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# Modern pollen assemblages from grazed vegetation in the western Pyrenees, France: a numerical tool for more precise reconstruction of past cultural landscapes

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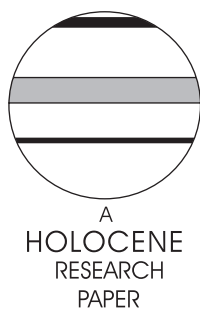
**Abstract:** Modern pollen assemblages from grazed vegetation in the Pyrenees Mountains (France) were studied with the aim of providing a calibrated model for reconstructing past pastoral activities. The modern analogues were selected to cover the major gradients of grazing pressure and degree of openness. The vegetation was surveyed by means of the synusial integrated method, assessing the structure and the patchiness of the pastoral phytoceonoses. A correlative model (Redundancy analysis) was devised relating 61 modern pollen spectra with 37 explanatory vegetation and land-use variables. It was shown that wooded, open grazed and nitrophilous sites are clearly separated from one another and that the model can be simplified using three relevant vegetation types as explanatory variables: dry heathland, semi-open oak forest and overgrazed community, respectively related to gradients of openness, soil richness and grazing pressure. When reconstructing past pastoral activities with fossil pollen spectra, it is important to consider scale-dependent influences of plant species. Low frequencies of well-dispersed taxa such as *Artemisia*, Chenopodiaceae, *Plantago lanceolata* and *Plantago major/media* must be interpreted with care since they reflect more regional, rather than local, input into the pastoral landscape. In contrast, the simultaneous occurrence of Asteroideae, Cichorioideae, *Cirsium*-type, *Galium*-type, Ranunculaceae, *Stellaria*-type and *Potentilla*-type pollen is clearly related to grazing on a local scale. Calculation of Davis indices also shows that Cichorioideae, *Galium*-type and *Potentilla*-type indicate the very local presence of the corresponding plants. These pastoral plant indicators may have a limited geographical validity, ie, mountainous regions with crystalline bedrock, which may indeed also provide the framework for the application to fossil spectra of the modern pollen/vegetation/land-use models presented here.

**Key words:** Integrated synusial approach, modern pollen, vegetation history, land use, pastoral indicators, scale, numerical analyses, western Pyrenees, France.

## Introduction

The reliability of pollen analysis as a tool for the reconstruction of past vegetation depends on good calibration between present pollen deposition and vegetation, and on the precise understanding of how current species composition is reflected in pollen assemblages. In attempting to evaluate not only human presence but also the nature, extent and duration of human activity, it is important to be able to recognize which specific plant community or individual taxon is representative of a certain type of land use such as cultivation, pasturing, trampling and human settlement or mowing.

The interpretation of anthropogenic activity in pollen diagrams relies on several complementary approaches. The most common approach is the 'indicator species' approach, which uses the ecological characteristics of different species,

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especially those favoured by human activity and today found mainly in human-induced vegetation types (Behre, 1981; Vorren, 1986; Hicks, 1988). Another interpretation tool is the 'comparative approach': comparisons of modern and fossil pollen spectra using all taxa, therefore a community-based approach (Wright, 1967). A wide range of communities/pollen assemblages is needed to increase our understanding of past landscapes and past land-use changes. In northern Europe, modern pollen assemblages and related vegetation, as well as land-use data, have been used to provide a basis for numerical comparisons (Berglund and Ralska-Jasiewiczowa, 1986; Berglund *et al.*, 1986; Gaillard *et al.*, 1992, 1994; Hicks and Birks, 1996; Hjelle, 1999a; Räsänen, 2001). These studies identified pollen assemblages and taxa indicators of various human-induced vegetation types. Despite these valuable contributions to the interpretation of pollen diagrams, the pollen/vegetation/land-use relationships found in northern Europe are not necessarily applicable in other areas, such as the mountainous regions of Mediterranean Europe (Galop, 1998; Galop *et al.*, 2003; Court-Picon, 2005). Many pollen diagrams from the western Pyrenees Mountains have been produced recently (Galop, 1998; Galop *et al.*, 2003), but no reconstruction of past vegetation or landscape units by means of comparisons of modern and fossil pollen spectra has been attempted so far.

Therefore, the objectives of the present study in the Pyrenees Mountains were:

- to investigate pollen representation of trees and herbs in modern pollen assemblages from characteristic vegetation types;
- to assess the major gradients in modern pollen assemblages and relate these to measured environmental variables;
- to test whether different vegetation types with their specific vegetation structure, as described by the integrated synusial approach, can be used efficiently to express the vegetation/pollen relationship;
- to establish whether various degrees of openness and grazing pressure produce significantly distinct modern pollen spectra, and to identify pollen taxa characteristics of pastoral activities.

The comparative approach requires a search for modern analogues of past landscapes and vegetation communities. Owing to the elevation and the steep slopes, grazing seems to have always been the main land-use practice in the Iraty Mountains of the Basque Country. Today, farmers maintain traditional land-use practices based on transhumance from the valley to the summer pastures. The main activity is sheep raising for milk and cheese. This production system necessitates, for each shepherd and his flock, small enclosures for gathering the herd, a milking corridor, a hut for cheese production and specific patches in summer pastures. It also calls for extensive and intensive pastures, some with forested areas and some treeless.

The modern analogues used for establishing the pollen/land-use relationship should present, as far as possible, ecological conditions similar to those prevailing in the past (Gaillard *et al.*, 1992). Moss polsters are commonly used as surface samples for local modern pollen deposition (Gaillard *et al.*, 1992; Hicks and Birks, 1996; Hjelle, 1998). They are assumed to record an average of several years of pollen deposition (Bradshaw, 1981; Heim, 1970), which is recommended since previous investigations have shown annual variation in pollen productivity (Hicks, 2001; Hicks *et al.*, 2001; van der Knaap *et al.*, 2001; Räsänen *et al.*, 2004). Moreover, the modern pollen assemblage should be a good analogue of a fossil pollen assemblage, which

usually covers more than one year of pollen deposition. However, contradictory views exist as to the timespan of pollen deposition covered by mosses (Cundill, 1991; Räsänen *et al.*, 2004).

## Methods

### Study area and sampling design

The data presented in this study were collected within the interdisciplinary research programme 'Palaeo-environment and dynamics of human activities in the Pyrenees Mountains' (Galop *et al.*, 2004). A field site for the programme was selected in the Iraty Mountains in the Basque Country (western part of the Pyrenees chain in southern France) and lies between 700 and 1500 m a.s.l. The silicate bedrock and acidic soils present there induce abundant peat deposits in small basins.

The landscape is hilly and characterized by a mosaic of vegetation types variously affected by pastoral activity. On sloping grounds the vegetation is dominated by heather moorland of *Calluna vulgaris*, *Erica* sp., *Molinia coerulea* and patches of *Ulex europaeus* and *Pteridium aquilinum*, still used for animal litter. Some slopes, especially the steepest ones, are dominated by deciduous forest patches of beach and oak. Intensive grazed pastures are prevalent on the smooth mountain crests.

Our investigations focused on a small watershed centred on the topogenic Sourzay's peat bog with the aim of investigating modern pollen/vegetation and pollen/land-use relationships in a mosaic pasture–woodland landscape, and to use these relationships in the interpretation of fossil pollen records from the same area. The modern analogues were selected near the fossil sequence to assess the effect of the vegetation structure on the pollen record. For collection of the modern pollen and related vegetation data, a preferential design was selected with stratification based on degree of landscape openness and current land use along four axes across the watershed and centred on the fossil pollen record site (Figure 1). Thus, the major relevant vegetation communities and gradients of grazing pressure, from open to forested areas, were covered. The transects were chosen so as to exclude as much as possible any areas disturbed by thalwegs, streams and human activities other than pastoral ones. Some relevant vegetation types such as grazed oak forests or enclosures were absent from the study site. The modern analogue data set was therefore completed outside the watershed.

