediments, vol 3. Terrestrial, algal, and siliceous indicators. Kluwer Academic Publishers, Dordrecht, pp 5–32

Blanco E, Casado MA, Costa M et al (1997) Los bosques ibéricos. Una interpretación geobotánica. Editorial Planeta, , Barcelona

Bresinsky A, Körner C, Kadereit JW, Neuhaus G, Sonnewald U (2013) Strasburger's plant sciences: Including prokaryotes and fungi. Springer, Berlin

Broothaerts N, Robles-López S, Abel-Schaad D et al (2018) Reconstructing past arboreal cover based on modern and fossil pollen data: a statistical approach for the Gredos Range (Central Spain). Rev Palaeobot Palynol 255:1–13. https://doi.org/10.1016/j.revpalbo.2018.04.007

Bunting MJ (2003) Pollen–vegetation relationships in non-arboreal moorland taxa. Rev Palaeobot Palynol 125:285–298. https://doi.org/10.1016/S0034-6667(03)00005-8

Cañellas-Boltà N, Rull V, Vigo J, Mercadé A (2009) Modern pollen–vegetation relationships along an altitudinal transect in the central Pyrenees (southwestern Europe). Holocene. https://doi.org/10.1177/0959683609345082

Carracedo V, Cunill R, García-Codron JC, Pèlachs A, Pérez-Obiol R, Soriano JM (2018) History of fires and vegetation since the Neolithic in the Cantabrian Mountains (Spain). Land Degrad Dev. https://doi.org/10.1002/ldr.2891

Carrión JS (2002) A taphonomic study of modern pollen assemblages from dung and surface sediments in arid environments of Spain. Rev Palaeobot Palynol 120:217–232. https://doi.org/10.1016/S0034-6667(02)00073-8

Castro-Parada A, Muñoz-Sobrino C (2022) Variations in modern pollen distribution in sediments from nearby upland lakes: implications for the interpretation of paleoecological data. Rev Palaeobot Palynol 306:104765. https://doi.org/10.1016/j.revpalbo.2022.104765

Catrufo-Ferreño R, Aira-Rodríguez MJ (1990) Evaluación de los vegetales de superficie como captadores del polen actual. An Asoc Palinol Leng Esp 5:11–18

Connor HE (1998) Breeding systems in New Zealand grasses XII. Cleistogamy in *Festuca*. New Zealand J Bot 36:471–476. https://doi.org/10.1080/0028825X.1998.9512585

Connor SE, van Leeuwen JFN, Rittenour TM, van der Knaap WO, Ammann B, Björck S (2012) The ecological impact of oceanic island colonization—a palaeoecological perspective from the Azores. J Biogeogr. https://doi.org/10.1111/j.1365-2699.2011.02671.x

Cugny C, Mazier F, Galop D (2010) Modern and fossil non-pollen palynomorphs from the Basque mountains (western Pyrenees, France): the use of coprophilous fungi to reconstruct pastoral activity. Veget Hist Archaeobot 19:391–408. https://doi.org/10.1007/s00334-010-0242-6

Díaz-Fernández PM (1994) Relations between modern pollen rain and mediterranean vegetation in Sierra Madrona (Spain). Rev Palaeobot Palynol 82:113–125

Díaz-González TE, Penas Á (2017) The High Mountain Area of Northwestern Spain: The Cantabrian Range, the Galician-Leonese Mountains and the Bierzo Trench. In: Loidi J (ed) The vegetation of the Iberian Peninsula. Springer, Cham, pp 251–321

Ejarque A, Miras Y, Riera S (2011) Pollen and non-pollen palynomorph indicators of vegetation and highland grazing activities obtained from modern surface and dung datasets in the eastern Pyrenees. Rev Palaeobot Palynol 167(123):139. https://doi.org/10.1016/j.revpalbo.2011.08.001

Fægri K, Iversen J (1989) Textbook of pollen analysis, 4th edn. Wiley, Chichester

