

# Comparison of understory plant community composition and soil characteristics in *Quercus pyrenaica* stands with different human uses

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## Abstract

The species composition of the plant community and the soil characteristics in *Quercus pyrenaica* ecosystems according to the degree of disturbance and the type of human intervention (burning, cutting, livestock grazing) were compared. Four types of oak communities were selected, each with five replicates: oak shrublands (SL), dehesas (DE) or open woodlands used for grazing, and two types of mature oak forest, one with abundant shrub biomass in the understory (FS) and the other with little shrub biomass in the understory (FO). A total of 175 species were found in the 20 sites studied, 52 appeared in a single site. The dehesas were the most different regarding species composition, with 30 species only found there. This was verified by a qualitative similarity analysis, in which the five dehesas formed a group clearly distinguishable from the other sites; the oak shrublands also formed a group, but it was not possible to distinguish between the mature oak forests with and without a shrubby understory. However, the soil characteristics were similar across all sites and differences could only be detected in organic matter and nitrogen content, which were significantly higher in the mature forests without a shrubby understory. When the plant community and soil characteristics were analysed as a whole using a canonical correspondence analysis, the separation of the dehesas was observed on the first axis, due to its greater richness and abundance in herb species, especially annuals. The other sites were ordered on the second axis, with greater differences between the oak shrublands, associated with higher shrub species cover, and the mature open forests, associated with forest herb species and a soil with a higher nitrogen, organic matter and cation exchange content. The mature forests with abundant shrub biomass were in an intermediate position. Therefore, although the differences in soil were not important and many species were common to all types of *Q. pyrenaica* communities, the type of human intervention did determine changes, as shown by the results of the multifactorial analyses. In addition, given that all the community types presented some species which were not found in the other types, greater biodiversity would be attained by preserving all of them.

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## 1. Introduction

The species composition and characteristics of a forest understory depend to a great extent on both past and present events, including the frequency and intensity of disturbances (Bormann and Likens, 1979). Forest management is one of the human disturbances that affects species diversity and composition, as well as forest structure and function (Hunter, 1999; Tybirk and Strandberg, 1999). In addition, these disturbances usually produce alterations in the soil processes (Kimmins, 1987). However, there are not always clear relationships among soil properties and forest management (Rubio et al., 1999).

It is generally assumed that after tree harvesting total species richness increases in temperate forests, mostly due to the establishment of shade intolerant ruderal species (Bormann and Likens, 1979; Elliott et al., 1997). Other types of management, like grazing, determine changes in species composition and in species diversity, but the effects are not the same for all forest ecosystems (González-Hernández and Silva-Pando, 1996; Krzic et al., 2003; Weisberg and Bugmann, 2003; Onaindia et al., 2004). Many authors found no changes in the diversity values as a result of management but did find changes in species composition (Fredericksen et al., 1999; Brososke et al., 2001; Nagaike et al., 2003). However, the opposite occurred in other cases, as in the study by Schumann et al. (2003), where differences in total species richness appeared between harvest gaps and controls but the species composition overlapped considerably. As regards effects of forest management on the

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edaphic characteristics and their relation to understory vegetation, some authors found a clear influence on understory composition but there were not a clear correlation between management and soil features (Rubio et al., 1999; Krzic et al., 2003). However, Strandberg et al. (2005) showed that conservational management can increase both soil nutrient availability and floristic diversity. On the other hand, Härdtle et al. (2003), studying different deciduous forest, found that soil conditions had a vegetation type specific effect on the understory.

Due to a long history of human occupation, hardwood forests have been confined to the least suitable zones for agriculture in southern Europe, normally in mountainous regions or those with lesser quality soils. Most of these forests have been used to obtain wood or firewood or for grazing, which has degraded the vegetation and soil (Gallardo et al., 1999; Moreno and Gallardo, 2002). *Quercus pyrenaica* oak forests, whose main distribution area is the Iberian Peninsula, have been linked to these types of land uses, which have conditioned their present characteristics (Calvo et al., 1999; Luis-Calabuig et al., 2000). On the other hand, in the last decades the decrease in the rural population has led to abandoning or reducing these uses, determining new changes, like the recovery of oak forests in old grazing or crop areas, or the proliferation of shrubby species in the understory, as wood was no longer taken and livestock no longer passed through.