### Field method

*Vegetation data*
A set of 71 vegetation relevés from various forest types (oak, beech), heath and wet vegetation communities was collected from both grazed and ungrazed areas during the summer of 2001. Vegetation analysis was undertaken according to the integrated synusial approach (Gillet *et al.*, 1991, 2002; Gillet and Gallandat, 1996), which is a method based on the Braun-Blanquet approach (Braun-Blanquet, 1964), but allows better structural description and characterization of plant communities in their landscape context (Figure 2). This method aims at:

- describing complex vegetation structures, taking into account both horizontal and vertical heterogeneity;
- emphasizing functional and dynamic links between various constituent elements among several spatio-temporal organization levels.
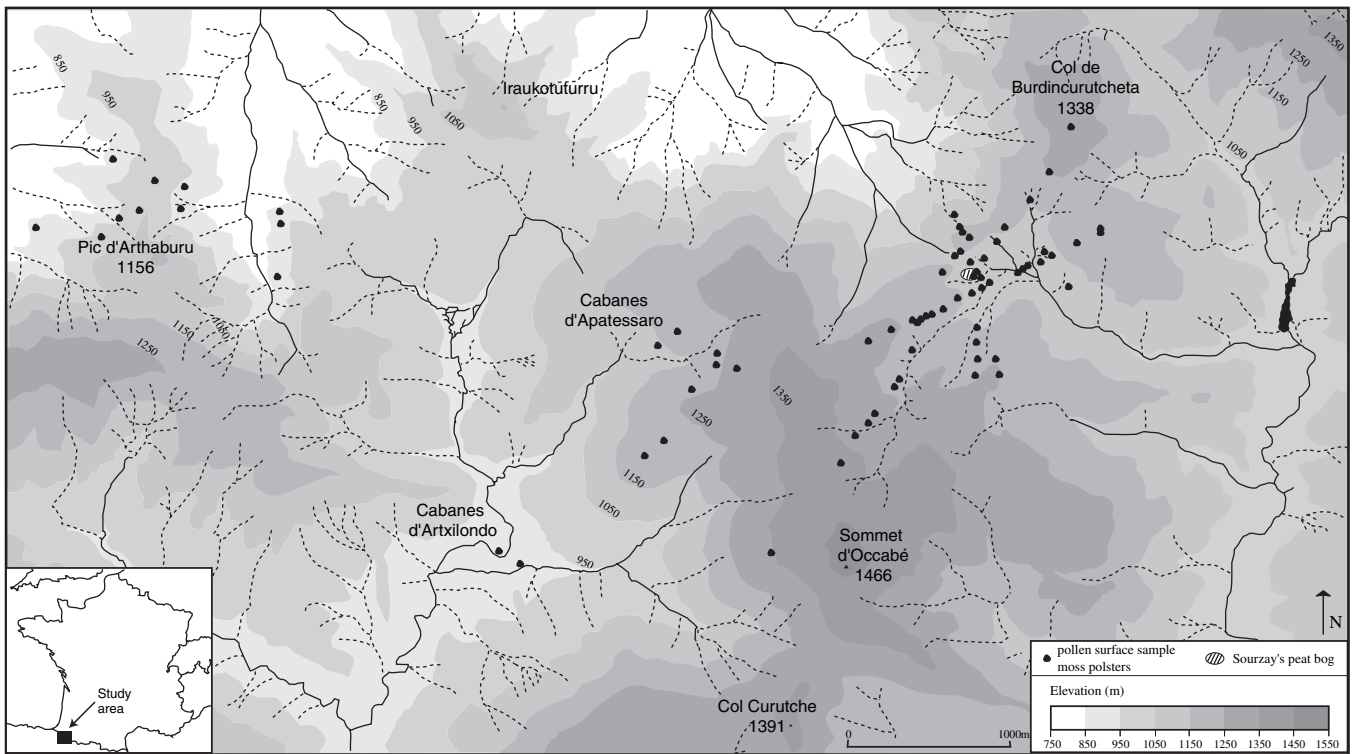
**Figure 1** The study area in southern France and the Iraty mountains of the Pays Basque. Location of the 71 modern analogues (solid circles) where pollen samples (moss polsters) and related vegetation data were collected. In the vicinity of the fossil pollen sequence (Sourzay's peat bog), the modern analogues are located along four transects with a stratification based on the degree of grazing and openness

Only two levels were considered in this study, those of the synusia and the phytocoenosis. The synusia is an elementary one-layered concrete vegetation unit (patch) directly linked to uniform environmental conditions. Thus, every synusia is a floristically, physiognomically and ecologically homogeneous vegetation unit. In the field, several vegetation stands were divided vertically and horizontally into synusiae, each therefore undergoing sampling for a floristic relevé. The synusial relevé



**Figure 2** Schematic representation of the two integration levels used for vegetation description, according to the integrated synusial method (adapted from Gillet and Gallandat, 1996)

furnishes a semi-quantitative description, according to Braun-Blanquet (1964), of the species occurring in the sample patch. Synusiae are organized in space and in time within phytocoenosis, as elements of a mosaic or a zoning of stratal communities (Gillet and Gallandat, 1996). Thus, a phytocoenosis is a complex of synusiae (herb, shrub and tree synusiae), functionally strongly linked in both space (mosaics, stratification) and time. A phytocoenotic relevé also furnishes a semi-quantitative description of the synusiae observed in a concrete phytocoenosis. The investigated sites presented homogeneous vegetation (floristically and structurally) on a minimal surface of 100 m$^2$ (not necessarily a square), which was the surveyed surface for each phytocoenosis. Vascular plant nomenclature follows Tutin *et al.* (1964–1980).

### Sampling of moss polsters
In the present study, moss polster samples were taken down to but not including the soil, and collected at the end of the flowering season, September 2001 (Räsänen *et al.*, 2004). Moss species vary from site to site, but whenever possible species producing dense life forms were chosen (Boyd, 1986). For the wet sites, *Sphagnum* sp. was the only available species and the upper green part (the first 4 cm) was collected.

For each phytocoenosis, and on the entire surface of the vegetation relevé, ten mosses were sampled and mixed together into one sample per site (Gaillard *et al.*, 1992).

### Environmental variables
The sampling sites were classified into categories according to the degree of grazing, dunging and trampling pressure, assessed as the proportion of the surveyed surface showing signs of recent cattle activity. On an ordinal scale, classes ranged from 0 to 3 as follows: (0) no pressure, (1) pressure < 5% of the surface, (2) pressure between 5 and 50% of the surface, (3) pressure > 50% of the surface. Livestock type (absence/presence nominal variable) was also taken into
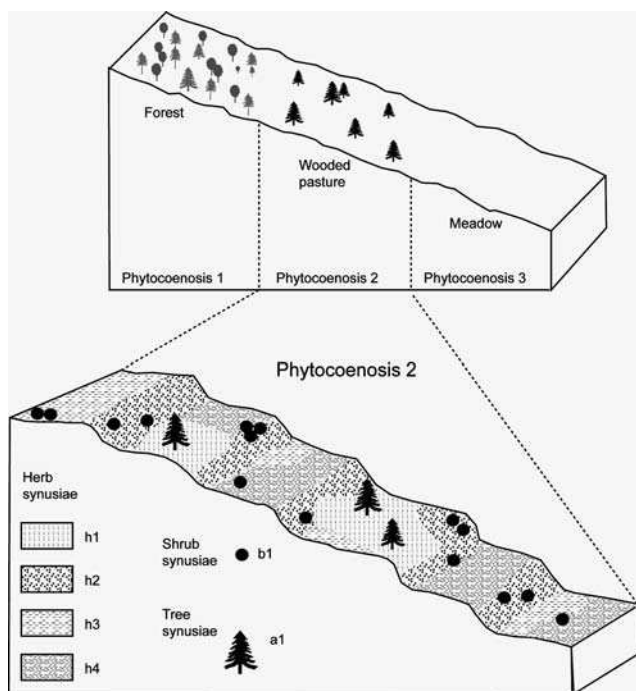
account, designated as sheep, horse, cow or pig, since livestock in this region was not mixed for all 71 sites. The altitude, slope (quantitative variables), aspect, nature of bedrock (absence/presence nominal variable) were measured or identified for each phytocoenosis. The aspect was transformed into a quantitative variable based on a trigonometric measure for both the north and east scales (eg, for the N-NE aspect the measure on the north scale was sin $67.5 = 0.92$ and on east scale cos $67.5 = 0.38$). In order to investigate how variation in the pollen data might be explained by the main gradients in the vegetation data, phytocoenosis typology was used, providing explanatory qualitative variables. Each plant community, 13 in all, was expressed as a presence/absence nominal variable.

For each phytocoenosis, mean soil depth (ten measures taken, randomly spread over the surveyed surface) was measured and soil samples were taken from the top 10 cm of soil, which corresponded to the A horizon, homogenized and pooled into one sample per surveyed surface (Gaillard *et al.*, 1992, 1997). A subsample was then air dried. The fraction (%) of coarse material ($> 2$ mm) was determined by the sieving procedure. The fresh sample was used for pH (KCl) and pH ($H_2O$) measurements. Organic matter (%), derived from the ash content, and total N (%) were analysed. These classical methods followed standard procedures (Anderson and Ingram, 1993). The water-holding capacity was obtained by saturating the soil sample over 96 hours, removing the excess water by filtration and oven drying the sample. The potential water content (% of dry soil) was obtained by the weight difference between saturated and dry soil.

Altogether, 37 explanatory variables were recorded and divided into five general categories: edaphic, geologic, geomorphologic, land use and vegetation variable types.