Furlanetto G, Ravazzi C, Badino F, Brunetti M, Champvillair E, Maggi V (2019) Elevational transects of modern pollen samples: site-specific temperatures as a tool for palaeoclimate reconstructions in the Alps. Holocene 29:271–286. https://doi.org/10.1177/0959683618810395

Garcia LC, Eubanks MD (2019) Overcompensation for insect herbivory: a review and meta-analysis of the evidence. Ecology 100:e02585. https://doi.org/10.1002/ecy.2585

García-Amorena I, Morla C, Rubiales JM, Gómez Manzaneque F (2008) Taxonomic composition of the Holocene forests of the northern coast of Spain, as determined from their macroremains. Holocene 18:819–829. https://doi.org/10.1177/0959683608089218

García-Antón M, Ruiz-Zapata B, Ugarte FM (1989) Análisis geomorfológico y palinológico de la Turbera de Saldropo, Barazar, Zeanuni, Bizkaia. Lurralde (san Sebastián) 12:25–44

García-Antón M, Gil-Romera G, Pagés JL, Alonso-Millán A (2006) The Holocene pollen record in the Villaviciosa Estuary (Asturias, North Spain). Palaeogeogr Palaeoclimatol Palaeoecol 237:280–292. https://doi.org/10.1016/j.palaeo.2005.12.004

García-Moreiras I, Sánchez JM, Muñoz-Sobrino C (2015) Modern pollen and non-pollen palynomorph assemblages of salt marsh and subtidal environments from the Ría de Vigo (NW Iberia). Rev Palaeobot Palynol 219:157–171. https://doi.org/10.1016/j.revpalbo.2015.04.006

Gil-García MJ, Valiño MD, Valdeolmillos Rodríguez A, Ruiz-Zapata MB (2002) Late-glacial and Holocene palaeoclimatic record from Sierra de Cebollera (northern Iberian Range, Spain). Quat Int 93–94:13–18. https://doi.org/10.1016/S1040-6182(02)00003-4

Gómez-Lobo A, Gil-García MJ, Atienza M, Ruiz-Zapata MB (1996) Evolución de la paleovegetación en el noroeste del Sistema Ibérico (Soria), durante los últimos 7000 BP. Bot Macaronés 23:233–240

González-Pellejero R, Allende F, López-Sáez JA, Frochoso M, Alba-Sánchez F, Abel-Schaad D (2014) Dinámicas naturales y antrópicas en los paisajes vegetales de los valles internos de Cantabria occidental (Norte de España). B Asoc Geogr Esp. https://doi.org/10.21138/bage.1747

González-Porto AV, Díaz-Losada E, Saa-Otero MP (1993) Aportación al conocimiento de la dinámica de la lluvia polínica en la Sierra del Buyo (Lugo, N.O. de España). Nova Acta Cient Compostel Biol 4:41–48

Grimm EC (1991) Tilia and tiliagraph. Illinois State Museum, Springfield

Hambäck PA (2001) Direct and indirect effects of herbivory: feeding by spittlebugs affects pollinator visitation rates and seedset of *Rudbeckia hirta*. Écoscience 8:45–50. https://doi.org/10.1080/11956860.2001.11682629

Heim J (1963) Recherches sur les relations entre la végétation actuelle et le spectre pollinique récent dans les Ardennes Belges. Bull Soc Roy Bot Belg 96:5–92

Heim J (1970) Les relations entre les spectres polliniques récents et la végétation actuelle en Europe occidentale. Université de Louvain, Laboratoire de Palynologie et de Phytosociologie, Louvain-la-Neuve, Thèse

Hladun KR, Adler LS (2009) Influence of leaf herbivory, root herbivory, and pollination on plant performance in *Cucurbita moschata*. Ecol Entomol 34:144–152. https://doi.org/10.1111/j.1365-2311.2008.01060.x

Iglesia-Rodríguez A (2010) Efecto del fuego sobre la germinación y el banco de semillas edáfico de Ericáceas de Galicia. Tesis Doctoral, Universidade de Santiago de Compostela, Santiago de Compostela