In a previous study carried out in *Q. pyrenaica* communities with different uses and degrees of disturbance, the structure of the tree layer and understory diversity were compared (Tárrega et al., 2006) and no clear relationship was found between the type of management and species diversity. Our current study is intended to show whether the type of management conditions changes in plant species and soil in these communities. Specifically, the aims are: (a) to determine whether there are differences in plant species composition across management types, (b) to analyse whether the intensity and type of human intervention have any effect on soil characteristics and (c) to study the relationship between the understory community and edaphic conditions. Four types of communities were compared: communities of shrubby oaks (SL, oak shrublands, result of secondary succession after abandoning grazing and halted by fire, or the progressive destruction of mature forests by felling and fires), dehesas (DE, open woodland with few shrubs, currently used as pasture), mature forests with practically no woody species in the understory (FO, forests with open understory, the result of grazing or exploitation for firewood) and mature forests with abundant woody species in the understory (FS, forests with shrubby understory, where these uses have been abandoned).

## 2. Materials and methods

Twenty *Q. pyrenaica* communities were selected, five of each type. The shrubby oak communities (SL) were identified physiognomically by a great density of small stems resulting from vegetative resprouting as a response to disturbances. The dehesa communities (DE) were the result of a traditional

livestock sustainable management method in which the forest was cleared, leaving a low density of trees which were pruned to favour crown development at the expense of height growth. In the study communities they were used as communal pastures by livestock (sheep and sometimes cows) and it was difficult to establish the livestock load due to high variability. The other two forest community types represented a lesser degree of human intervention, the difference between them being the higher (FS) or lower (FO) abundance of woody species in the understory.

To minimise the variability, geographically close communities were selected (situated in León province, NW Spain, 42°36'–42°49'N, 4°52'–5°11'W), altitude between 920 and 1300 m, with no slope or one of less than 10%, subhumid Mediterranean climate (mean annual temperature 10.9 °C, mean annual precipitation 927 mm, dry period in July and August, according to the Ministerio de Agricultura, 1980) and humic cambisol type soil (Forteza et al., 1987). The specific location of each community and a description appear in Tárrega et al. (2006).

A systematic sampling method was used for the plant community study. Two perpendicular transects of about 40 m were established in each community and ten 1 m<sup>2</sup> quadrats, each 3 m apart, were sampled in each transect. The first quadrat of each transect was randomly selected. All the species present in each quadrat were recorded, quantifying their abundance as a cover percentage (visually estimated). Cover values higher than 100% were due to layer superposition. Sampling was conducted in June and July 2004.

Soil sampling was conducted in September 2004. Five samples, approximately 8 m apart, were collected in each site, taking the first 10 cm, which were homogenised to obtain a uniform sample of the characteristics of the site as a whole. The depth of the litter layer was measured at the same soil sampling points. The soil samples were air-dried and passed through a 2 mm mesh sieve for later analysis. The pH, organic matter, total nitrogen, cation exchange capacity (C.E.C.), and available calcium, potassium, magnesium and sodium were determined in each sample, in accordance with the official methods of soil analysis (M.A.P.A., 1994).

Plant species composition was compared across study communities by a qualitative affinity analysis. Those only appearing on one community (52 species) were not included in the analysis. Thus, a table of qualitative data with 123 species (1 = species present, 0 = species absent) was analysed, using percentage disagreement as a similarity index and the U.P.G.M.A. technique as clustering method. The software used was Statistica 6.0.

An analysis of variance was conducted to determine whether there were significant differences in soil variables and for cover values of annual species, herbaceous perennial species, woody species, and species richness. In all cases five replicates were considered. The Scheffe test was applied for post hoc comparisons when the ANOVA was significant ( $p \leq 0.05$ ). Sample normality was checked using the Kolmogorov–Smirnov test and homogeneity of variances with the Cochran test.