## Laboratory methods

Moss samples were treated according to standard procedures (Faegri and Iversen, 1989) by boiling in 10% NaOH for 45 min, sieving, treating with 40% HF (to digest fine silica), $ZnCl_2$ (to eliminate clay material), and acetolysis (one part $H_2SO_4$ and nine parts acetic anhydride, heated in water bath for 8 min). Samples were mounted in glycerol, and pollen were identified to the most precise taxonomic level possible, using pollen keys (Faegri and Iversen, 1989; Moore *et al.*, 1991; Reille, 1992).

As the focus of this study is the effect of the vegetation structure on the pollen assemblages, pollen from trees, dwarf-shrubs and herbs were thus included in the analysis. A minimum of 400 pollen grains was counted per sample, and a total of 113 pollen and spore taxa were recorded. Moreover, as one of the main goals was to investigate the plant–pollen relationships on a local scale, some taxa were excluded from the pollen sum. Only pollen taxa of plants potentially present in the flora of the region were included in the analysis. For example, pollen of *Olea* was excluded and considered exogenous as it comes from cultivated areas in Spain, far from the study area. The calculation sum, used to obtain percentages of the pollen taxa in numerical analyses, excludes exogenous and aquatic taxa as well as fern spores. In all, 28 taxa were excluded. Thus, the modern pollen data set consists of 71 samples and 85 pollen taxa.

## Data analysis

### Vegetation typology
The vegetation was described through examination of 71 phytocoenotic relevés and 256 synusial relevés among these phytocoenoses. Synusial typology was first carried out based on the comparison and classification of the synusial relevés using floristic-statistical tools to identify syntaxa (typological

units of this organization level). These tools combine step by step various applications such as ordinations and clustering using different options of the package MULVA-5 (Wildi and Orloci, 1996). The analytical procedure was performed separately on the data of each layer, herb, shrub and tree. The optimal number of groups of relevés and species was determined by comparing the results of the various classifications using criteria such as concentration analysis and contingency coefficient provided in the package. The phytocoenotic relevés were compared using the same numerical tools and classified into coenotaxa (typological units of this organization level).

### Association and representation indices
In order to understand the pollen–plant relationships at the taxonomic level used for pollen analysis, plant taxa were grouped according to pollen morphological types. For the vegetation, the species list was first derived from all the synusial relevés included in each phytocoenotic relevé. Taxa occurring only as plants or only in the pollen assemblages were excluded from the calculation of the Davis indices of association (A), under-representation (U) and over-representation (O) (Davis, 1984; Hjelle, 1997; Bunting, 2003). These indices are based on presence–absence data of the taxon list and are defined as follows:

$$A = B_0(P_0 + P_1 + B_0)^{-1}$$

$$U = P_1(P_1 + B_0)^{-1}$$

$$O = P_0(P_0 + B_0)^{-1}$$

Where $B_0$ is number of samples in which both the pollen type and its associated plant are present, $P_0$ is number of samples in which the pollen type is present in the surface sample but not the plant taxa and $P_1$ is number of samples in which the pollen type is not present in the surface sample but the plant taxa is present in the vegetation.

Ordination by principal component analysis (PCA) was used to display the relationship between the calculated indices (A, U, O as descriptors) and the pollen taxa (objects). PCA used a covariance matrix with the eigenvectors adjusted by variance. The taxa were then classified into groups using agglomerative hierarchical clustering with proportional-link linkage, and a connection of 0.7. Euclidian distance was used. PCA and cluster analysis were implemented respectively by the CANOCO program for Windows 4.0 (Leps and Smilauer, 2003; Ter Braak and Smilauer, 1998) and Progiciel R (Casgrain and Legendre, 2001).

### Pollen/vegetation/environment relationships
Direct gradient analyses were considered appropriate for exploration and testing patterns of modern pollen variation in relation to environmental and anthropogenic explanatory variables. The fitting model depends on whether the pollen taxa respond roughly linearly to gradients (linear response), or perform best around some environmental optima (unimodal response) (Ter Braak and Smilauer, 1998). Preliminary Detrended Canonical Correspondence Analysis (DCCA) showed that this data set has a gradient length of 1.309 standard deviation units of species turnover (SD). This implied that linear-based methods of data analysis such as Redundancy Analysis (RDA) were suitable in this case (Ter Braak and Prentice, 1988).

RDA attempts to explain pollen taxa responses by ordination axes that are constrained to be linear combinations of the 37 explanatory variables available, including the 13 coenotaxa (vegetation communities). Thirteen pollen taxa present only

once in the 71 pollen assemblages were omitted. The pollen percentage data was log-transformed [ln $(ay+c)$ with $a=1$ and $c=1$) and double-centred. Forward selection and Monte Carlo test with 999 unrestricted permutations were run to check statistical significance and to select the best explanatory variables for further analysis. The permutation tests were later applied to the canonical axes.

First, the investigated matrix contained the pollen data set and 37 independent variables from 71 modern analogues. In preliminary RDA, pollen assemblages from enclosures and wetland communities were clearly separated from the remaining sites, but were also clearly different from fossil spectra (included passively) (Mazier, Galop, Cugny, Buttler, Legaz and Rendu, unpublished data, 2005). These sites contained some characteristic taxa in large proportion and their assemblages were quite different from the other plots, causing a long gradient in the ordinations, which resulted in a poor separation of the other samples. Ten sites and consequently two explanatory variables were therefore omitted for further RDA, resulting in the use of 61 sites, 73 pollen taxa and 35 environmental variables, of which 13 were retained for their significance, the others being passively presented in the ordination diagrams (or given as covariable).

Three main predictor variables, three vegetation groups, which had the best correlation with the first three ordination axes, were used for more precise analyses. In order to define the weight of each taxon for these three nominal variables, partial RDA was performed separately on each one. The species scores on the first canonical axis of each analysis were then considered descriptors in a new ordination using Principal Component Analysis (PCA). PCA used a covariance matrix with the eigenvectors adjusted to the square root of their variance, divided by the standard deviation (symmetric scaling $\sqrt{\lambda_h/s_i}$).

All ordination analyses were implemented by the CANOCO program for Windows 4.0 (Ter Braak and Smilauer, 1998) and diagrams constructed by Progiciel R (Casgrain and Legendre, 2001) and refined by Illustrator 10.

# Results

## Phytocoenosis typology

The numerical analysis of the 256 synusial relevés resulted in 21 syntaxa (cluster group): 4 within trees, 3 within shrubs and 14 within the herb layer (Table 1 presents the species composition for the herb syntaxa). The comparison and the classification of the 71 phytocoenotic relevés made it possible to identify 13 coenotaxa (Table 2) divided into two main groups: anthropogenic (4) and 'natural' communities (9). These plant communities can be ordered along a gradient of anthropogenic influence and degree of openness. Here, we describe only the three main coenotaxa, which are found as significant explanatory variables in the redundancy analysis.

Coenotaxon No. 2 occurs mainly on small areas and reflects a community type composed of two herb syntaxa. The syntaxon **H4** (*Rumex acetosella–Galium saxatile*) is correlated with intense livestock activity inducing areas of urination and defecation, as well as bare soil areas. The vegetation of the patch presents a short and sparse canopy dominated by *Rumex acetosella* and *Galium saxatile*. The other syntaxon **H3** (*Trifolium repens–Poa annua*) reflects grazed dense vegetation. This short grass patch is dominated by grazed-area species such as *Poa annua*, *Trifolium repens*, *Stellaria media* ssp. *media* and *Cerastium fontanum* ssp. *fontanum*. Coenotaxon No. 2 depends directly on the daily routine of the livestock, mainly

sheep, and presents a high pastoral value. This overgrazed community is often found on mountain crests.

Coenotaxon No. 7 describes large areas of dry mountain-slope heathland, composed of seven syntaxa. The principal syntaxa are **H9** (*Ulex europaeus–Calluna vulgaris*), **H5** (*Potentilla erecta–Agrostis curtisii*) and **H14** (*Pteridium aquilinum–Agrostis curtisii*). This high-altitude community presents heathland species, with a dominance of *Agrostis curtisii*, *Potentilla erecta*, *Danthonia decumbens*, *Deschampsia flexuosa*, *Vaccinium myrtillus*, *Calluna vulgaris*, *Ulex europaeus*, *Erica vagans*, *Erica cinerea*, *Erica tetralix* and *Pteridium aquilinum*. Its species composition is closely related to coenotaxon No. 6, which includes **H8** in addition (*Calluna vulgaris–Vaccinum myrtillus*), and results from colonization by *Ulex europaeus* and *Pteridium aquilinum*, induced through a decrease in grazing pressure.