Iriarte-Chiapusso MJ, Muñoz-Sobrino C, Ramil-Rego P, Rodríguez-Guitián M (2001) Análisis palinológico de la turbera de San Mamés de Abar (Burgos). In: Fombella Blanco MA, Fernández González D, Valencia Barrera RM (eds) Palinología. Diversidad y aplicaciones. Trabajos del XII Simposio de Palinología (APLE), León, 1998. Universidad, Secretariado de Publicaciones, León, pp 87–93

Iriarte-Chiapusso MJ, Muñoz-Sobrino C, Goméz-Orellana L, Ramil-Rego P (2006) Dinámica del paisaje en la Reserva de la Biosfera del Urdaibai durante el Holoceno. In: Cadiñanos Aguirre JA, Ibabe Lujanbio A, Lozano Valencia P, Meaza Rodríguez G, Onaindia Olalde M (eds) III Congreso Español de Biogeografía. Universidad del País Vasco/Euskal Herriko Unibertsitatea, Leioa, Comunicaciones, pp 113–117

Jackson ST, Lyford ME (1999) Pollen dispersal models in quaternary plant ecology: assumptions, parameters, and prescriptions. Bot Rev 65:39–75. https://doi.org/10.1007/BF02856557

Lara-Ruiz J (2019) Manual de Polinización de la Flora Ibérica. Bubok, Madrid

Leunda Esnaola M (2019) Millennial scale vegetation and fire dynamics at high altitudes in the central Pyrenees. Tesis Doctoral, Universidad de Zaragoza, Zaragoza

Li Y, Nielsen AB, Zhao X, Shan L, Wang S, Wu J, Zhou L (2015) Pollen production estimates (PPEs) and fall speeds for major tree taxa and relevant source areas of pollen (RSAP) in Changbai Mountain, northeastern China. Rev Palaeobot Palynol 216:92–100. https://doi.org/10.1016/j.revpalbo.2015.02.003

López-Merino L (2009) Paleoambiente y antropización en Asturias durante el Holoceno. Universidad Autónoma de Madrid, Madrid, Tesis Doctoral

López-Merino L, López Sáez JA, López García P (2006) Estudio palinológico de la turbera litoral holocena de Las Dueñas (Cudillero, Asturias, España). Rev Esp Micropaleontol 38:299–308

López-Merino L, Martínez-Cortizas A, López-Sáez JA (2010) Early agriculture and palaeoenvironmental history in the North of the Iberian Peninsula: a multiproxy analysis of the monte areo mire (Asturias, Spain). J Archaeol Sci. https://doi.org/10.1016/j.jas.2010.03.003

López-Merino L, Martínez-Cortizas A, Reher GS, López-Sáez JA, Mighall TM, Bindler R (2014) Reconstructing the impact of human activities in a NW Iberian Roman mining landscape for the last 2500 years. J Archaeol Sci 50:208–218. https://doi.org/10.1016/j.jas.2014.07.016

López-Sáez JA, Alba-Sánchez F, López-Merino L, Pérez-Díaz S (2010) Modern pollen analysis: a reliable tool for discriminating *Quercus rotundifolia* communities in central Spain. Phytocoenologia 40:57–72. https://doi.org/10.1127/0340-269X/2010/0040-0430

López-Sáez JA, Sánchez-Mata D, Alba-Sánchez F, Abel-Schaad D, Gavilán RG, Pérez-Díaz S (2013) Discrimination of Scots pine forests in the Iberian Central System (*Pinus sylvestris* var. *iberica*, Pinaceae) by means of pollen analysis. Phytosociological Considerations Lazaroa 34:191–208. https://doi.org/10.5209/rev_LAZA.2013.v34.n1.43599

López-Vila J, Montoya E, Cañellas-Boltà N, Rull V (2014) Modern non-pollen palynomorphs sedimentation along an elevational gradient in the south-central Pyrenees (southwestern Europe) as a tool for holocene paleoecological reconstruction. Holocene 24:327–345. https://doi.org/10.1177/0959683613518593