For the joint comparison of all the results a canonical correspondence analysis was conducted, using the CANOCO program (Ter Braak, 1991). Species appearing on only one community were not used for this analysis. The depth of the litter layer and the soil variables were included as environmental variables, disregarding pH, C/N ratio and C.E.C. because they had lower variability in the study sites and thus provided little information.

### 3. Results

The most frequent species across all communities were *Galium aparine*, *Festuca rubra*, *Carex muricata*, *Cruciata glabra*, *Agrostis capillaris*, *Arenaria montana*, *Avenula marginata* and *Lotus corniculatus*, as well as *Q. pyrenaica* sprouts (Table 1). On most communities, except the oak shrublands, the perennial herbs were those with the greatest

Table 1  
Most frequent, abundant or representative annual, perennial herbs and woody species in the studied community types

	SL			DE			FS			FO		
	Fr	Cov. mean	Cov. S.D.	Fr	Cov. mean	Cov. S.D.	Fr	Cov. mean	Cov. S.D.	Fr	Cov. mean	Cov. S.D.
Annual herbs												
<i>Aira caryophylla</i>	3	0.3	0.6	5	13.9	7.6	2	0.1	0.2	2	0.1	0.1
<i>Cerastium glomeratum</i>	2	0.1	0.1	5	5.1	2.7						
<i>Cynosurus echinatus</i>	1	0.1	0.1	5	5.6	4.3						
<i>Galium aparine</i>	5	1.3	2.0	5	2.8	3.1	5	2.7	2.5	5	0.9	0.9
<i>Melampyrum pratense</i>	3	3.7	6.9				4	3.3	3.3	3	6.3	8.1
<i>Petrorhagia prolifera</i>				5	2.3	1.9						
<i>Tuberaria guttata</i>				5	14.1	9.0				1	0.1	0.2
<i>Vulpia bromoides</i>				5	11.9	10.8	1	0.1	0.2	1	0.1	0.1
Perennial herbs												
<i>Agrostis capillaris</i>	4	3.0	3.1	5	29.1	6.6	4	3.2	2.0	4	3.8	4.4
<i>Anemone nemorosa</i>										2	4.4	7.8
<i>Anthoxanthum odoratum</i>	2	0.5	0.9	2	0.4	0.7	4	0.9	1.3	4	5.2	9.8
<i>Arenaria montana</i>	5	2.8	1.4	2	0.5	0.9	5	4.0	3.4	5	1.6	2.0
<i>Avenula marginata</i>	5	5.9	4.7	3	2.7	2.9	4	4.2	3.4	5	6.6	8.1
<i>Bellis perennis</i>				4	3.7	5.6				1	0.1	0.1
<i>Brachypodium pinnatum</i>	3	8.0	10.0	2	1.1	2.3	5	7.6	4.4	2	6.4	8.8
<i>Carex muricata</i>	5	4.7	4.8	4	6.7	7.0	5	2.6	1.2	5	2.5	3.0
<i>Cruciata glabra</i>	5	3.6	2.4	4	1.3	1.3	5	5.1	4.9	5	4.9	3.2
<i>Festuca paniculata</i>	3	0.9	1.3									
<i>Festuca rubra</i>	5	10.0	7.1	5	10.1	7.3	5	10.5	1.6	5	14.0	5.9
<i>Helleborus foetidus</i>							3	0.1	0.1	2	1.6	3.3
<i>Hieracium castellanum</i>				4	6.7	5.8						
<i>Hieracium murorum</i>							1	0.4	0.9	3	0.7	0.7
<i>Hieracium gr. pilosella</i>	3	2.3	2.7	5	6.8	3.3	2	0.2	0.4	3	0.8	1.4
<i>Holcus mollis</i>				2	0.4	0.7	5	11.1	10.7	3	5.8	6.9
<i>Lathyrus niger</i>							2	0.2	0.4	3	2.4	2.8
<i>Lotus corniculatus</i>	4	2.3	3.0	5	3.1	0.8	5	0.3	0.1	3	0.1	0.3
<i>Melittis melissophyllum</i>							1	0.2	0.4	1	0.2	0.3
<i>Physospermum cornubiense</i>				1	0.1	0.1	4	0.7	1.0	5	4.1	7.0
<i>Pteridium aquilinum</i>							2	4.6	7.2	2	3.7	8.0
<i>Stellaria holostea</i>				1	0.1	0.1	3	3.6	4.6	5	4.2	2.5
<i>Veronica chamaedrys</i>										2	1.0	1.7
Woody species												
<i>Calluna vulgaris</i>	4	7.6	12.0	2	1.1	2.2	3	6.7	11.6	1	0.2	0.3
<i>Chamaespartium tridentatum</i>	2	2.0	2.7									
<i>Crataegus monogyna</i>	2	0.1	0.1	3	0.2	0.3	5	3.1	3.5	5	1.9	0.9
<i>Erica arborea</i>							5	12.0	7.4			
<i>Erica tetralix</i>	2	3.1	5.9									
<i>Erica umbellata</i>	3	7.4	11.6	1	0.6	1.3				1	0.1	0.1
<i>Genista florida</i>	1	0.1	0.1				2	1.1	1.5	3	1.6	2.0
<i>Lithodora diffusa</i>	3	0.9	1.5	1	0.2	0.5	4	2.7	2.9	4	5.5	6.7
<i>Lonicera periclymenum</i>							2	1.6	2.2	1	0.1	0.2
<i>Prunus spinosa</i>							2	0.2	0.3	3	0.3	0.3
<i>Quercus pyrenaica</i>	5	52.5	14.4	5	5.0	4.4	5	22.9	12.8	5	10.6	7.7