Coenotaxon No. 12 corresponds to open oak forest with a low and sparse canopy. This community includes three herb syntaxa (**H5**, **H9** and **H6** (*Vaccinium myrtillus–Deschampsia flexuosa*)), one shrub (**B21**) and two tree syntaxa (patches of oak trees alone (**A17**), and mixed beech and oak (**A16**)). The herb vegetation is dominated by *Agrostis curtisii*, *Potentilla erecta*, *Calluna vulgaris*, *Ulex europaeus*, *Deschampsia flexuosa* and *Vaccinium myrtillus*. This coenotaxon corresponds to poor soils on slopes outside the Sourzay watershed.

## Association and representation indices

Only 32 taxa were found both as plants and as pollen in one or more phytocoenoses. The relationships between the different taxa and the calculated indices are summarized in the PCA scatter plot (Figure 3). The first axis explains 55.9% of the index variation, and is strongly related to the presence of both pollen and corresponding plants (eg, Poaceae, Cyperaceae). It separates strongly associated taxa, plants and pollen present in over 65% of the samples (*Galium*-type and *Potentilla*-type), from unassociated taxa occurring infrequently in the vegetation and pollen rain (eg, Rosaceae, *Rumex obtusifolius*). The second axis captures 40.1% of the variation and differentiates over-represented taxa, most often found only as pollen (eg, *Abies*, *Quercus* tot, *Urtica dioica*, Brassicaceae and *Plantago lanceolata*), from under-represented taxa often found only as plants (eg, *Sorbus*, *Polygala*, *Erica tetralix*).

Good agreement is found in the results of the two methods, ordination and classification, with strongly associated taxa of group 5 and associated taxa of group 3 on the right-hand side of the first axis. Group 1 clearly indicates over-represented taxa on the positive side of the second axis. Group 2 is centred and represents weakly associated types with low A values and relatively high U and O values. Group 4 constitutes a mixed group with unassociated, under-represented and weakly associated types. Table 3 summarizes the calculated indices for selected taxa in this study and also in previous ones, based on the classification of Bunting (2003).

## Pollen/vegetation/environment relationships

Redundancy analysis (RDA) was used to describe the major gradients in the modern pollen assemblages and to relate these patterns to the environmental and anthropogenic variables. This correlative model also tests whether different degrees of openness and grazing pressure produce statistically distinct modern pollen spectra.

Among the 37 explanatory variables, 14 contribute significantly to the correlative model, using forward selection and Monte Carlo permutation tests ($P \leq 0.05$, 999 permutations). Pudding rock, mainly represented in some places of our study area, was found significant. This variable was considered to be a covariable as we did not want to interpret its effect. Therefore, a

**Table 1**  Synthetic presentation of the herb synusial elementary syntaxa (SyE) of the Iraty Mountains pastoral landscape

| Syntaxon no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of synusial relevés | 4 | 5 | 5 | 18 | 50 | 32 | 6 | 9 | 21 | 8 | 6 | 5 | 6 | 11 |
| *Urtica dioica* | V:2 | r:+ | | | | | | | | | | | | |
| *Cirsium eriophorum* | IV:2 | r:2 | | | r:+ | | | | | | | | | |
| *Cirsium palustre* | V:2 | | | | | | | | | | r:+ | r:1 | | |
| *Cirsium vulgare* | IV:2 | | | | | | | | | | r:1 | | | |
| *Rumex obtusifolius* ssp. *obtusifolius* | | V:1 | | r:1 | | | | | | | | | | |
| *Taraxacum officinale* | | V:1 | r:+ | r:+ | r:+ | | | | | | r:r | | | |
| *Ranunculus repens* | | V:2 | | | | | | | | | | | | |
| *Achillea millefolium* ssp. *millefolium* | | IV:1 | | | | | | | | | | | | |
| *Cynosurus cristatus* | | IV:2 | | | | | | | | | | | | |
| *Lolium perenne* | r:+ | IV:2 | r:+ | | | | | | | | | | | |
| *Holcus lanatus* | | III:2 | | | | | | | | | | | | |
| *Capsella bursa-pastoris* | | III:+ | | | | | | | | | | | | |
| *Plantago lanceolata* | | III:1 | r:+ | r:1 | | | | | | | | | | |
| *Stellaria media* ssp. *media* | r:1 | V:2 | V:1 | II:2 | r:+ | | r:1 | | | | | | | |
| *Cerastium fontanum* ssp. *fontanum* | r:+ | V:1 | V:2 | IV:2 | r:+ | r:2 | | | | | | | | |
| *Trifolium repens* | r:+ | V:2 | III:2 | III:2 | | r:1 | | r:2 | | | II:2 | | | |
| *Poa annua* | | V:2 | V:3 | III:2 | r:+ | I:2 | II:2 | | | | | | | |
| *Rumex acetosella* | | II:+ | | V:2 | r:2 | I:2 | | r:3 | | | | | | |
| *Danthonia decumbens* | | | r:+ | I:1 | V:2 | | | | r:1 | II:1 | II:2 | r:+ | | r:+ |
| *Galium saxatile* | | r:1 | r:1 | V:2 | V:2 | IV:2 | IV:2 | r:3 | r:2 | II:2 | r:2 | | | |
| *Agrostis curtisii* | | | III:2 | V:2 | III:2 | III:1 | | | r:3 | | | r:+ | r:1 | II:3 |
| *Potentilla erecta* | | | II:+ | IV:1 | V:2 | II:1 | | | r:1 | V:2 | V:2 | | | |
| *Carex flacca* | | | II:1 | | V:2 | IV:2 | II:2 | r:2 | I:1 | r:1 | IV:1 | | | |
| *Deschampsia flexuosa* | | | r:1 | I:1 | II:1 | V:3 | V:2 | r:2 | r:2 | | r:2 | IV:1 | II:1 | II:2 |
| *Fagus sylvatica* H. | | | | | r:+ | III:1 | II:2 | | r:+ | | r:r | | r:3 | |
| *Vaccinium myrtillus* | | | | I:+ | II:2 | IV:2 | IV:2 | V:3 | III:1 | | r:+ | | | |
| *Oxalis acetosella* | | | | | | | V:3 | | | | | | | |
| *Calluna vulgaris* | | | | | II:+ | I:1 | | V:3 | V:2 | IV:2 | IV:1 | | | r:5 |
| *Ulex europaeus* | | | | | r:+ | | | | V:3 | | | | | |
| *Erica vagans* | | | | | I:1 | r:2 | | r:+ | V:2 | | | | | |
| *Erica cinerea* | | | r:+ | | r:1 | | | r:+ | IV:2 | | | | | |
| *Erica tetralix* | | | | | I:1 | | | III:2 | V:2 | V:2 | IV:2 | | | |
| *Molinia caerulea* ssp. *caerulea* | | | | | III:2 | | | | r:2 | V:2 | IV:2 | IV:2 | | |
| *Viola palustris* ssp. *palustris* | | | | | | | | | | | V:2 | | | |
| *Parnassia palustris* | | | | | | | | | | r:2 | V:2 | | | |
| *Narthecium ossifragum* | | | | | r:+ | | | | | II:2 | IV:2 | | | |
| *Juncus acutiflorus* | | | | | | | | | | | II:1 | V:3 | | |
| *Eriophorum angustifolium* | | | | | | | | | | IV:2 | II:2 | IV:2 | | |
| *Carex echinata* | | | | | | | | | | IV:2 | III:1 | III:2 | | |
| *Carum verticillatum* | | | | I:+ | I:+ | | | | | III:+ | V:1 | II:2 | | |
| *Wahlenbergia hederacea* | | | | | r:1 | | | | | II:1 | III:2 | | | |
| *Juncus effusus* | III:2 | | II:+ | | | r:+ | r:2 | | | r:1 | II:+ | III:2 | V:5 | II:3 |
| *Agrostis capillaris* | III:2 | V:2 | V:2 | V:2 | III:2 | V:2 | III:2 | II:1 | | II:2 | III:1 | IV:2 | III:1 | II:2 |
| *Pteridium aquilinum* | | | II:+ | r:+ | I:1 | II:2 | | | r:1 | | | | r:3 | V:4 |

Names are given according to the main featuring species (grey bars). Each elementary syntaxon is described by a specific list of species (differential species in grey). Only the differential species are listed Relative frequency (RF) classes are indicated for each species in each syntaxon; r: species represented in less than 10% of the relevés or in a single relevé; I: $10\% \leq RF \leq 20\%$; II: $20\% \leq RF \leq 40\%$; III: $40\% < RF \leq 60\%$; IV: $60\% < RF \leq 80\%$; V: RF $> 80$. Mean abundance-dominance values are also indicated according to the Braun-Blanquet scale. The syntaxa are: H1, *Urtica dioica–Cirsium palustre*; H2, *Rumex obtusifolius–Poa annua*; H3, *Trifolium repens–Poa annua*; H4, *Rumex acetosella–Galium saxatile*; H5, *Potentilla erecta–Agrostis curtisii*; H6, *Vaccinium myrtillus–Deschampsia flexuosa*; H7, *Oxalis acetosella–Deschampsia fexuosa*; H8, *Calluna vulgaris–Vaccinium myrtillus*; H9, *Ulex europaeus–Calluna vulgaris*; H10, *Molinia coerulea–Erica tetralix*; H11, *Viola palustris–Parnassia palustris*; H12, *Juncus acutiflorus–Eriophorum angustifolium*; H13, *Juncus effusus–Agrostis capillaris*; H14, *Pteridium aquilinum–Agrostis curtisii*.

partial RDA ordination diagram of 61 pollen assemblages and 13 explanatory variables such as vegetation units and other environmental variables was performed (Figure 4).