Mariscal B (1983) Estudio polínico de la turbera del Cueto de la Avellanosa, Polaciones (Cantabria). Cad Lab Xeol Laxe 5:205–226

Mariscal B (1986) Análisis polínico de la turbera del Pico Sertal, de la Sierra de Peña Labra. Reconstrucción de la paleoflora y de la paleoclimatología durante el Holoceno en la zona oriental de la Cordillera Cantábrica. In: López-Vera F (ed) Quaternary climate in western mediterranean. Proceeding of the Symposium on Climatic Fluctuations during the Quaternary in the Western Mediterranean Regions, Madrid, Jun. 16–21, 1986. Universidad Autónoma de Madrid, Madrid, pp 205–220

Mariscal B (1987) Estudio palinológico de la flora holocénica de Cantabria aspectos paleo-climáticos. Universidad Complutense de Madrid, Madrid, Tesis Doctoral

Mariscal B (1989) Comparacion palinologica entre una turbera de la cordillera central y unas turberas de la cordillera cantabrica. In: II. European Paleobot. Conference. Universidad Complutense de Madrid, Madrid, p 28

Mariscal B (1993) Variacion de la vegetacion holocena (4300–280 BP) de Cantabria a traves del analisis polinico de la turbera del Alsa. Estudios Geol 49:63–68. https://doi.org/10.3989/egeol.93491-2338

Mazier F (2001) Validation des signatures polliniques du pastoralisme en moyenne montagne pyrénéenne. Etude des relations végétation/pluie pollinique actuelle et pratiques pastorales. DEA Laboratoire de Chrono-Ecologie UMR 6565 CNRS. Université de Franche-Comté, Besançon

Mazier F, Galop D, Brun C, Buttler A (2006) Modern pollen assemblages from grazed vegetation in the western Pyrenees, France: a numerical tool for more precise reconstruction of past cultural landscapes. Holocene 16:91–103. https://doi.org/10.1191/0959683606hl908rp

Mazier F, Galop D, Gaillard M-J et al (2009) Multidisciplinary approach to reconstructing local pastoral activities: an example from the Pyrenean Mountains (Pays Basque). Holocene 19:171–188. https://doi.org/10.1177/0959683608098956

Menéndez-Amor J, Florschütz F (1963) Sur les éléments steppiques dans la végétation quaternaire de l'Espagne. Bol R Soc Esp Hist Nat Secc Geol 61:121–133

Ministerio para la Transición Ecológica y el Reto Demográfico (MITECO) (2023) Mapa Forestal de España, máxima actualidad. https://www.miteco.gob.es/es/cartografia-y-sig/ide/descargas/biodiversidad/mfe.html

Moore PD, Webb JA, Collison ME (1991) Pollen analysis. Blackwell Scientific Publications, Oxford

Morales-Molino C, Devaux L, Georget M, Hanquiez V, Sánchez-Goñi MF (2020) Modern pollen representation of the vegetation of the Tagus Basin (central Iberian Peninsula). Rev Palaeobot Palynol 276:104193. https://doi.org/10.1016/j.revpalbo.2020.104193

Morales-Molino C, Leunda M, Morellón M et al (2022) Millennial land use explains modern high-elevation vegetation in the submediterranean mountains of southern Europe. J Biogeogr 49:1779–1792

Moreno A, Stoll H, Jiménez-Sánchez M, Cacho I, Valero-Garcés B, Ito E, Lawrence Edwards R (2010) A speleothem record of glacial (25–11.6 kyr BP) rapid climatic changes from northern Iberian Peninsula. Glob Planet Change 71:218–231. https://doi.org/10.1016/j.gloplacha.2009.10.002

Mothershead K, Marquis RJ (2000) Fitness impacts of herbivory through indirect effects on plant–pollinator interactions in *Oenothera macrocarpa*. Ecology 81:30–40. https://doi.org/10.2307/177131

