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Modern pollen–vegetation relationships along an altitudinal transect in the central Pyrenees (southwestern Europe)

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Abstract: Modern proxy-calibration studies are a powerful tool for paleoecological interpretation. This paper analyzes the relationships among modern pollen rain, vegetation and altitude in the central Pyrenees, where several paleo-palynological studies have been developed, but a modern analog survey is still unavailable. The work analyzes the pollen content of moss polsters from different vegetation communities along an altitudinal transect, as well as the flora and vegetation using the Braun-Blanquet system. DCCA showed that altitude satisfactorily explains both vegetation (r^2 = 0.988) and pollen (r^2 = 0.841) gradients. Besides the complexity of pollen–vegetation relationships, some regularities were found to be useful for paleoecological and paleoenvironmental interpretation. In general, altitudinal vegetation and pollen patterns show similarities, but pollen belts and boundaries are less well defined, likely because of the homogenizing effect of upward wind transport. Palynological differentiation of montane from subalpine/alpine belts is straightforward from the trends of the more significant pollen types, mainly the low-altitude deciduous trees and the high-mountain herbs. Palynological differences between subalpine and alpine belts, which boundary coincides with the treeline, are more subtle and need quantitative criteria and complementary proxies. From an individual point of view, four main groups of pollen were distinguished, in relation to their usefulness as vegetation and altitudinal indicators: (1) very good indicators, (2) good indicators, (3) non indicators, and (4) allochthonous pollen types. The first two groups resulted to be useful as indicator taxa for modern analogs for paleovegetational and paleoaltitudinal reconstruction, while the latter two groups should be interpreted with caution in paleoenvironmental studies.

Key words: Pollen rain, vegetation belts, mountains, Pyrenees.

Introduction

Studies of modern pollen assemblages and their relationship with vegetation and key environmental factors, or calibration studies, are one of the best tools for qualitative and quantitative reconstruction of paleovegetation and paleoenvironments (Birks and Birks, 1980). Characterizing modern pollen assemblages in a particular region, in relation to the vegetation features and the environmental factors involved, has been recognized as an essential step in studies about its environmental history (Jackson and Williams, 2004; Gosling *et al*., 2005). The interpretation of past pollen records solely in terms of the known biology of the taxa involved is puzzling, because of uncertainties related with pollen production, dispersal and preservation, as well as the identity, location and extent of pollen source, and the size and local characteristics of the catchment area (Birks and Birks, 1980; Faegri *et al*., 1989; Moore *et al*., 1991; Traverse, 1994; Tyson, 1995). Calibration studies overcome problems related to these factors, providing a straightforward correlation between pollen signal, vegetation and environmental features (Jackson and Williams, 2004). The more recent developments in this type of study include quantitative calibrations of modern pollen assemblages in terms of climatic and other environmental parameters, to obtain training sets and transfer functions, useful for reliable quantitative paleoenvironmental reconstruction (Birks, 1995, 1998). Studies on modern pollen assemblages have been developed in different parts of the world, mostly in Europe (eg, Hicks, 1992,

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1993; Hjelle 1997, 1999; Van der Knaap *et al*., 2001; Bunting, 2002, 2003; Nielsen and Vad Odgaard, 2005; Court-Picon *et al*., 2005, 2006; Mazier *et al*., 2006; Finsinger *et al*., 2007; Räsänen *et al*., 2007), North and South America (eg, Behling *et al*., 1997; Bush, 2002; Markgraf *et al*., 2002; Berrío *et al*., 2003; Weng *et al*., 2004; Gosling *et al*., 2005; Whitmore *et al*., 2005; Rull, 2006; Graf and Chmura, 2006), Africa (eg, El Ghazali and Moore, 1998; Elenga *et al*., 2000; Gajewski *et al*., 2002; Watrin *et al*., 2007), Asia (Anupama *et al*., 2000; Yu *et al*., 2004; Shen *et al*., 2006; Djamali *et al*., 2009; Luo *et al*., 2009), and Australia (Dodson, 1982; Walker, 2000). In southern Europe, however, only a few surveys are available, mainly in the Alps and the Pyrenees (Court-Picon *et al*., 2005, 2006; Mazier *et al*., 2006; Ortu *et al*., 2006; Finsinger *et al*., 2007).

The paleoecological significance of the Pyrenees largely relies on the fact that they have been recognized as one of the potential glacial refuge areas from which European forest trees expanded during the postglacial warming (Brewer *et al*., 2002; Terhürne-Berson *et al*., 2004; Magri, 2008; Benito *et al*., 2008). Palynology, together with macrofossil analysis and molecular phylogeography, has been decisive for such a realization. From a palynological point of view, the northern slope of this range has been more intensively studied (see reviews by Jalut *et al*., 1992; Reille and Lowe, 1993; and Visset *et al*., 1996) than the southern one, where studies by Montserrat (1992), Peñalba (1994), Riera *et al*. (2004) and González-Sampériz *et al*. (2006), among others, are worth mentioning. So far, one single study on modern pollen–vegetation relationships has been published, located in the northern slope (Mazier *et al*., 2006). On the southern slope, climate reconstructions are based on aquatic organisms such as chironomids, diatoms and chrysophycean cysts but not pollen (Catalan *et al*., 2002; Pla and Catalan, 2005). The only pollen-based climate reconstruction attempted so far in this region (Pla and Catalan, 2005) used a continental-wide data set of modern pollen assemblages extracted from the European Pollen Database (EPD) and related bioclimatic values as developed by Cheddadi *et al*. (1996). All former interpretations have been based only on the known ecology of the taxa represented in pollen diagrams. The use of large, continental-scale data sets as modern analogs for mountain environments is problematic because the accuracy of paleoclimatic estimations possibly influenced by the following factors: (1) the ‘multiple-analog’ problem, where the fossil assemblage is similar to several modern samples originated from areas with different climatic conditions (Birks, 1998; Finsinger *et al*., 2007); this problem is particularly important when a small number of pollen taxa of high taxonomic rank, for example at family level, are used in the calibration (Birks, 1998); (2) the scarcity of surface samples from the subalpine and alpine belts in the data bases used for paleoclimate reconstruction; (3) the effect of wind-driven uphill transport of tree pollen into the subalpine and alpine zones; (4) the great dependence of relative pollen percentages in spectra from elevated sites to the local physiographic conditions (slopes, exposure to dominant winds) (Ortu *et al*., 2006); (5) the multiple analyst problem, since samples are commonly analyzed by a number of different analysts, and taxonomic consistency in the identifications may become an issue when quantitative paleoenvironmental reconstructions are implemented (Birks, 1998; Finsinger *et al*., 2007). A new methodology for mountains is proposed by Ortu *et al*. (2006). This includes more local studies along altitudinal gradients oriented to facilitate the interpretation of past vertical shifts and changes in vegetation composition, in order to infer past climate changes and land-use changes (Ortu *et al*., 2006). The works of Court-Picon *et al*. (2005, 2006) in the Alps, and Rull (2006) in the Andes are examples of this procedure.

In this paper, we analyze the pollen rain captured in surface samples (mosses), in relation to the flora and vegetation, in an altitudinal transect of the central Pyrenees, from the montane to the alpine vegetation belts. The area belongs to a national park and is relatively well preserved. The general aim is to improve paleoecological interpretations based on pollen, and the particular objectives are the following: (1) to assess the pollen and vegetation gradients, to test if altitude is a controlling factor for their variation and, if so, to define their altitudinal patterns; (2) to establish qualitative and quantitative relationships between pollen rain and vegetation patterns, in order to use them for paleoecological reconstruction in future studies; and (3) to derive consistent pollen–altitude correlations, both collectively and individually, to find potential indicator taxa useful for paleoclimate reconstructions. In fact altitudinal biotic gradients are largely controlled by climatic factors, especially temperature (Court-Picon *et al*., 2005).

Methods

Study area

This research has been carried out in the central Pyrenees (Val d’Aran, NW Catalonia), between about 42°37′–42°45′N and 0°43′–1°01′E (Figure 1). The transect studied lies in the headwaters of river Garona, draining to the north, and includes a sector of Val d’Aiguamòg, and several individual sites from Val del Garona, Val de Valarties, and Circ de Colomèrs, in the peripheral zone of the ‘Aiguestortes i Estany de Sant Maurici’ National Park, created in 1955. Biogeographically, the area studied is mainly of boreoalpine and Eurosiberian character, but Mediterranean elements appear in the lower parts. The climate is influenced by the Atlantic regime, which determines moderate to high precipitation with virtually no water deficit throughout the year. Measured mean annual temperatures range from 9.5°C (Vielha, 974 m a.s.l.) to 2.7°C (Pòrt dera Bonaigua, 2200 m a.s.l.), varying at a rate of 0.55°C/100 m altitude. Total annual precipitation in these two stations is of 968 mm and 1210 mm, respectively, with two maxima, one in the spring (April–March) and another in the fall (November) (Bolós and Capdevila, 1994). The vegetation is arranged in a typical altitudinal succession defining three main belts (montane, subalpine and alpine), the boundaries of which vary with local topographic and climatic conditions, as well as human disturbance. The treeline is situated in the subalpine/alpine boundary. The main human activities are cattle raising and forest exploitation which, in the study area, are restricted to the lowermost altitudes. Recently, tourism has displaced other economic activities, but the zone remains relatively undisturbed in comparison with other comparable Pyrenean regions.