Fr: frequency or number of sites where the species appeared. Cov.: mean and standard deviation cover values for the five sites of each community type. SL: oak shrublands, DE: dehesas, FS: oak forests with shrubby understory, FO: oak forests with open understory.

Table 2

Mean values and standard deviation (S.D.) of annual, perennial herbs and woody species cover, and mean and standard deviation values of species richness of each community type, as well as total species richness, number of common species (species appearing in all the five sites of each community type), number of exclusive species (species appearing in one or more sites of this community type but not in the other community types), number of species appearing only in one site and total species richness

	SL		DE		FS		FO		ANOVA results	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	F-test	p-Value
Annual spp. cover	6.5	5.8 <b>a</b>	75.6	37.0 <b>b</b>	8.8	4.4 <b>a</b>	8.0	9.2 <b>a</b>	15.25	<0.001
Perennial herb cover	68.2	23.8	105.7	23.5	85.8	26.7	102.9	37.8	1.84	0.18
Woody spp. cover	79.1	20.2 <b>a</b>	8.6	7.1 <b>b</b>	56.8	6.2 <b>a</b>	27.2	16.8 <b>b</b>	24.90	<0.001
Mean and S.D. richness	42.4	13.2	55.6	8.8	45.6	3.6	42.9	10.9	2.00	0.16
Total richness	90		104		89		94			
No. of common spp.	10		23		18		12			
No. of exclusive spp.	18		30		13		18			
No. of spp. in only 1 site	13		14		10		15			

SL: oak shrublands, DE: dehesas, FS: oak forests with shrubby understory, FO: oak forests with open understory. Results of analysis of variance were also included (when  $p < 0.05$ , different letters within a row indicate significant differences by Scheffe test). Total richness considering all the community types = 175.