Muñoz-Sobrino C, Ramil-Rego P, Gómez-Orellana L, Díaz-Varela RA (2005) Palynological data on major Holocene climatic events in NW Iberia. Boreas 34:381–400. https://doi.org/10.1111/j.1502-3885.2005.tb01108.x

Ortega-Villazán MT, Morales-Rodríguez CG (2015) El clima de la Cordillera Cantábrica castellano-leonesa: diversidad, contrastes y cambios. Investigaciones Geogr 63:45–67. https://doi.org/10.14198/INGEO2015.63.04

Peñalba MC (1994) The history of the Holocene vegetation in northern Spain from pollen analysis. J Ecol 82:815–832. https://doi.org/10.2307/2261446

Peñalba MC, Arnold M, Guiot J, Duplessy J-C, de Beaulieu J-L (1997) Termination of the last glaciation in the Iberian Peninsula inferred from the pollen sequence of Quintanar de la Sierra. Quat Res 48:205–214. https://doi.org/10.1006/qres.1997.1922

Penas Á, del Río S, Herrero L, Ladero M (2017) The Duero Basin. In: Loidi J (ed) The vegetation of the Iberian Peninsula. Springer, Cham, pp 395–437

Pérez-Díaz S, López-Sáez JA, Pontevedra-Pombal X, Souto-Souto M, Galop D (2016) 8000 years of vegetation history in the northern Iberian Peninsula inferred from the palaeoenvironmental study of the Zalama ombrotrophic bog (Basque-Cantabrian mountains, Spain). Boreas 45:658–672. https://doi.org/10.1111/bor.12182

Pérez-Obiol R, Roure JM (1985) Relaciones entre la vegetación y su espectro polínico en Cataluña. An Asoc Palinól Leng Esp 2:329–338

Pérez-Obiol R, García-Codron JC, Pèlachs A, Pérez-Haase A, Soriano JM (2016) Landscape dynamics and fire activity since 6740 cal yr BP in the Cantabrian region (La Molina peat bog, Puente Viesgo, Spain). Quat Sci Rev 135:65–78. https://doi.org/10.1016/j.quascirev.2016.01.021

Pérez-Obiol R, Soriano JM, Nadal J, Lurbe L, Sánchez-Morales M, Pèlachs A (2019) Les poblacions d'*Abies alba* a la Mata de València d'Àneu a partir de l'anàlisi i el calibratge pol·línic. In: La investigació al Parc Nacional d'Aigüestortes i Estany de Sant Maurici. XI Jornades sobre Recerca al Parc Nacional d'Aigüestortes i Estany de Sant Maurici. Parc Nacional d'Aigüestortes i Estany de Sant Maurici, Lleida, pp 213–220

Pérez-Obiol R, Sànchez M, Pèlachs A, Nadal J, Cunill R, Badia A (2021) Modern pollen rain on an elevational gradient in the catalan Pyrenees. In: Florenzano A, Clò E (eds) Mediterranean Palynology Societies Symposium 2021. Abstracts Book. Modena, pp 46–47

Piotrowska K (2008) Pollen production in selected species of anemophilous plants. Acta Agrobot 61:41–52. https://doi.org/10.5586/aa.2008.005

Pohl F (1933) Freilandversuche zur Bestäubungsökologie der Stieleiche. Beiträge zur Morphologie und Biologie des Pollens IV. Beih Bot Cbl 55:673–692

Pohl F (1937) Die Pollenkorngewichte einiger windblütiger Pflanzen und ihre ökologische Bedeutung. Beiträge zur Morphologie und Biologie des Pollens VII. Beih Bot Cbl 57:113–173

Prentice C, Guiot J, Huntley B, Jolly D, Cheddadi R (1996) Reconstructing biomes from palaeoecological data: a general method and its application to European pollen data at 0 and 6 ka. Clim Dyn 12:185–194. https://doi.org/10.1007/BF00211617

Ramil-Rego P, Muñoz-Sobrino C, Rodríguez-Guitián M, Gómez-Orellana L (1998) Differences in the vegetation of the north Iberian Peninsula during the last 16,000 years. Plant Ecol 138:41–62. https://doi.org/10.1023/A:1009736432739