Axis 1 shows a clear gradient from open land to forest vegetation types. It contrasts open land such as CoE No. 7, usually treeless dry heathland, with wooded sites, such as more or less open beech forest. CoE No. 7 and the North are respectively correlated, negatively ($r = -0.42$), and positively ($r = 0.47$), to axis 1. Indeed, beech forests, represented by CoE No.9, 10 and 11 included as passive variables, are generally found on northern slopes. Axis 2 appears to represent a soil richness gradient, and is positively linked with loss on ignition and total N ($r = 0.40$ and 0.36, respectively), whereas the vegetation type CoE No. 12, oak forest on poor soils, presents a negative correlation ($r = -0.37$). Thus, axis 2 contrasts the nitrophilous features of an overtrampled community (CoE No. 3) with oak forest. Axis 3 better expresses a grazing pressure gradient with sites intensively grazed and trampled on the positive side on the axis. CoE No. 2, an overgrazed community, is strongly linked with axis 3 ($r = 0.50$) and correlated to

**Table 2** Synthetic presentation of the elementary coenotaxa that constitute the Iraty mountains pastoral landscape

| Coenotaxon no. | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Number of phytocoenotic relevés | 3 | 3 | 3 | 4 | 6 | 9 | 15 | 4 | 6 | 7 | 6 | 4 | 1 |
| H2 *Rumex obtusifolius–Poa annua* | V:4 | | | | | | | | | | | | |
| H1 *Urtica dioica–Cirsium palustre* | V:3 | | | | | | | | | | | | |
| H3 *Trifolium repens–Poa annua* | | V:3 | | | | | | | r:2 | | | | |
| H4 *Rumex acetosella–Galium saxatile* | | V:4 | V:4 | V:2 | | | r:4 | | | | | | |
| H13 *Juncus effusus–Agrostis capillaris* | | r:4 | | V:4 | | | | | | | r:4 | | |
| H11 *Viola palustris–Parnassia palustris* | | | | | V:3 | | | | | | | | |
| H12 *Juncus acutiflorus–Eriophorum angustifolium* | | | | | V:4 | | | | | | | | |
| H10 *Molinia coerulea–Erica tetralix* | | | | | IV:2 | | | | | | | | |
| H8 *Calluna vulgaris–Vaccinium myrtillus* | | | | | | r:4 | II:4 | r:4 | III:4 | r:2 | r:3 | | |
| H5 *Potentilla erecta–Agrostis curtisii* | | | | | | V:4 | V:3 | | | r:2 | | IV:3 | |
| H9 *Ulex europaeus–Calluna vulgaris* | | | | | | | V:3 | | | | | V:3 | |
| H14 *Pteridium aquilinum–Agrostis curtisii* | | | r:5 | r:3 | | r:2 | I:4 | V:4 | | | | | |
| H6 *Vaccinium myrtillus–Deschampsia flexuosa* | | | | | | r:3 | r:4 | V:2 | V:2 | V:2 | r:1 | III:2 | V:2 |
| A15 *Fagus sylvatica* | | | | | | | | | V:4 | V:3 | V:3 | | |
| B19 *Fagus sylvatica* | | | | | | | | | | V:2 | IV:3 | | |
| H7 *Oxalis acetosella–Deschampsia flexuosa* | | | | | | | | | | | V:2 | | |
| A16 *Quercus robur–Fagus sylvatica* | | | | | | r:2 | | | | | | III:2 | |
| A17 *Quercus robur* | | | | | | | | | | | | III:2 | |
| B21 *Quercus robur–Fagus sylvatica* | | | | | | | r:1 | | | | | r:3 | |
| B20 *Fagus sylvatica–Abies alba* | | | | | | | | | | | | | V:3 |
| A18 *Fagus sylvatica–Abies alba* | | | | | | | | | | | | | V:4 |

Each coenotaxon (CoE) is described by a list of syntaxa, numbered according to Table 1 for the herb layers (H: 1–14); the tree (A: 15–18) and shrub (B: 19–21) syntaxa are not presented in detail (see explanation in Table 1). The dominant SyE are listed (grey bars). The coenotaxa are: CoE 1, cattle enclosure; CoE 2, overgrazed lawn; CoE 3, overtrampled lawn; CoE 4, grazed wet vegetation; CoE 5, mire vegetation; CoE 6, heathland; CoE 7, encroached heathland; CoE 8, fern fallow; CoE 9, open beech forest; CoE 10, semi-open beech forest; CoE 11, dense beech forest; CoE 12, semi-open oak forest; CoE 13, isolated site.

pastoral activities (grazing and trampling). On the negative side of axis 3, sites from CoE No.7 and 12 are related to low grazing pressure.

The investigated vegetation types represent the major relevant gradients in the modern pollen data. The first three axes respectively correspond to CoE No. 7 (dry heathland), CoE No. 12 (semi-open oak forest) and CoE No.2 (overgrazed community). These vegetation units are clearly related to the degree of openness, soil richness and grazing pressure, respectively. Therefore, in an attempt to identify indicator taxa for each of these three ecological trends, these coenotaxa were used individually as main predictors in partial RDA. The resulting species scores were further considered variables in a principal component analysis (PCA). In the ordination diagram (Figure 5), Ericaceae, *Erica tetralix*, *Sanguisorba minor*, associated to Poaceae, are positively linked with the degree of openness. As expected, *Fagus* and *Pinus* are related to forested sites. *Abies* and *Plantago* sp. are also correlated to forested sites and soil richness (more obvious on the plots of axes 1 and 3). The taxon *Potentilla* type occurs mainly in wet conditions with Apiaceae. Other data show that *Potentilla*-type and Apiaceae are mainly found in the peatbogs (Mazier *et al.*, unpublished data, 2005).

Cichorioideae, Ranunculaceae, *Stellaria*-type, *Cirsium*-type, *Galium*-type and Asteroideae, are connected with the grazing pressure, whereas Chenopodiaceae, *Plantago lanceolata* and *Plantago major/media* are negatively correlated to grazing pressure.

*Urtica dioica*, *Rumex*, Scrophulariaceae and Rubiaceae are associated with soil richness. Several taxa are found close to the axes origin, such as *Rumex obtusifolius*, *Artemisia*, *Betula*, *Vaccinium-Rhododendron*, *Lotus*-type and Fabaceae. This suggests that these pollen taxa have little relationship to the measured variables represented by the three selected coenotaxa. Indeed, they are commonly recorded in low abundance in

most of the sites, and thus are not characteristic of the investigated vegetation types.

# Discussion

## Herb and tree pollen representation

The indices of Davis A, O and U provide some basic information on the general pollen–vegetation relationships of the mosaic vegetation of the Iraty Mountains, such as heathland, pastoral vegetation, and oak and beech forest. Table 3 presents the results of previous studies, in particular of Bunting (2003) and Hjelle (1997) who give indices for main taxa from Scottish and Norwegian heath communities, respectively. *Potentilla*-type and Poaceae are strongly associated, and *Cirsium*-type, *Pteridium aquilinum* are weakly associated for the three data sets. *Plantago major/media* has been found unassociated and *Plantago lanceolata* over-represented in both the Pyrenees and Scottish data sets. These comparisons indicate that these indices can be applied widely to different regions and also to different habitats.

Several taxa commonly used as anthropogenic indicator taxa, which were lightly or not at all investigated in the local vegetation communities, are recorded at low values in a very high proportion (60–90%) of the surface samples, such as *Artemisia*, Chenopodiaceae and *Plantago lanceolata* (the latter observed three times in the 71 vegetation relevés). This suggests that sporadic, low percentages of these taxa in palaeorecords need not necessarily be indicative of local pastoral activity, but may originate from long-distance transport.