cover in the understory, even exceeding 100% in some sites (Table 2). The annual species were abundant in the dehesas while their cover was below 10% in the other sites. Woody species dominated the oak shrublands with almost 80% cover, and were also abundant in the mature forests with shrubby understory, with over 50% cover; the lowest cover was recorded in the dehesas where they did not reach 10%. Differences were detected between oak shrublands and forests with shrubby understory versus dehesas and forests with open understory. The total number of species recorded was 175, of which 52 appeared in only one site. The highest species richness, as a mean and as a total per community type, was found in the dehesas, which also included the highest number of species that did not occur in other community types (exclusive species). The lowest number of exclusive species was recorded in the mature forests with shrubby understory, though they included 13 species that were found nowhere else. Also another 11 species were shared by the two types of mature forests (FO and FS) did not appear in the other community types. The dehesas also shared the highest number of common species (23 species)

appearing in the 5 sites, while the oak shrublands only had 10 species common to the 5 sites. Comparison of the species composition using an analysis of qualitative similarity (Fig. 1) showed the greatest similarity among the five dehesas, while all the other sites formed another group. Within this group a subgroup formed by the oak shrublands, and another in which the mature forests are mixed without a clear separation between FS and FO.

The depth of the litter layer varied between 2.7 and 4 cm across all study sites (Table 3). The soils of the study sites presented a moderately acid pH with abundant organic matter and nitrogen, good nutrient levels and a C/N ratio between 14.8 and 17.3. The soil characteristics did not differ among the sites, except for the mature open forests, which had a higher organic matter, nitrogen and sodium content.

When the relationship between plant species richness and cover and the soil variables was analysed, significant results were obtained only for woody cover, which showed a positive correlation with the C/N ratio (Spearman  $R = 0.46$ ,  $p = 0.04$ ) and Ca (Spearman  $R = 0.46$ ,  $p = 0.04$ ) and a negative correlation with K (Spearman  $R = -0.56$ ,  $p = 0.01$ ).

In the plane defined by the first two axes of the canonical correspondence analysis (cumulative percentage variance of species–environmental relation = 56%, Monte Carlo test results:  $F$ -ratio = 2.55,  $p = 0.01$ ) the location of all the dehesa communities was seen at the positive end of the first axis, contrary to all the environmental variables, and associated with herb species such as *Scleranthus annuus*, *Bellis perennis*, *Bromus hordeaceus*, *Aira caryophylla*, *Cynosurus echinatus*, *Petrorhagia prolifera*, *Tuberaria guttata*, *Vulpia bromoides*, etc. (Fig. 2a and b; Tables 1 and 3). The other communities were at the negative end of the first axis, observing a grouping in terms of the second axis with the oak shrublands at the negative end, associated with shrub species like *Erica umbellata*, *Halimium alyssoides*, *Erica tetralix* and *Chamaespartium tridentatum* and herbs like *Festuca paniculata* and *Carex nigra*. The mature open forests were associated with soils with a higher organic matter, nitrogen and cation exchange content, and were located at the positive end of the second axis. They