Räsänen S (2001) Tracing and interpreting fine-scale human impact in northern Fennoscandia with the aid of modern pollen analogues. Veget Hist Archaeobot 10:211–218. https://doi.org/10.1007/PL00006932

Rebelo AG, Siegfried WR, Oliver EGH (1985) Pollination syndromes of *Erica* species in the south-western Cape. South Afr J Bot 51:270–280

Reille M (1992) Pollen et spores d'Europe et d'Afrique du Nord. Laboratoire de Botanique Historique et Palynologie, Université d'Aix-Marseille III, Marseille

Reille M (1998) Pollen et spores d'Europe et d'Afrique du Nord, Supplément 2. Laboratoire de Botanique Historique et Palynologie, Université d'Aix-Marseille III, Marseille

Sainz-Ollero H, Sánchez de Dios R, García-Cervigón Morales A (2010) La cartografía sintética de los paisajes vegetales españoles: una asignatura pendiente en geobotánica. Ecología 23:249–272

Salas L (1993) Análisis palinológico de la turbera de Pico Ano, implicaciones de las variaciones climáticas del Holoceno final.

In: Fumanal García MP, Bernabeu J (eds) Estudios sobre Cuaternario, medios sedimentarios, cambios ambientales, hábitat humano. Universitat de València, València, pp 179–183

Sánchez-Goñi MF, Hannon GE (1999) High-altitude vegetational pattern on the Iberian mountain chain (north-central Spain) during the holocene. Holocene 9:39–57. https://doi.org/10.1191/095968399671230625

Sánchez-Morales M, Pèlachs A, García-Codron JC, Carracedo V, Pérez-Obiol R (2022) Landscape dynamics and fire regime since 17,550 cal yr BP in the Cantabrian region (La Molina peat bog, Puente Viesgo, Spain). Quat Sci Rev 278:107373. https://doi.org/10.1016/j.quascirev.2022.107373

Servera-Vives G, Mus Amezquita M, Snitker G, Florenzano A, Torri P, Estrany Bertos J, Mercuri AM (2022) Modern analogs for understanding pollen-vegetation dynamics in a Mediterranean mosaic landscape (Balearic Islands, Western Mediterranean). Holocene 32:716–734

Stockmarr JA (1971) Tablets with spores used in absolute pollen analysis. Pollen Spores 13:615–621

Strauss SY, Conner JK, Rush SL (1996) Foliar herbivory affects floral characters and plant attractiveness to pollinators: implications for male and female plant fitness. Am Nat 147:1098–1107. https://doi.org/10.1086/285896

Sugita S, Gaillard M-J, Broström A (1999) Landscape openness and pollen records: a simulation approach. Holocene 9:409–421. https://doi.org/10.1191/095968399666429937

Van Geel B, Aptroot A (2006) Fossil ascomycetes in Quaternary deposits. Nova Hedwigia 82:313–329. https://doi.org/10.1127/0029-5035/2006/0082-0313

Van Zeist W, Timmers RW, Bottema S (1970) Studies of modern and Holocene pollen precipitation in southeastern Turkey. Palaeohistoria 14(1968):19–39

Vazquez-Gomez R, Peinado-Lorca M (1993) Relations between modem pollen rain and vegetation in the Sierra de Guadarrama (Madrid, Spain). Ecol Mediterr 19:59–76. https://doi.org/10.3406/ecmed.1993.1715

Von Engelbrechten S (1998) Late-glacial and Holocene vegetation and environmental history of the Sierra de Urbión, North-Central Spain. Doctoral Thesis, University of Dublin, Trinity College, Dublin

Wilmshurst JM, McGlone MS (2005) Origin of pollen and spores in surface lake sediments: comparison of modern palynomorph assemblages in moss cushions, surface soils and surface lake sediments. Rev Palaeobot Palynol 136:1–15. https://doi.org/10.1016/j.revpalbo.2005.03.007

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.