Sampling and sample processing

A total of 33 sampling sites (ARAN-1 to ARAN-33) along an altitudinal transect from 868 m to 2585 m were used for this study (Figure 1). In each site, two-four moss polsters were collected in an area of ~10 m^2 and mixed into one single sample per site. The vegetation was accurately described using the Braun-Blanquet system, which is commonly used in the Pyrenees (Vigo, 1976; Folch, 1981; Bolós, 2001). In this system, a semi-quantitative abundance-dominance index is used to estimate the plant cover for each species, according to the following scale: 5 (>75%), 4 (50–75%), 3 (25–50%), 2 (5–25%), 1 (<5%), + (scarce), r (rare). The altitude was measured with a GPS device. Moss samples were used because of their known suitability as pollen traps and their frequent occurrence in the transect. Furthermore, their pollen content is an average pollen assemblage of several years, as it occurs in sediments, and provides a better record of local vegetation than soil samples, superficial lake sediments or artificial traps (Räsänen *et al*., 2004, 2007; Wilmshurst and McGlone, 2005; Mazier *et al*., 2006). Samples were processed according to standard laboratory

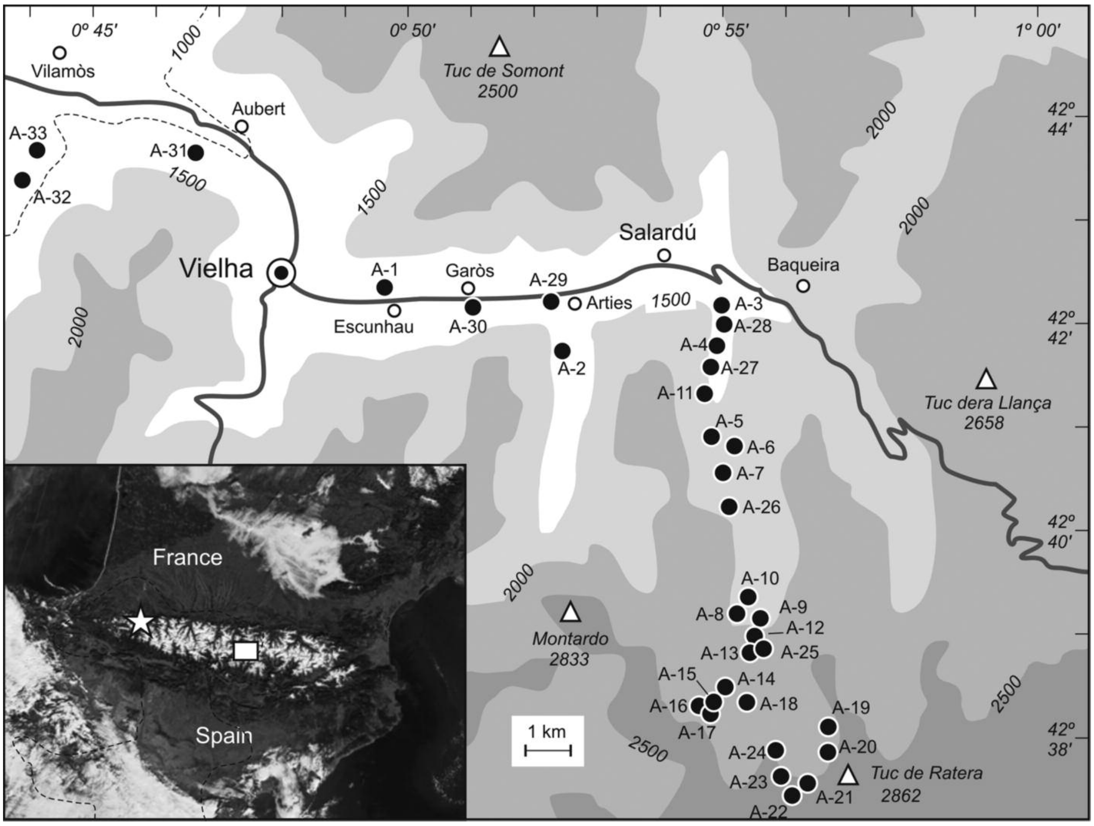

Figure 1 Location map. Sampling sites are indicated by black dots. Open dots are towns and triangles represent the highest peaks of the area. The region studied is indicated by a white rectangle in the satellite image. The approximate location of the study by Mazier *et al.* (2006) is denoted by a star

procedures (Faegri *et al*., 1989; Moore *et al*., 1991), including KOH digestion, sieving, HCl and HF treatment, and acetolysis (see online supplementary data). Two *Lycopodium* tablets (batch 124961, 12,542 spores/tablet) were added to each sample before chemical processing as exotic marker. Microscopic slides were mounted in silicone oil.

Pollen analysis and data management

Pollen was identified to the lowest taxonomic level possible, with the aid of a pollen key (Moore *et al*., 1991), a pollen atlas (Reille, 1992), and the reference collection of the Autonomous University of Barcelona. Pollen counting was conducted until the saturation of diversity and a minimum of 300 pollen grains per sample (Rull, 1987). On many slides *Pinus* was superabundant, and counts of local pollen types were increased, in order to reach statistically representative numbers. In order to minimize the effect of the eventual uneven distribution of pollen grains on the slide, counting was made on regular transects along the whole slides. Aquatic and semi-aquatic taxa (Cyperaceae and Juncaceae) were excluded from the pollen sum, which includes only pollen. Diagrams were plotted with *psimpoll* 4.26 (Bennett, 2002). The zonation was conducted using the method of optimal splitting by information content (Bennett, 1996). Detrended Canonical Correspondence Analysis (DCCA) was used as direct gradient analysis, to elucidate the relationships between pollen or vegetation as a whole and environmental factors, with altitude as the only constraining variable (Barendregt *et al*., 1995; Manly, 1998). Rare elements (those designed with '+' and 'r' in the vegetation analysis, and those below 2% of the total in pollen analysis) were removed from the analysis. DCCA was preferred to Principal Components Analysis (PCA) because the wide altitudinal range considered suggested unimodal instead of linear responses of taxa (Jongman *et al*., 1995). The response of each pollen taxon to the altitude was approached through the Weighed Averaging method (ter Braak, 1995), using the *C2* 1.4 software (Juggins, 2003). Individual pollen–plant relationships were studied using the Spearman rank-order correlation coefficient (Siegel and Castellan, 1988), because the data on plant abundance are semi-quantitative. DCCA and the Spearman coefficient calculations were performed with *MVSP* 3.1 (Kovach, 1999). The indices of coincidence (A), under-representation (U), or over-representation (O) were calculated, to describe the relationship between pollen types and their parent taxa (Hjelle, 1997; Bunting, 2003; Mazier *et al*., 2006). These indices are based on presence-absence data and are defined as follows:

$$A = b_0/ (p_0+p_1+b_0);\ U = p_1/ (p_1+ b_0);\ O = p_0/ (p_0+ b_0) \qquad (1)$$

where b_0 is number of samples in which both the pollen type and its parent plant are present, p_0 is number of samples in which the pollen type is present and the parent plant absent, and p_1 is number of samples in which the parent plant is present and the pollen type absent. All these indices range between 0 and 1. Using these parameters, pollen types are classified into: SAT, Strongly Associated Types ($A > 0.65$); AT, Associated Types (A between 0.50 and 0.65); ORT, Over-Represented Types (low A, high O and $U = 0$); WAT, Weakly Associated Types (low A and relatively high O and U); UT, Unassociated Types ($A = 0$ and high O and U) (Mazier *et al*., 2006).

Results

Vegetation

Based on the altitudinal arrangement of vegetation, three main altitudinal belts were described in the study area (Figure 2): (1) montane, below 1600 m elevation, (2) subalpine, between 1600

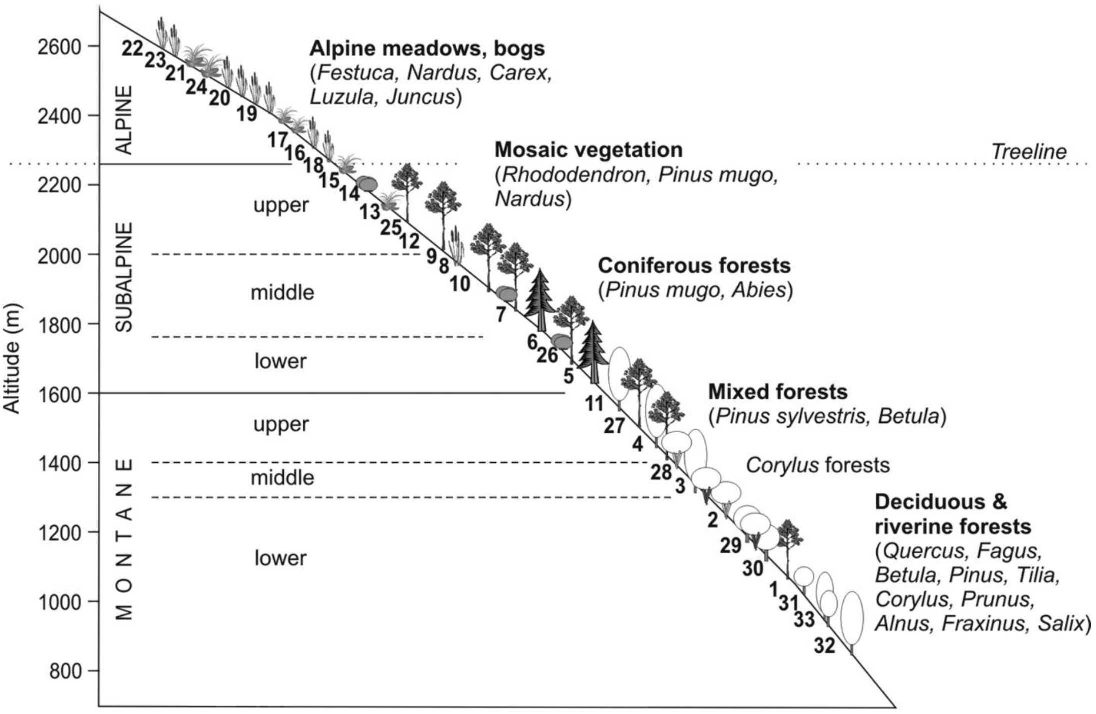

Figure 2 Sketch of the altitudinal arrangement of vegetation and the vegetation belts defined in this study. Numbers correspond to sampling sites (see also supporting online material)