Some discrepancies were observed between these three data sets, ie, *Calluna vulgaris* which is strongly associated in Bunting (2003) and associated in the Iraty data set (this study), and the *Vaccinium*-type which is strongly associated in Scotland and weakly associated in this study. Apiaceae, *Rumex*,
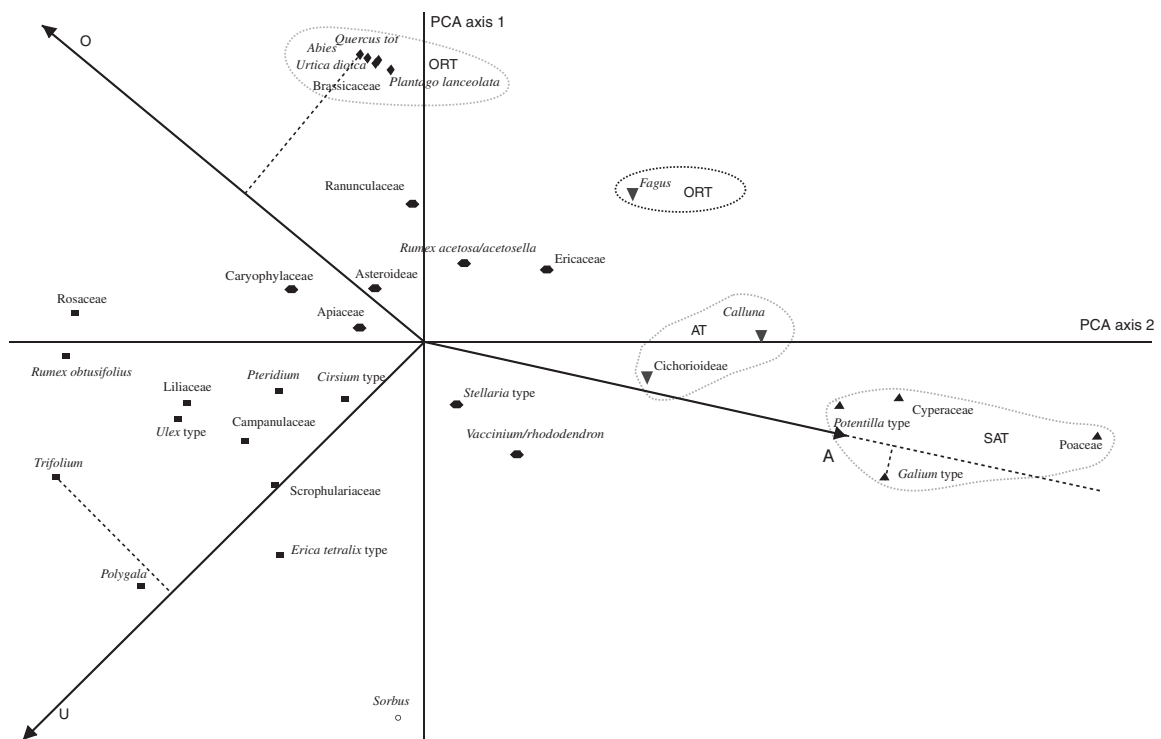
**Figure 3** Principal Component Analysis (PCA) using Davis's indices of association (A), under-representation (U) and over-representation (O) (Davis, 1984). Groups according to the clustering are indicated with different symbols: 1, ◆; 2, ●; 3, ▼; 4, ■; 5, ▲. The eigenvalues of the first three principal component axes are 0.135 (55.9%), 0.099 (40.9%) and 0.008 (3.2%), respectively

Ranunculaceae are over-represented in Bunting's data set and weakly represented in this study, while the *Trifolium*-type is associated in Hjelle (1998) and weakly associated in this study.

The dissimilarities between the three data sets might be explained by differences in environmental factors between regions, such as climate, edaphic conditions and land use (Broström *et al.*, 2004). Grazing influence on flowering and pollen production of grasses is well documented (Groenman-van Waateringe, 1993; Hjelle, 1998), thus it may be that Poaceae produce less pollen in anthropogenic coenotaxa. Another explanation may be the differences in pollen production for species included in large taxonomic groups such as Poaceae, Apiaceae and Ranunculaceae (Broström, 2004). A further reason may be the differences in sampling design and in method used for vegetation inventories (Bunting and Hjelle, unpublished data, 2004).

Broström *et al.* (2004) calculated relative pollen productivity estimates (PPEs) for 11 herb taxa related to *Poaceae* (used as reference taxon) and compared PPEs for herbs (Broström *et al.*'s study) and trees (data set of Sugita *et al.*, 1999). She showed that most herb taxa have higher PPEs than *Poaceae*, for example *Calluna vulgaris*, *Rumex acetosa*-type and *Plantago lanceolata*. It is outlined in many studies that the presence of *Plantago lanceolata* in fossil pollen assemblages should be interpreted with caution, especially in pastoral areas on crystalline substrate, such as in our case. This taxon is characterized by long-distance transport and may originate from a wider landscape, for example, from valley floors in our case. Cichorioideae and Cyperaceae have lower PPEs, whereas *Potentilla*-type and Rubiaceae (*Galium*-type) have relatively higher PPEs than *Poaceae* (Broström *et al.*, 2004). We obtained similar results, showing that these taxa can be considered good local indicators and are important in inferring past land uses from local pollen diagrams. Broström *et al.* (2004) also showed that most of the common tree taxa such as *Pinus*, *Quercus* and *Fagus* produce six to eight times as much pollen per unit area as Poaceae. This emphasizes the underestimation of past open

land from fossil records when translating the AP/NAP ratio into open areas (Sugita *et al.*, 1999). The overestimation of *Pinus* is well known (Heim, 1970; Broström *et al.*, 1998, 2004). Pine is considered a high pollen producer and a long-distance disperser, which implies a significant regional input. This explains the important proportion of pine recorded in all the 71 surface samples, *Pinus* presents high proportion in beech forest and in fern fallow with dense canopy of *Pteridium aquilinum* (Mazier *et al.*, unpublished data, 2005). *Pteridium aquilinum* forms a closed canopy at four sites grouped into the CoE No. 8 community, dominated by *Pteridium aquilinum* and *Agrostis curtisii*. It is surprising that *Pteridium* spores were not found in the pollen samples from these four sites, whereas it occurred in high proportion in one site of CoE No. 9 (more than 20%), just before a small mountain dominated by this species. This may be due to preferential spore dispersal in relation to prevailing winds. The interpretation of *Pteridium* occurrence in pollen diagrams should be interpreted with caution (Tinsley, 2001).

We must keep in mind that, because of annual variability in pollen productivity, the use of moss polsters could be critical when studying pollen–vegetation relationships, and identifying pollen indicators of plant communities. Interannual variation in pollen productivity is well documented, at least for tree taxa, and has been shown to be related to climatic variability (Hicks, 2001; B. Odgaard, personal communication, 2004). Moreover, the exact number of deposition years in a moss polster is not known and differs from 1 to 10 years according to the authors (Heim, 1970; Bradshaw, 1981; Cundill, 1991; Räsänen *et al.*, 2004). Räsänen *et al.* (2004) suggest that pollen assemblages in the green part of moss polsters represent more than one but less than two years of pollen deposition.

## Correlative model of pollen/vegetation/ environment relationships

We focused on the pollen/plant/environment relationships as explored by Redundancy Analysis (a detailed presentation of

**Table 3** Indices of association and representation from three different studies (this study; Bunting, 2003; and Hjelle, 1997) based on the classification of Bunting (2003)