and 2250 m, and (3) alpine above 2250 m. The montane zone is characterized by deciduous forests (sometimes mixed with conifers), and could be further subdivided into three altitudinal layers. The detailed floristic analysis of each site can be seen in the online supporting material. The lower layer (up to 1300 m) is characterized by deciduous forests (mostly *Querco-fagetea*) and riverine forests of several types. Human disturbance is frequent at this altitude, as evidenced by towns, pasture and cultivation, often abandoned and replaced by secondary forests. The main forests at this level are: (1) deciduous oak forests, dominated by *Quercus petraea* with birch (*Betula pendula*), ash (*Fraxinus excelsior*) and beech (*Fagus sylvatica*), (2) mixed forests dominated by beech with pine (*Pinus sylvestris*), (3) forests with *Tilia platyphyllos*, *Prunus avium* and hazel (*Corylus avellana*), and (4) forests with *Prunus avium*, *Corylus avellana* and *Fraxinus excelsior* with abundant *Brachypodium sylvaticum*. Along rivers and streams, there are three types of riverine forests: (1) alder (*Alnus glutinosa*) forests with ash (*Fraxinus excelsior*), (2) ash forests with *Brachypodium sylvaticum*, and (3) willow (*Salix* sp.) forests. The middle layer is a thin layer ranging from 1300 to 1400 m, characterized by deciduous mixed forests with abundant *Corylus avellana* (*Actaeo-Coryletum*). The upper layer (1400–1600 m) is dominated by pine (*Pinus sylvestris*) forests with hazel. The subalpine belt is formed basically by coniferous forests of two types: (1) silver fir (*Abies alba*) forests with *Rhododendron ferrugineum* (*Rhododendro-Pinetum uncinatae abietetosum*) at the lowest part (up to 1750 m), and pine forests of *Pinus mugo* ssp. *uncinata* (*Rhododendro-Pinetum uncinatae*) from 1750 to 2250. Swamps within this belt are characterized by communities of *Scirpus cespitosus* (*Narthecio-Trichophoretum caespitosi*), associations of reeds and sedges (*Juncus pyrenaeus, Carex rostrata* and *Caltha palustris* with *Epilobium palustre*), and peat bogs dominated by *Sphagnum* sp. The uppermost part of the subalpine belt (2000–2250 m) is characterized by a mosaic vegetation constituted by scrubs of *Rhododendron* sp. with scattered pines (*Pinus mugo* ssp. *uncinata*) and patches of *Nardus* sp. meadows, in a more or less open vegetation, which is the transition between the coniferous forests and alpine meadows. The alpine belt is dominated by meadows of *Nardus stricta* (*Selino-Nardetum*) or *Festuca eskia* (*Selino pyrenaei-Festucetum eskia*), with frequent swamps and bogs dominated by sedges (mainly *Carex* sp.), in the more humid areas. In the context of this study, it is interesting to note that in the lowlands below the study area, mostly in the south, some typical Mediterranean elements, notably *Quercus ilex* and the cultivated *Olea europaea* var. *europaea*, are common and locally abundant. Both are absent in the studied transect.

The high species–environment correlation obtained in the DCCA (r = 0.988, $\alpha < 0.001$) shows that altitude satisfactorily explains the species distribution gradient in statistical terms. In a biplot of the site scores using the first two axes, four groups can be recognized (Figure 3). Group 1 includes the sites of the lower part of the transect, up to 1710 m, characterized by different types of deciduous forests (ash forest, mixed oak forest, hazel forest, birch forest). Group 2 includes sites that support coniferous forests of silver fir and pines, located at middle elevations (1640 to 1980 m). Site A-26 from group 1 is noteworthy as it is covered by an open pine forest, more proper of group 2. Group 3 is formed by herbaceous bogs and meadows that correspond to the highest altitudinal belt (1830–2590 m). Finally, group 4 is represented by one single site (ARAN-10, 1910 m), bearing some particular features. The sample is from a peat bog around a small lake, with different species composition than other similar sites. The bog is dominated by *Sphagnum* sp., *Carex lasiocarpa, Menyantes trifoliata*, and *Drosera* sp. The general arrangement of sampling sites suggests that axis 1 reflects the main altitudinal gradient of samples and vegetation, confirming the importance of altitude for explaining the vegetation array. According to the position of these four groups, the treeline, represented by the uppermost boundary of the transition zone, located at 2250 m elevation, may be situated around the score 6.0 of this axis. Axis 2 is more difficult to interpret, as most samples are situated around middle values. However, the position of groups 2 and 4 (conifer forests and a peat bog, respectively, both in the subalpine belt) suggests some gradient related to forested and open vegetation at intermediate altitudinal levels.

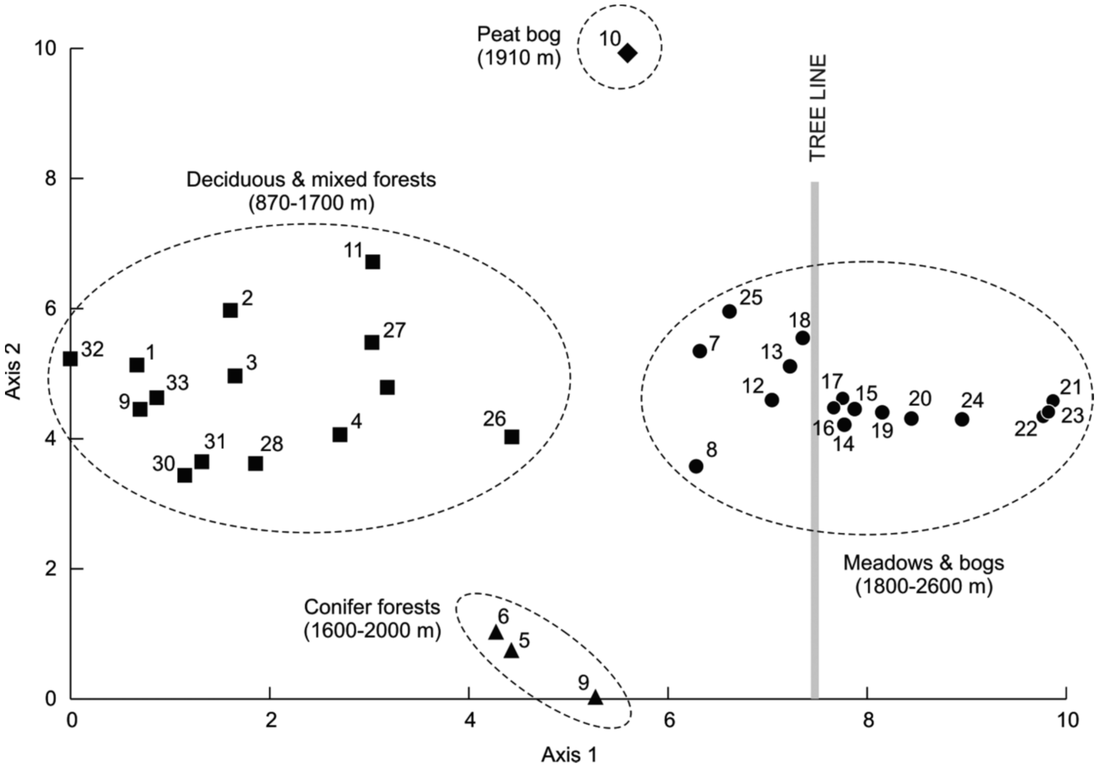

Figure 3 Biplot of the first two DCCA axes for the vegetation data set, representing the dispersion and grouping of sampling sites, according to the vegetation types defined

Pollen

A total of 126 pollen and spore types were recorded, of which 55 were selected for this study. The pollen results are depicted in a percentage diagram, which includes only the pollen types over >2% of total abundance (Figure 4), minor elements are shown in Table 1. The figure is clearly dominated by tree pollen types, while herbaceous species and shrubs are more poorly represented. The more abundant pollen type is *Pinus*, which reaches more than 80% of total pollen sum, and rarely is less than 50%. At high altitudes, herbaceous pollen becomes more abundant (especially above 2100 m), while trees and shrubs experience a small decrease. Three zones were found to be statistically significant. Zone I (from the base to 970 m) shows a low taxonomic richness, and is dominated by *Alnus*, followed by *Betula* and *Quercus*. Notably, *Pinus* and *Corylus* are comparatively low. Among herbs, Poaceae is also scarce, whereas most of the other types are absent. Zone II ranges from 970 m to 1790 m and is characterized by the dominance of *Pinus* and the relatively high abundance of *Corylus*, combined with the low representation of Poaceae. Other deciduous trees, such as *Betula, Fraxinus* and *Salix* are important in some samples of this zone. Herbs are still scarce or absent. Zone III embraces all samples above 1790 m and is characterized by relatively high abundance of Poaceae and Cyperaceae, and low tree and shrub pollen, except for pine. Besides grasses, other herb pollen types present correspond to Chenopodiaceae-Amaranthaceae, *Plantago* and Apiaceae. In general, there is an increase in both abundance and diversity of herbaceous pollen (see also Table 1). Fern spores are generally scarce in most samples and highest abundance of psilate and verrucate monoletes occur in samples from Zone II. Among minor elements (<2% of the total), none is restricted to the montane belt, though Boraginaceae is more common in the lowermost levels. *Juglans* occur mostly in the montane and the subalpine belts, with one single occurrence in the lower alpine belt. The other pollen types occur from 1600 m upwards. *Populus, Ulmus, Bartsia, Potamogeton* and *Viola* occur only in the subalpine zone, while *Phyteuma*, *Euphrasia* and *Gentiana* occur only in the alpine belt, above the treeline.

The WA-optimum and tolerance measure the probability of finding a given pollen type at a certain altitude. Figure 5 shows two extreme examples, one from a lower-altitude taxon (*Corylus*) and another from the alpine belt (Cyperaceae). In the first case, the maximum probability occurs around 1500 m, while in the second; the optimum is at about 2260 m. The same information, for taxa represented in the pollen diagram, is depicted in Figure 6, where it is evident that pollen types from deciduous trees concentrate at lower altitudes, while herb pollen optima are at higher elevations. The pollen of evergreen trees (*Abies*, *Quercus ilex*-type, *Pinus* and *Olea*) and *Fagus* lie in an intermediate position. Two shrub types (*Buxus* and *Corylus*) have their optima close to the deciduous trees, whereas two others (Ericaeae) have their maxima close to the treeline. As in the case of vegetation, there is a well defined altitudinal gradient that explains the distribution of pollen content of the different samples (species–environment correlation: $r = 0.841$, $\alpha < 0.001$), which is represented by axis 1 (Figure 7). The contact between groups II and III is around samples A-9 and A-12, situated around 2000 m, which coincides with the upper limit of the forest–meadows transition zone. Axis two has a lower separation power, but it clearly segregates the two low-altitude samples (A-32 and A-33). The first is dominated by *Alnus* and the second is co-dominated by *Betula* and *Quercus* (deciduous), hence, this axis discriminates the pollen signal of two of the more frequent low-altitude forests.

Discussion and conclusions

Pollen–vegetation relationships

The altitudinal belts defined for the vegetation and the altitudinal pollen zones obtained from the diagram differ in several ways. Pollen Zone I lie at the base of the montane belt, while Zone II

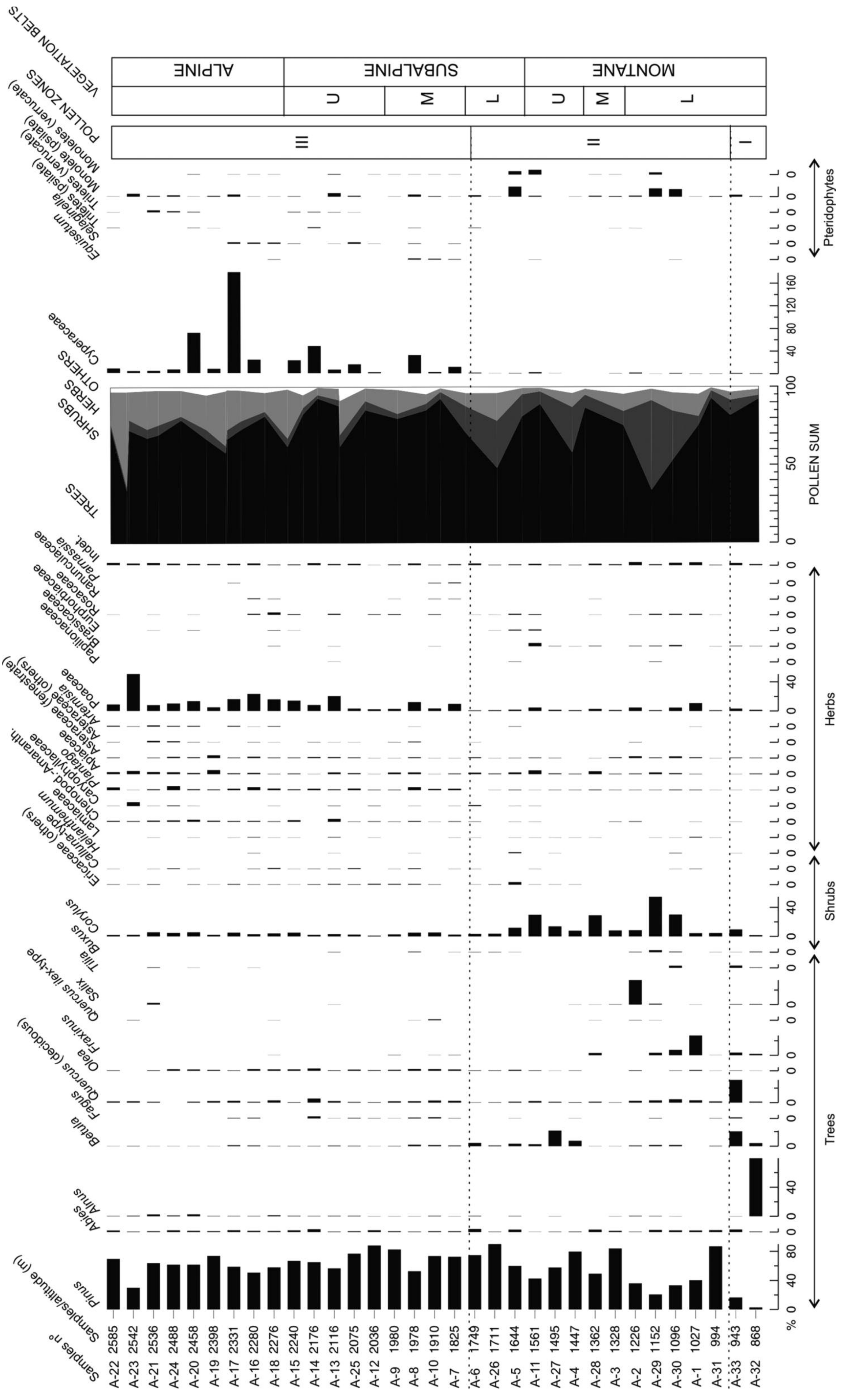

Figure 4 Pollen diagram including the pollen types over 2% of total abundance. Elements outside the pollen sum (Cyperaceae and pteridophytes) are represented at the right side of the summary column

Table 1 Presence/absence data for the pollen types below 2% of total abundance, not represented in the pollen diagram (Fig. 4). A = Alpine, S = Subalpine, M = Montane belts.

Sample (altitude m)	Vegetation belts	BORAGINACEAE	URTICACEAE	*Juglans*	*Populus*	*Ulmus*	*Bartsia*	*Polygonum*	*Potamogeton*	*Viola*	*Eucalypus*-t	LILIACEAE	*Lonicera*	*Campanula*	*Saxifraga*	*Phyteuma*	*Euphrasia*	*Gentiana*
2585	A	–	+	–	–	–	–	–	–	–	–	–	–	–	–	+	–	+
2542	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2536	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–
2488	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2458	A	–	–	–	–	–	–	–	–	–	–	+	–	–	+	+	–	–
2398	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2331	A	–	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–
2280	A	–	–	–	–	–	–	+	–	–	–	+	–	+	–	–	–	–
2276	A	–	+	+	–	–	–	–	–	–	–	+	–	–	–	+	–	–
2240	A	–	–	–	–	–	–	–	–	–	+	–	–	+	–	–	–	–
2176	S	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–
2116	S	–	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–
2075	S	–	–	+	–	–	–	–	–	–	+	+	–	–	–	–	–	–
2036	S	–	–	–	–	–	–	–	–	–	–	–	+	–	–	–	–	–
1980	S	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1978	S	–	–	+	–	–	–	–	–	–	+	+	–	–	–	–	–	–
1910	S	+	–	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–
1825	S	–	–	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–
1749	S	–	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–
1711	S	–	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–
1644	S	–	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
1561	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1495	M	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1447	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1362	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1328	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1226	M	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1152	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1096	M	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
1027	M	+	–	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–
994	M	+	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
943	M	–	–	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–
868	M	+	+	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

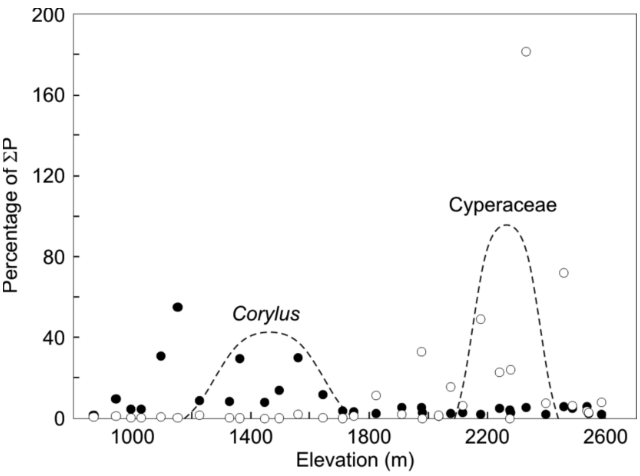

Figure 5 Example of WA estimations for optima and tolerance, using two extreme situations, one from low altitude pollen type (*Corylus*, solid circles) and another from a high altitude element (*Cyperaceae*, open circles)

embraces most of the montane belt and the lower half of the subalpine belt, including the transition zone. Zone III coincides with the upper half of the subalpine belt and the entire alpine belt. The lower montane vegetation belt can be characterized by the presence of pollen from deciduous trees such as (in ascending order) *Alnus*, *Betula*, *Quercus* (deciduous), *Fraxinus* and *Salix*, which are absent in the upper levels (Figure 4). In the middle and upper montane belts, the assemblages are almost exclusively composed of *Pinus*, which is dominant, and lower quantities of *Corylus*, with the local presence of *Betula* in the uppermost levels. The subalpine belt is absolutely dominated by *Pinus* pollen. Poaceae and Cyperaceae start to appear in low quantities, and the pollen from the deciduous trees of the montane belt is virtually absent. In the alpine belt, the same situation is maintained, though grasses and sedges may be locally more abundant than *Pinus*. The upper forest limit has no particular palynological signal that allows its identification. The altitudinal arrangement of WA-optima is consistent with the formerly defined vegetation belts, except for some interesting cases. The montane belt is characterized by the optima of trees and low-elevation shrubs, all of them characteristic of the deciduous forests. The subalpine belt shows a mixture of tree pollen from the conifer forests and *Fagus*, herbs and Ericaeae shrubs. It is interesting that *Olea* and *Quercus ilex*-type have their optimum within this belt, around 2020 and 1810 m, respectively, though their parent plants are absent from the transect, which suggests an efficient upward wind dispersal. In this case, the treeline is clearly marked by the end of tree and shrub pollen optima.