| Pollen taxon | A | U | O | Bunting (2003) | Hjelle (1997) |
|---|---|---|---|---|---|
| Unassociated types (UT) | | | | | |
| *Anagallis* | 0.00 | 1.00 | 1.00 | | |
| *Centaurea jacealnigra* | 0.00 | 1.00 | 1.00 | | |
| Fabaceae | 0.00 | 1.00 | 1.00 | UT | |
| *Ilex* | 0.00 | 1.00 | 1.00 | | |
| Labiatae | 0.00 | 1.00 | 1.00 | | |
| *Lotus*-type | 0.00 | 1.00 | 1.00 | | WAT |
| *Parnassia*-type | 0.00 | 1.00 | 1.00 | | |
| *Plantago major/media* | 0.00 | 1.00 | 1.00 | no plant | WAT |
| Strongly associated types (SAT) | | | | | |
| Poaceae | 0.96 | 0.01 | 0.03 | SAT | SAT |
| Cyperaceae | 0.73 | 0.10 | 0.20 | AT | |
| *Galium*-type | 0.72 | 0.22 | 0.10 | Rubiaceae ORT | AT |
| *Potentilla*-type | 0.67 | 0.16 | 0.23 | SAT | AT |
| Associated types (AT) | | | | | |
| *Calluna* | 0.58 | 0.12 | 0.38 | SAT | ORT |
| Comp. SF Cichorioideae | 0.48 | 0.27 | 0.41 | | SAT |
| Over-represented types (ORT) | | | | | |
| Abies | 0.04 | 0.00 | 0.96 | | |
| *Urtica dioica* | 0.05 | 0.00 | 0.95 | no plant | no plant |
| *Plantago lanceolata* | 0.06 | 0.00 | 0.94 | ORT | SAT |
| Brassicaceae | 0.06 | 0.00 | 0.94 | no plant | WAT |
| *Quercus* tot. | 0.08 | 0.00 | 0.92 | | |
| *Fagus* | 0.38 | 0.00 | 0.62 | | |
| Under-represented types (URT) | | | | | |
| *Sorbus* | 0.11 | 0.89 | 0.00 | | |
| Weakly associated types (WAT) | | | | | |
| *Polygala* | 0.03 | 0.97 | 0.50 | no pollen | URT |
| *Trifolium* | 0.06 | 0.93 | 0.80 | | SAT (*Trifolium repens* type) |
| *Erica tetralix*-type | 0.16 | 0.82 | 0.44 | | SAT |
| *Rumex obtusifolius* | 0.05 | 0.75 | 0.95 | ORT (*Rumex*) | no plant |
| Scrophulariaceae | 0.19 | 0.74 | 0.57 | | |
| *Ulex*-type | 0.14 | 0.74 | 0.77 | | |
| Campanulaceae | 0.18 | 0.71 | 0.67 | | AT |
| Liliaceae | 0.14 | 0.71 | 0.78 | no plant | |
| Rosaceae | 0.02 | 0.67 | 0.98 | | |
| *Pteridium* | 0.20 | 0.61 | 0.71 | WAT | WAT |
| *Cirsium*-type | 0.25 | 0.56 | 0.64 | WAT | WAT |
| *Vaccinium/Rhododendron* | 0.38 | 0.49 | 0.41 | SAT (*Vaccinium* type) | WAT (*Vaccinium* type) |
| *Stellaria*-type | 0.33 | 0.47 | 0.53 | | |
| Apiaceae | 0.23 | 0.44 | 0.71 | ORT | SAT |
| Caryophyllaceae | 0.16 | 0.44 | 0.81 | no plant | |
| Comp. SF Asteroideae | 0.23 | 0.37 | 0.74 | | AT (*Achillea* type) |
| *Rumex acetosa/acetosella* | 0.28 | 0.25 | 0.69 | ORT (*Rumex*) | SAT |
| Ranunculaceae | 0.20 | 0.20 | 0.79 | ORT (*Ranunculus acris* type) | SAT (*Ranuculus acris* type) |
| Ericaceae | 0.35 | 0.19 | 0.61 | | |

Indices of association (A), over-representation (O) and under-representation (U) for taxa present in both plant and pollen data sets. Strongly associated types: A > 65%; Associated types: 50% < A < 65%; Over-represented types: low A values, high O values and U = 0; Weakly associated types: low A values and relatively high values for both U and O; Unassociated types: A = 0 and high O and U values.

the pollen-diagram will be published elsewhere; Mazier *et al.*, unpublished data, 2005).

*Advantage of a synusial approach for studying vegetation*
The significant explanatory variables of the canonical axes were edaphic conditions (total N, loss on ignition, pH), geomorphology (aspect North, linked to forested sites), plant communities (CoE No. 2, 3, 4, 6, 7, 8 and 12) and land use (grazing, trampling). The results show that the vegetation units under consideration, which better reflect vegetation structure than a classical relevé, can be used efficiently to explain the major environmental gradients in pollen data. Dry heathland,

semi-open oak forest and overgrazed community best reflect the gradients of landscape openness, soil richness and grazing pressure, respectively. RDA axis 1 separates open land from beech sites (both lightly grazed) that are contrasted mainly on the basis of Poaceae and *Fagus*. Poaceae is mainly represented in the CoE No. 7 community, a dry heathland corresponding to an early succession stage of the *Ulex europaeus* invasion. Broström *et al.* (1998) demonstrated that Poaceae may be representative of all types of open land. However, this study shows a difference in the proportion of Poaceae within vegetation types induced by human activity, since this taxon decreases in both the overgrazed CoE No. 3 and No. 2
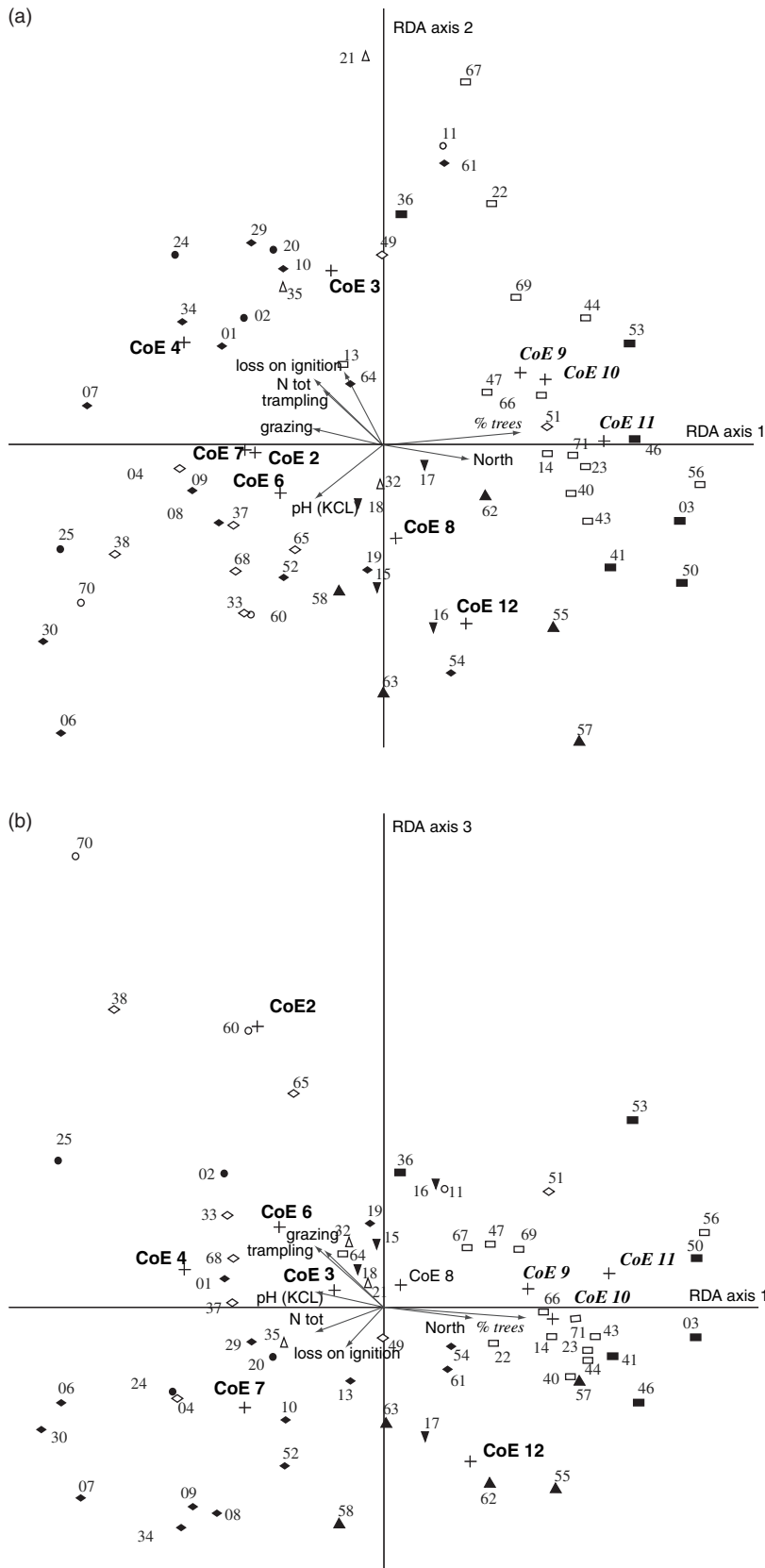
**Figure 4** Redundancy analysis (RDA) of the modern pollen assemblages, using 13 explanatory variables (nominal variables are given with their centroïds (crosses) and quantitative variables with arrows), four passive variables (italic) and 61 pollen samples (points). The three first axes explain respectively 17.9, 6.2 and 5.4% of the total variation in the modern pollen data, and are all significant (*P* < 0.001 after 999 permutations). The vegetation types, ie, elementary Coenotaxa (CoE) are: ○, CoE2; △, CoE3; ●, CoE4; ◇, CoE6; ◆, CoE7; ▼, CoE8; □, CoE9/10; ■, CoE11; ▲, CoE12. (a) Sites scores and environmental variables on RDA axes 1 and 2. (b) Site scores and environmental variables on RDA axes 1 and 3
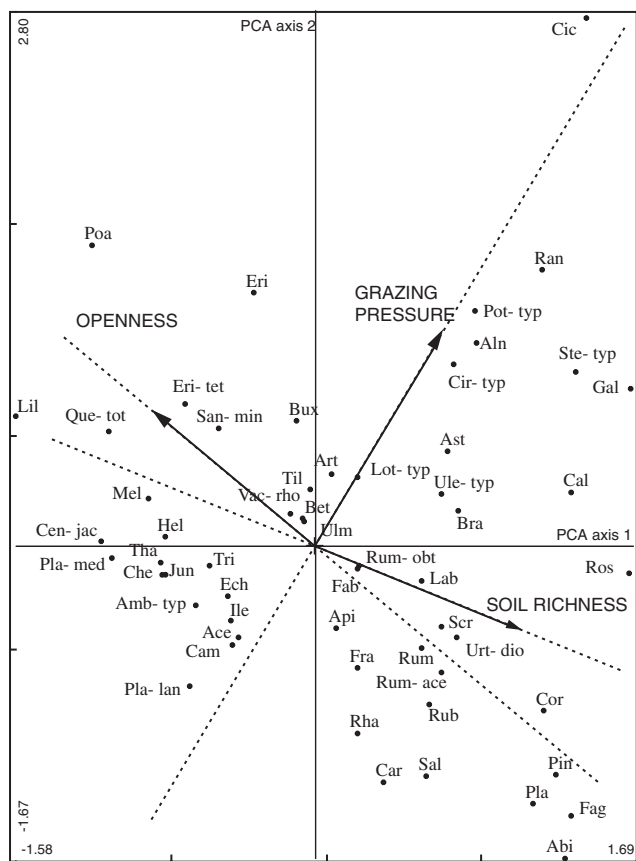
**Figure 5** Principal Component Analysis (PCA) using the scores of a separate RDA with coenotaxa CoE No. 7 (dry heahland), indicative of vegetation openness, CoE No. 12 (semi-open oak forest), indicative of low soil richness, and CoE No. 2 (overgrazed community), indicative of high grazing pressure. Axis 1 and 2 represent 85% of the total variance. Abbreviations: Abi, *Abies*; Ace, *Acer*; Aln, *Alnus*; Amb-typ, *Ambrosia*-type; Api, Apiaceae; Art, *Artemisia*; Ast, Asteroideae; Bet, *Betula*; Bra, Brassicaceae; Bux, *Buxus*; Cal, *Calluna*; Cam, Campanulaceae; Car, Caryophyl-laceae; Cen-jac, *Centaurea jacea*; Che, Chenopodiceae; Cic, Cichoriodeae; Cir-typ, *Cirsium*-type; Cor, *Corylus*; Ech, *Echium*; Eri, Ericaceae; Eri-tet, *Erica tetralix*; Fab, Fabaceae; Fag, *Fagus*; Fra, *Fraxinus*; Gal, *Galium*-type; Hel, *Helianthemum*;, Ile, *Ilex*; Jun, *Juncus*; Lab, Labiateae; Lil, Liliaceae; Lot-typ, *Lotus* type; Mel, *Melampyrum*; Poa, Poaceae; Pla, *Plantago*; Pla-lan, *Plantago lanceolata*; Pla-med, *Plantago major/media*; Pin, *Pinus*; Que-tot, *Quercus total*; Pot-typ, *Potentilla*-type; Ran, Ranunculaceae; Rha, *Rhamnus*; Rub, Rubiaceae; Rum, *Rumex*; Rum-ace, *Rumex acetosa/acetosella*; Rum-obt, *Rumex obtusifolius*; Ros, Rosaceae; Sal, *Salix*; San-min, *Sanguisorba minor*; Scr, Scrophulariaceae; Ste-typ, *Stellaria* type; Til, *Tilia*; Ulex-typ, *Ulex* type; Ulm, *Ulmus*; Urt-dio, *Urtica dioica*; Vac-rho, *Vaccinium/Rhododendron*