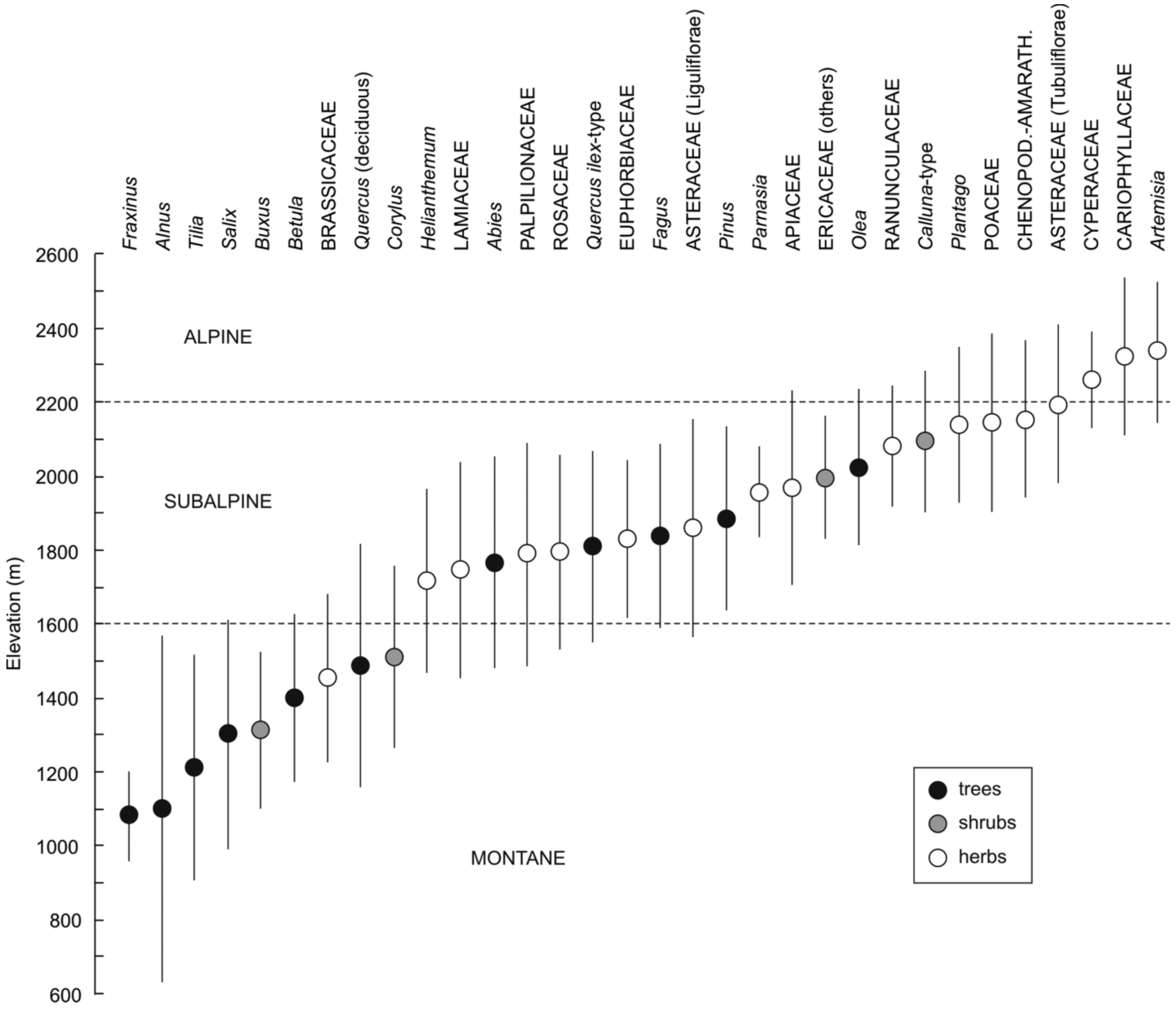

Figure 6 WA optima (circles) and tolerance (bars) for the elements represented in the pollen diagram

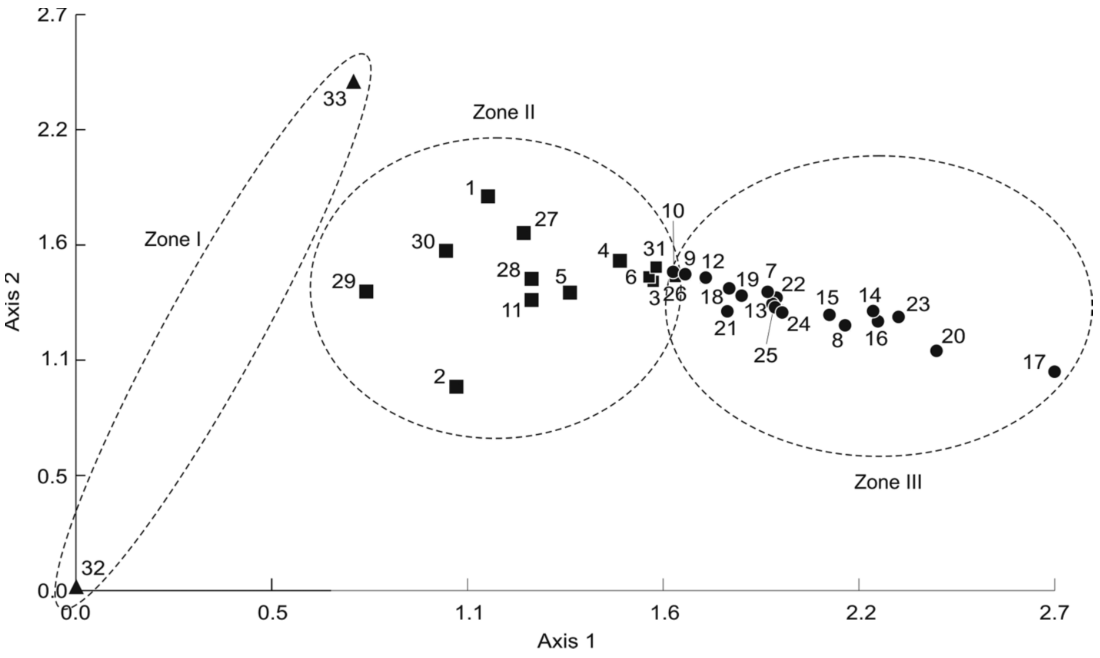

Figure 7 Biplot of the first two DCCA axes for the pollen data set, with sampling sites grouped according to the pollen zones obtained

The correlation coefficient for the major pollen types recorded is given in Table 2. Eleven taxa show significant correlations, ranging from 0.449 to 0.688. Considering the coincidence, over-representation and under-representation indices (Table 2), the more strongly associated types (SAT) are Apiaceae, Asteraceae (others), Cyperaceae and Poaceae, followed by (AT) Asteraceae (fenestrate), *Calluna*-type, *Fraxinus* and Rosaceae; whereas the less associated types (UT) are *Artemisia*, Chenopodiaceae-Amaranthaceae, Ericaceae (others), Euphorbiaceae, *Fagus*, *Gentiana*, *Helianthemum*, *Olea* and *Quercus ilex*-type. These patterns agree with a previous study carried out on the western Pyrenees (Mazier *et al*., 2006), where 11 of the 15 coincident taxa show the same degree of association, these are: Cyperaceae and Poaceae (SAT); *Calluna* (AT); *Abies*, *Fagus*, *Plantago* and *Quercus* (ORT); and Carypohyllaceae, Ericaceae, Liliceae and Ranunculaceae (WAT). Other pollen types are not comparable because the study of Mazier *et al*. (2006) was developed on a lower altitudinal level (below to 1500 m), in a region without Mediterranean influence, and highly disturbed by human activities. These indices measure the degree of association among pollen and their corresponding parent plants along the whole transect. The comparison of pollen percentages and parent plant values by taxon along the transect allowed the establishment of the following pollen groups (Figures 8–11).

Very good indicator pollen types (VGI)

The local occurrence and abundance of both pollen and parent taxa show the same altitudinal patterns. This is the case of *Fraxinus* and *Salix*, the first restricted to the montane belt, and the second present in the montane and the alpine belts (Figure 8). In the montane belt, both genera are represented by trees mainly of riverine forests. In the high mountain, the *Salix* pollen derives from the dwarf willow (*Salix herbacea*), which is present and locally abundant in some highermost sample plots. Ericaceae (others) also belongs to this group, but both pollen and parent plants are restricted to the subalpine and alpine belts.

Good indicator pollen types (GI)

The local occurrence and abundance of pollen types and parent taxa show similar altitudinal patterns. The best examples are *Betula* and *Corylus*, which pollen and species (*B. pendula, C. avellana*) are concentrated in the mountain belt (Figure 9). In both cases, the parent plant is absent from the upper belts, but their pollen is present in low abundances, likely because of wind dispersal. Other pollen types of this group are *Quercus* (deciduous), *Tilia*, *Alnus, Buxus* and Brassicaceae, in the montane belt; and *Plantago, Calluna*-type, Poaceae, Asteraceae (others) and Cyperaceae, mostly in the alpine belt. Apiaceae falls within this group, but it is not restricted to any particular altitudinal belt.

Non-indicator pollen types (NI)

There is no relationship between the altitudinal patterns of occurrence and abundance of pollen types and their parent taxa. This is the case of *Fagus*, of which parent plants (*F. sylvatica*) are restricted to the lowermost part of the montane belt (up to 1000 m), but its pollen reaches the alpine belt (up to 2300–2400 m), with a maximum around 2200 m (Figure 10). *Pinus* and *Abies* are similar, with their parent species (*P. sylvestris, P. mugo* ssp. *uncinata* and *A. alba*) growing at intermediate altitudinal levels, and their pollen more or less evenly distributed along the transect. Asteraceae (fenestrate) and Lamiaceae are also spread along the transect, but their parent plants are almost restricted to the alpine and montane belts, respectively. In the case of Ranunculaceae, Rosaceae, Fabaceae and Caryophyllaceae, there is no any regular relationship between pollen and parent plant patterns.

Allochthonous pollen types (A)

The pollen is present and relatively abundant, although the parent plants have not been found in any of the sites analyzed. The case of *Olea* is especially noteworthy, because this lowland Mediterranean tree is absent from the region and its surroundings, but its pollen occurs along the whole transect, reaching values of 2–3% in the subalpine and alpine belts (Figure 11). Chenopodiaceae-Amaranthaceae, *Helianthemum* and *Quercus ilex*-type are similar in the pattern, but with lower abundances.

Paleoenvironmental significance

The beneficial input that this type of study can provide for paleoenvironmental reconstruction is the existence of consistent pollen–vegetation altitudinal patterns and (ideally) key boundaries, useful

Table 2 Degree of association between abundance of pollen in moss samples and the abundance of source plants in vegetation plots. The Spearman rank-order correlation coefficient (R) measures the quantitative statistical relationship. The coincidence (A), overrepresentation (O) and underrepresentation (U) parameters and its derived classification into SAT (Strongly Associated Types), AT (Associated Types), ORT (Over-Represented Types), WAT (Weakly Associated Types) and UT (Unassociated Types) measure the degree of association based on presence/absence data (see methods for more details). Correlation coefficients significant at α < 0.01 are in bold.

Pollen taxa	R	A	0	U	Association
Abies	0.262	0.333	0.666	0.000	ORT
Alnus	0.297	0.032	0.967	0.000	ORT
Apiaceae	0.162	0.848	0.151	0.000	SAT
Artemisia	–0.192	0.000	1.000		UT
Asteraceae (fenestrate)	0.173	0.600	0.307	0.181	AT
Asteraceae (others)	0.320	0.757	0.193	0.074	SAT
Betula	**0.592**	0.281	0.718	0.000	ORT
Boraginaceae	0.343	0.222	0.500	0.714	WAT
Buxus	**0.454**	0.153	0.846	0.000	ORT
Calluna-type	**0.563**	0.619	0.350	0.071	AT
Caryophyllaceae	0.233	0.380	0.384	0.500	WAT
Chenopod.-Amaranth.	–0.241	0.000	1.000		UT
Corylus	**0.591**	0.272	0.727	0.000	ORT
Brassicaceae	**0.638**	0.352	0.600	0.250	WAT
Cyperaceae	**0.501**	0.774	0.200	0.040	SAT
Ericaceae (others)	**0.549**	0.440	0.541	0.083	WAT
Eurphorbiaceae	–0.207	0.000	1.000	1.000	UT
Fagus	0.282	0.090	0.909	0.000	ORT
Fraxinus	**0.688**	0.538	0.416	0.125	AT
Gentiana	–0.074	0.000	1.000	1.000	UT
Helianthemum	–0.137	0.000	1.000		UT
Lamiaceae	0.191	0.440	0.500	0.214	WAT
Liliaceae	0.011	0.125	0.500	0.857	WAT
Olea	–0.204	0.000	1.000		UT
Papilionaceae	0.000	0.344	0.333	0.583	WAT
Parnasia		0.384	0.000	0.615	WAT
Pinus	**0.572**	0.393	0.606	0.000	ORT
Plantago	**0.449**	0.280	0.718	0.000	ORT
Poaceae	**0.473**	1.000	0.000	0.000	SAT
Quercus (deciduous)	0.133	0.181	0.818	0.000	ORT
Quercus ilex-type		0.000	1.000		UT
Ranunculaceae	0.019	0.208	0.285	0.772	WAT
Rosaceae	0.079	0.606	0.130	0.333	AT
Salix	0.321	0.315	0.625	0.333	WAT
Tilia	0.244	0.142	0.833	0.500	WAT

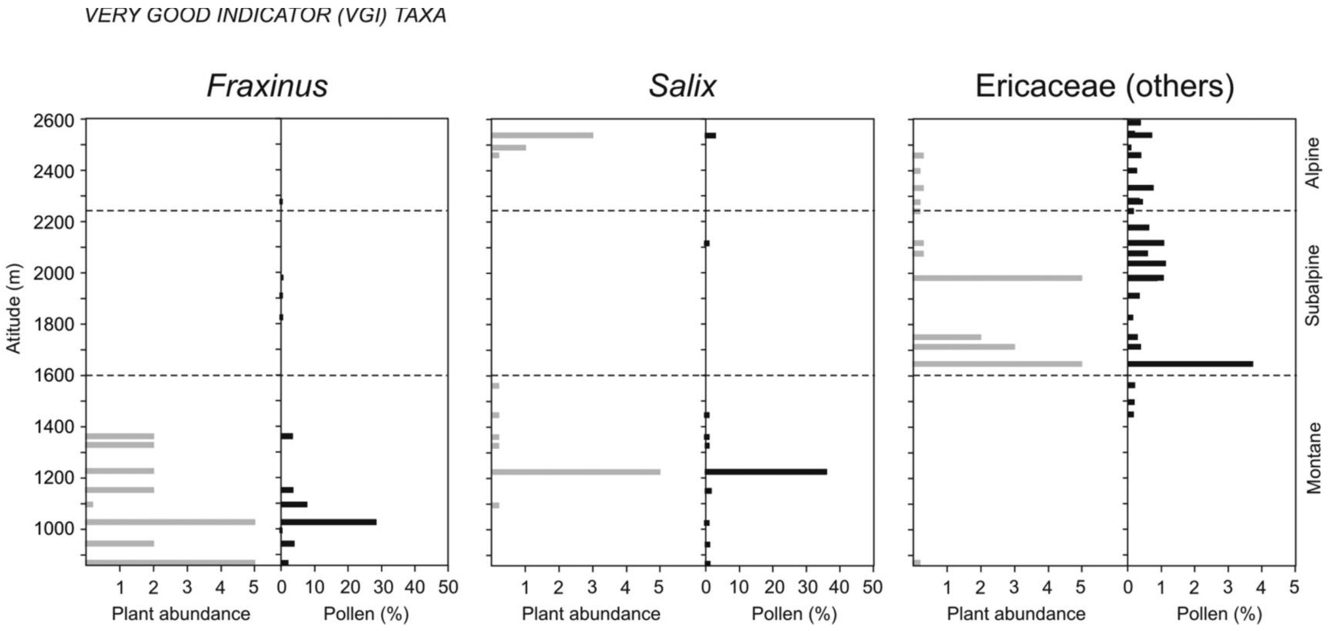

Figure 8 Comparison of plant abundance (grey bars) and pollen percentages (black bars) for the *Very Good Indicator* (VGI) taxa