communities. Nevertheless, the proportion of Poaceae is not the same in CoE No. 2, an overgrazed pasture and CoE No. 4, grazed wet vegetation. The integrated synusial approach provides some explanation for these dissimilarities between pastoral communities. Poaceae was mainly recorded in CoE No. 4 and 7, and indeed this may be explained by the presence of patches of *Juncus effusus* (CoE No. 4) and *Ulex europaeus* (CoE No. 7), both of which protect herbs from grazing, thus allowing the flowering of the grasses. Alternatively, another factor might be the animals' preference for some species. This seems to be verified for *Poa annua*, the main species in CoE No. 2 that has a higher pastoral value and a higher appetency as compared with *Agrostis curtisï*. Another explanation might be the differences in pollen productivity of the various species included in this large taxonomic group. High grazing pressure

induces a specific community, such as CoE No. 2, which presents patches of syntaxon **H4** (*Rumex acetosella–Galium saxatile*) on nearly bare soils, and syntaxon **H3** (*Trifolium repens–Poa annua*) in densely grazed micro-sites. This coeno-taxon seems to be the most reliable analogue for intensive pastoral activity. On the other hand, CoE No. 7 can be used as an analogue for extensive pastures and CoE No. 9, 10 or 11 for deciduous, mainly beech, forest. CoE No. 6 provides a situation of transition between extensive and intensive pas-tures. CoE No. 3 and 4 are more related with the soil richness, which may derive from grazing pressure.

*Pollen indicators of pastoral activities*

In the PCA analysis based on the three vegetation predictors CoE No. 7, 12 and 2, Cichorioideae, Ranunculaceae, *Stellaria*-type, *Cirsium*-type, *Galium*-type, Asteroideae and, to a lesser extent, *Potentilla*-type are strictly related to grazing pressure. Similar results were obtained in northern Europe (Hicks, 1988; Gaillard *et al.*, 1992, 1994; Hjelle, 1998, 1999a,b; Räsänen, 2001). It was found that Cichorioideae (Hjelle, 1999a), *Cirsium*-type (Hjelle, 1998), *Galium*-type (Gaillard *et al.*, 1992), *Potentilla*-type (Gaillard *et al.*, 1992; Hjelle, 1999a), and Ranunculaceae (Hjelle, 1999a) were characteristic of grazing. In this study *Plantago lanceolata*, Chenopodiaceae and *Plantago major/media*, the last two taxa being absent from the vegetation, are more common in sites on aspects N and NW and occur mainly in lightly grazed wooded sites. Their presence is related to the prevailing wind, which brings pollen from a wider landscape. Gaillard *et al.* (1992) showed that *Plantago lanceolata* is a mowing indicator in southern Sweden. According to Hicks and Birks (1996), Chenopodiaceae and *Rumex acetosa/acetosella* are related to human settlements. This may apply in our case for *Rumex acetosa/acetosella*, since this taxon was present in tracks and/or in the ploughed soils of CoE No. 3, but generally it was recorded sporadically in modern pollen assemblages and therefore cannot be a good pastoral indicator. In our case, the presence of the taxa Chenopodiaceae, *Plantago lanceolata* and *Artemisia* implies regional input.

*Urtica dioica* is related to soil richness (total N and loss on ignition) and does not constitute a strict pastoral indicator (Gaillard *et al.*, 1992), at least when low values are recorded (Mazier *et al.*, unpublished data, 2005). It is found in surface samples from enclosures, but the plant often grows outside, where dung has accumulated near stone walls.

## Conclusion

(1)    The correlative model, RDA of 61 modern pollen spectra and 35 external variables, shows that wooded, opened, grazed and nitrophilous sites are clearly separated from each other. The relevant variables are vegetation types CoE No. 7 (dry heathland), CoE No. 12 (semi-open oak forest) and CoE No. 2 (overgrazed community). These vegetation units are clearly related to degree of openness, soil richness and grazing pressure, respectively. Therefore, the synusial integrated ap-proach does provide a robust method for assessing vegetation structure and links between different patches (herbs, shrubs and trees), and also for relating modern pollen assemblages to environmental conditions.

(2)    The present study implies that, when reconstructing past pastoral activity, it is important to identify the scale of the landscape in question. In our case, *Artemisia*, Cheno-podiaceae, *Plantago lanceolata*, and *Plantago major/media* indicate regional human activity, and are not characteristic

of specific land use, whereas the simultaneous presence, in pollen assemblages, of Asteroideae, Cichoriodeae, *Cirsium*-type, *Galium*-type, Ranunculaceae, *Stellaria*-type and *Potentilla*-type is clearly associated with grazing on a local scale. Calculation of Davis indices also shows that Cichorioideae, *Galium*-type and *Potentilla*-type indicate very local presence of the corresponding plants. However, such pastoral indicators might be valid only for crystalline bedrock, and for this mountainous region.

(3)   The final aim of our project is to achieve a more precise reconstruction of the cultural landscape in this mountainous area on a local scale, comparing the modern pollen assemblages to local fossil pollen assemblages from a small bog (Galop *et al.*, 2003; Mazier *et al.*, unpublished data, 2005). Thanks to the interdisciplinary research programme 'Palaeoenvironment and dynamics of human activities in the Pyrenees Mountains' this site is now also well documented in microfossil, historical and archaeological data. All these data sets will be used to validate the results of the comparative approach.

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