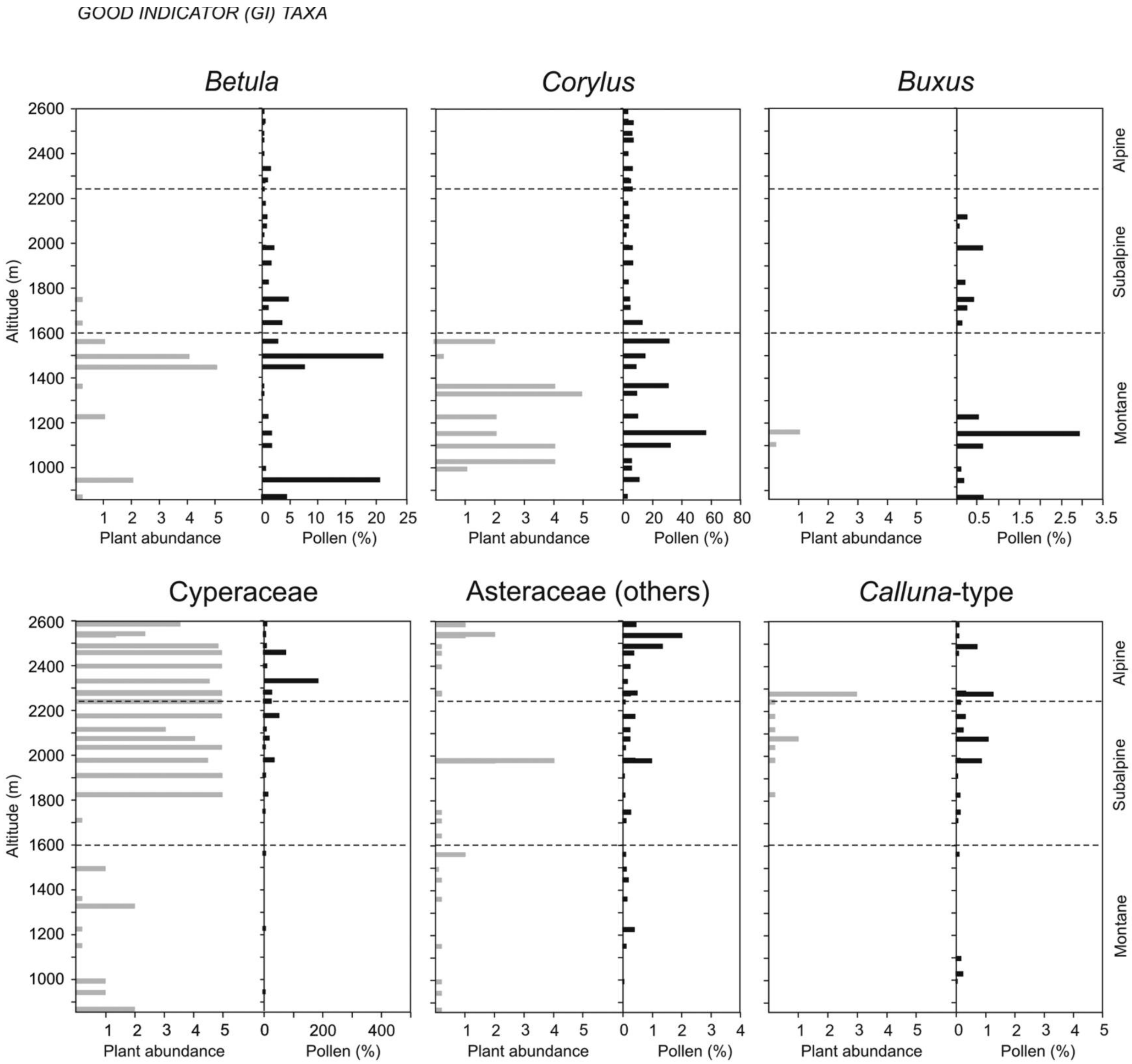

Figure 9 Comparison of plant abundance (grey bars) and pollen percentages (black bars) for selected *Good Indicator* (GI) taxa. Note that Cyperaceae are outside the pollen sum, so its percentages may exceed 100%

to record past vegetation changes linked to climatic and other environmental changes. This section analyzes the data obtained in the Pyrenean transect from this point of view. Taken globally, vegetation and palynological belts show an imperfect matching. Pollen belts tend to be wider and with less defined boundaries, which is likely due to the homogenizing effect of wind dispersal, especially from lower to upper altitudinal levels. This effect is clearly shown by pollen of conifer trees such as *Pinus* or *Abies*, which species do not penetrate into the alpine belt, but their pollen is recorded in high abundance up to the highest part of the transect (Figure 8). The superabundance of *Pinus* pollen in all mountain belts is also a common feature in modern pollen samples from the Alps (Court-Picon *et al*., 2005, 2006). The case of *Fagus* is also noteworthy, because the tree is present only at lower levels (<1000 m), but its pollen is recorded up to 2300–2400 m, with an optimum around 1800 m (Figure 6). Other deciduous trees (*Betula*, *Corylus*, *Quercus*, *Tilia* and *Alnus*) show also upward wind transport, but to a lesser extent. The reverse situation, ie, pollen widespread but the parent plants restricted to higher altitudes, is infrequent and has been only observed in the Asteraceae (others)-type (Figure 8). If we consider the pollen assemblage as a whole, the more clear distinction is between the montane belt and the upper ones, with the boundary situated slightly above (~150 m) the vegetation limit (Figure 4). Besides the consistent dominance of *Pinus* pollen at all levels (except for some samples at the base), the montane belt is the dominion of deciduous tree pollen, while the subalpine and alpine belts are characterized by assemblages dominated by grasses and sedges. In the altitudinal arrangement of the WA optima of the more significant pollen types, there is also a clear break in the montane/subalpine boundary, which reinforces the possibility of recognizing this limit palynologically. From a paleoecological point of view, this can be useful to differentiate between these two altitudinal levels in a pollen record, and to reconstruct their potential vertical displacements. The key altitude, which marks this palynological differentiation, is ~1800 m. The lowermost part of the montane belt, with upper boundary around 950 m is also easy to differentiate palynologically by the abundance of *Alnus*, *Betula* and *Quercus* (deciduous), in front of the other deciduous trees, which

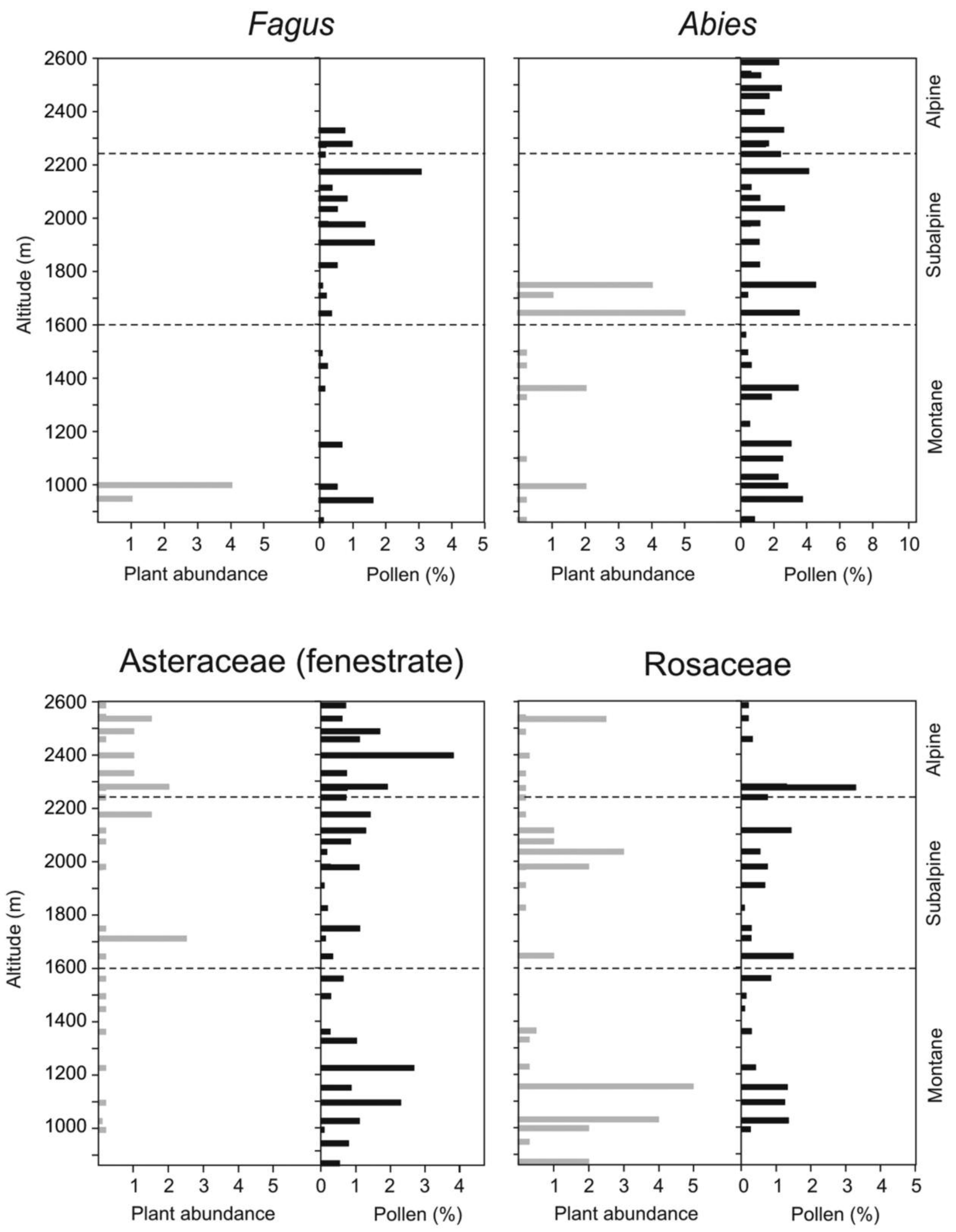

Figure 10 Comparison of plant abundance (grey bars) and pollen percentages (black bars) for selected *Non-Indicator* (NI) taxa

increase above this boundary. The precise altitudinal placement of the treeline is not easy only from a palynological point of view. The only change observed in the diagram is quantitative, and consists of a significant increase in Cyperaceae (around 2300 m), which diminishes upwards. Some minor elements (*Juglans*, *Artemisia*, *Phyteuma* and *Campanula*) can help broadly define the treeline interval, although they can not precisely identify its exact position (Table 1). The use of other types of evidence, such as macrofossils and conifer stomata remains, is needed to record past treeline displacements (Hansen, 1995; Tinner *et al*., 1996; Hicks, 2001; Seppä and Hicks, 2006; Finsinger *et al*., 2007).

The individual patterns of several pollen taxa can provide more information of potential utility for paleoecological reconstruction. The WA analysis (Figure 6) is useful because it provides a measure of the altitudinal range at which it is more probable to find a given pollen type. However, it should be taken into account that this does not always reflect the presence and/or abundance of the parent taxa at the same altitude, as discussed above, especially in cases such as *Olea* or *Quercus ilex*-type. Similarly, the WA optima and tolerance do not correctly estimate the abundance of pollen for taxa with high dispersion power, as for example *Pinus* or *Abies*, the pollen of which is widespread and with similar percentages along the whole sampling range, or for taxa with a skewed distribution (*Alnus*), or pollen types produced by several plant species present along the gradient (eg, Asteraceae, Apiaceae). Among the first, *Fraxinus* is an excellent paleoenvironmental indicator, as its pollen has a neat upper boundary of occurrence at ~1400 m (Figure 8). As stated before, *Salix* pollen is a good indicator of the local presence and abundance of its parent taxa, but it does not provide information about altitudinal or vegetational boundaries by itself. However, it can be highly informative in combination with other taxa (*Pinus*, *Corylus*, Poaceae, Cyperaceae), to discriminate between the lower montane and the alpine belts. Ericaceae (others) is also an excellent indicator of the montane/subalpine boundary, as it occurs almost only above it. The utility of GI types relies on their abundance patterns, and are the best proxies for the montane/subalpine boundary, which can be easily identified by a dramatic drop in *Betula*, *Corylus* and Brassicaceae around 1500–1600 m. Also in this group, *Quercus* (deciduous), *Tilia* and *Alnus* are excellent to characterize the lowermost montane belt, up

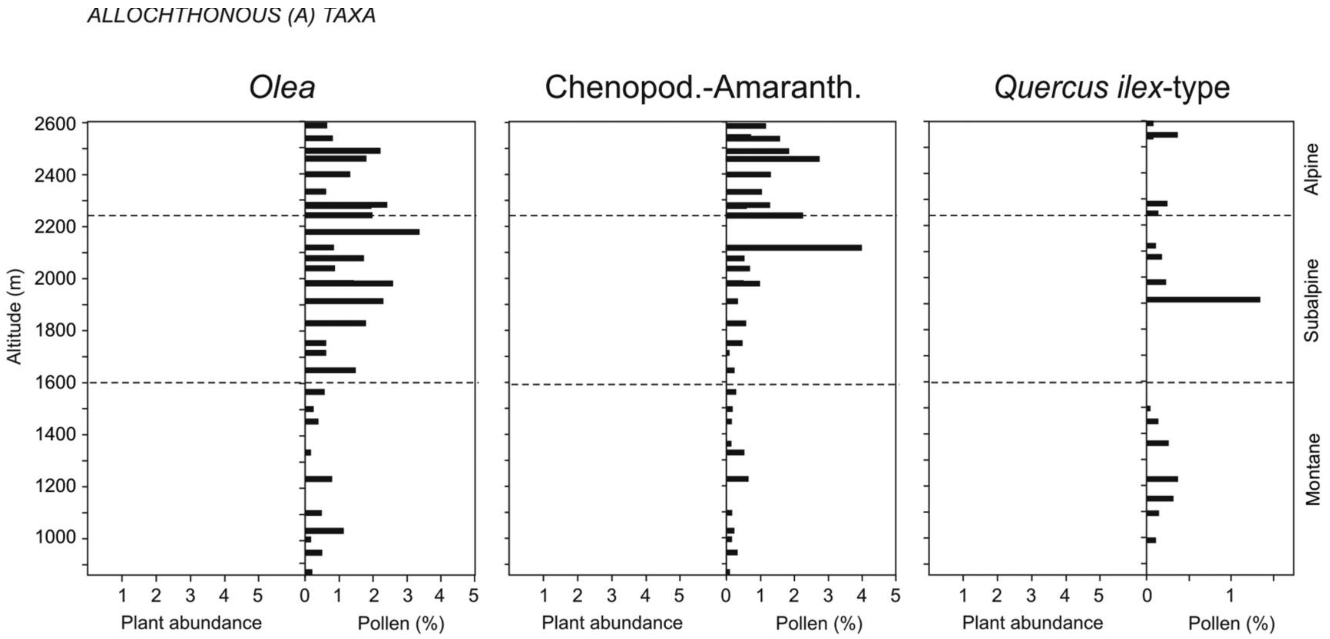

Figure 11 Comparison of plant abundance (grey bars) and pollen percentages (black bars) for *Allochthonous* (A) taxa

to 1000–1100 m, while Cyperaceae, *Calluna*-type and Asteraceae (others) are good indicators for altitudes above 2000 m. Among the NI pollen types, Caryophyllaceae only occurs in the subalpine and alpine belts. There is also a peak of Ranunculaceae pollen in the treeline, but it is not clear if this is a regular feature or a local phenomenon. The others do not show any indicator potential in relation to altitude. Concerning allochthonous pollen (A), *Olea* deserves special attention. The source plant for this pollen is mainly *Olea europaea* var. *europaea* (probably with minor contribution from the wild, uncommon *O. europaea* var. *sylvestris*), a tree commonly cultivated in the Mediterranean lowlands, the pollen of which has been considered an indicator of low altitude environments and warm climates (Osborne *et al*., 2000). In our transect, despite the absence of the parent plant, its pollen occurs regularly at any altitude, with maximum values around the treeline; therefore, its interpretation in terms of paleoclimate should be very careful. This is supported by the fact that *Olea* pollen is a usual component of the airborne pollen flora in the Mediterranean region and one of the main causes of allergies (De Linares *et al*., 2007). The pollen of *Olea* is not mentioned in previous studies to be found from the western Pyrenees (Mazier *et al*., 2006) or the Alps (Court-Picon *et al*., 2005, 2006; Ortu *et al*., 2006). The parent plants do not occur in the lowlands of these regions, and the known dispersion power of this pollen type is of about 50 km from its source (Osborne *et al*., 2000). However, in a survey covering most of the Italian peninsula and the Italian side of the Alps, the pollen of *Olea* and *Quercus ilex*-type showed their higher values in the lowlands, where the parent plant is present, but they also occur in many mountain samples, confirming the efficient upward dispersion power (Finsinger *et al*., 2007). The case of Chenopodiaceae-Amaranthaceae pollen is similar. Usually, the pollen of Chenopodiaceae is considered an indicator of human disturbance at lower altitudinal levels (Mazier *et al*., 2006), but the lack of sufficient taxonomic precision is a handicap for a sound interpretation. The potential sources for *Helianthemum* pollen are *H. nummularium*, a common species ranging from the lowlands to the alpine belt, and *H. oleandicum*, present in the pastures growing on calcareous substrates (Vigo, 1976). The absence of these species in the inventories (see online supporting material), however, prevents further discussion. The *Quercus ilex* pollen type is produced by *Quercus ilex* and *Q. coccifera*, both restricted to the adjacent Mediterranean lowlands. Although this type occurs irregularly and in lower abundance (< 0.5%, except for a peak in the middle subalpine belt) throughout the transect, it reaches the highermost elevations surveyed here, which warns against a straightforward interpretation of its presence in the pollen diagrams.

Natural versus anthropogenic changes

A high proportion of modern analog studies developed in Europe deal with landscapes highly modified by human activities (cultural landscapes), where pollen types indicative of human disturbance are frequent (eg, Gaillard *et al*., 1992, 1994; Hjelle, 1997, 1998, 1999; Court-Picon *et al*., 2005, 2006; Mazier *et al*., 2006; Ortu *et al*., 2006). This constrains the comparison of these works with our study, which is in a transect that has been under protection for more than 50 years. Mazier *et al*. (2006), working on the western Pyrenees, suggest that *Artemisia*, Chenopodiaceae and two *Plantago* species (*P. lanceolata* and *P. major/media*) are indicators of regional human action not related to any specific activity, while the simultaneous presence of Asteraceae, *Cirsium*-type, *Galium*-type, Ranunculaceae, *Stellaria*-type and *Potentilla*-type is associated with local grazing. In our study, taxa related to the indicators of regional human disturbance have been found, all of them concentrated in the upper altitudinal belts. The pollen of *Plantago* is a good indicator of the presence of the parent plant, and is more abundant from 1800 m upwards (Figure 8), but the only species found at these altitudes is *P. alpina* (see online supporting material), a typical high-mountain species (Vigo, 1976). The Chenopodiaceae-Amaranthaceae type is also more abundant above the montane belt, especially in the alpine level, but plants of these families have not been found in our study (Figure 8), suggesting that this pollen is transported upwards from more disturbed, lowland areas. In the case of *Artemisia*, its pollen is present almost only in the alpine belt, but the parent species remains unknown, because none of the two high-mountain species of this genus – *A. eriantha* and *A. gabriellae* (Vigo, 1976) – have been found along the transect (see online supporting material). Among the indicators of local grazing, only Asteraceae and Ranunculaceae types have been recorded, but it is not possible to know if these types are the same as those of Mazier *et al*. (2006). Other European pollen indicators or grazing (eg, *Potentilla,* *Juniperus, Trifolium*), mowing (eg, *Centaurea, Scleranthus, Polygonum*) or elements from ruderal communities such as *Rumex* or *Galium* (Behre, 1981; Hicks, 1988, 1992; Gaillard *et al*., 1992, 1994; Hicks and Birks, 1996; Hjelle, 1999), are absent from our transect. In the Alps, additional anthropogenic indicators of mowing, grazing and cultivation, as for example *Sanguisorba*, *Vicia*, *Onobrychis*, *Serratula*, *Sinapis* or *Papaver*, have been found in modern samples (Court-Picon *et al*., 2005, 2006), but they are equally absent from our transect. These results emphasize the potential of the transect of this study for recording natural environmental changes. Further work should be oriented to the study of nearby areas under higher human pressure, to obtain modern analogs for past human-induced ecological changes.

Final remarks

This work is a first step in a process towards the establishment of qualitative and quantitative relationships between modern pollen, vegetation, elevation and key environmental parameters (temperature, precipitation, etc.), in the central Pyrenees. A first attempt to explore this possibility using the data set analyzed here gave promising but still improvable preliminary results. Indeed, the use of Weighted Averaging-Partial Least Squares (WA-PLS) regression between the pollen set (48 variables, 33 cases) and altitude provided a determination coefficient of $r^2_{\text{jack}} = 0.375$ and a Root Mean Square Error of Prediction (RMSEP) of 427 m, which is about 26% of the total length of the altitude gradient. These values are still below the usual performance numbers for successful models in mountains elsewhere (Rull, 2006) and could be improved with the incorporation of more transects in adjacent areas, and the use of additional statistical tools (Ortu *et al*., 2006).

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