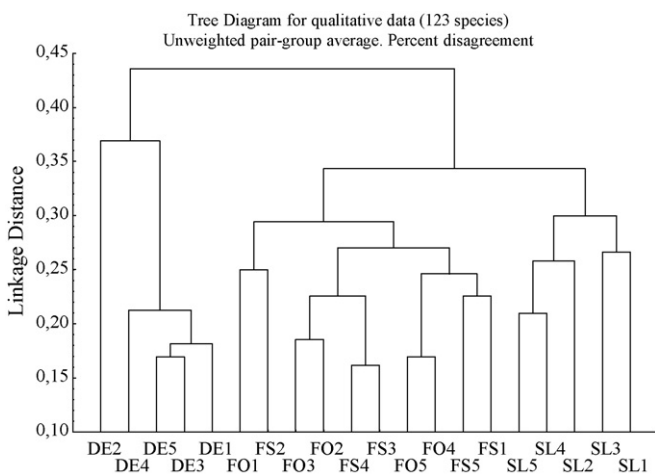
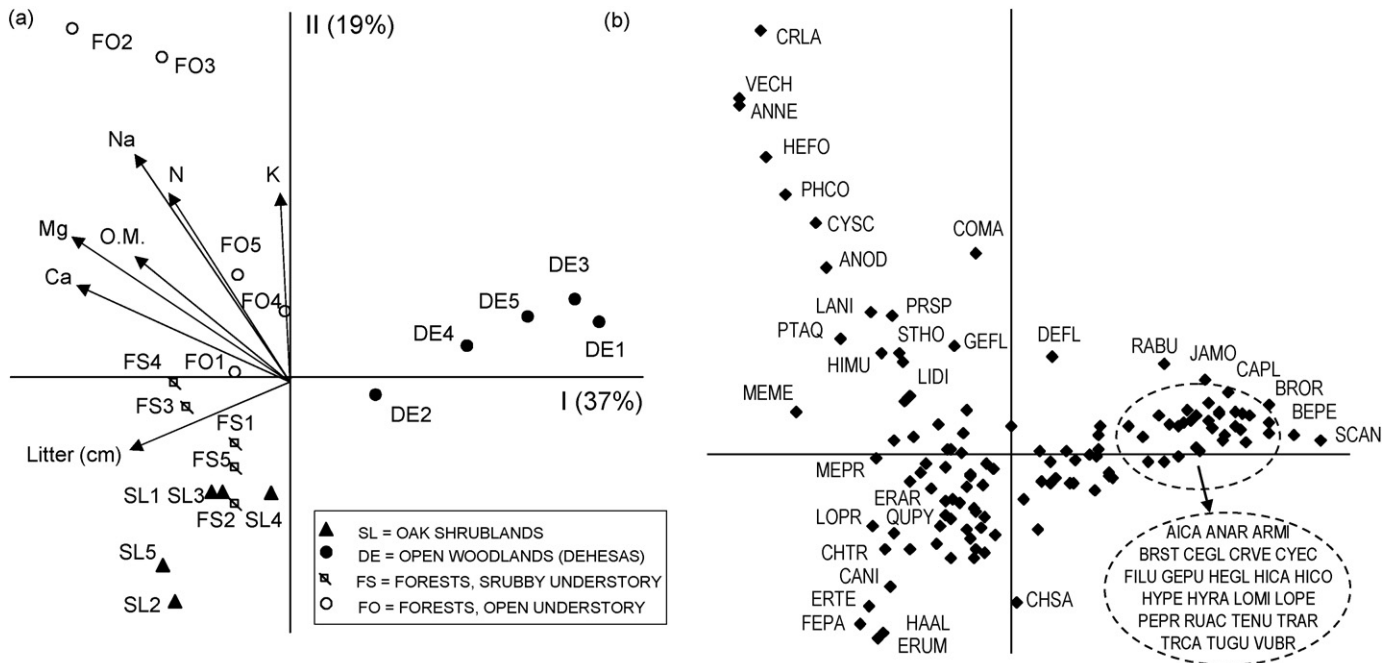


Fig. 1. Qualitative affinity analysis among the study communities (SL: oak shrublands, DE: dehesas, FS: oak forests with shrubby understory, FO: oak forests with open understory).

Table 3  
Mean values and standard deviation (S.D.) of the soil variables in the studied community types

	SL		DE		FS		FO		ANOVA results	
	Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.	F-test	p-Value
Litter (depth cm)	3.50	1.66	2.72	0.82	3.96	1.10	2.94	0.42	1.30	0.308
pH	5.20	0.69	5.12	0.21	5.50	0.30	4.88	0.38	1.62	0.225
Organic matter (%)	6.05	2.16 <b>a</b>	5.58	1.63 <b>a</b>	5.62	0.96 <b>a</b>	9.10	2.07 <b>b</b>	4.56	<b>0.017</b>
N (%)	0.21	0.05 <b>a</b>	0.21	0.07 <b>a</b>	0.19	0.04 <b>a</b>	0.36	0.09 <b>b</b>	7.48	<b>0.002</b>
C/N	16.6	2.12	15.8	2.37	17.3	1.16	14.8	0.93	1.98	0.158
C.E.C. (meq/100 g)	7.19	1.62	4.95	2.16	7.58	2.60	9.65	3.74	2.64	0.085
Ca (meq/100 g)	4.56	2.11	2.64	1.39	5.24	2.08	5.16	3.22	1.39	0.281
Mg (meq/100 g)	0.87	0.30	0.61	0.26	1.07	0.45	1.31	0.77	1.87	0.175
K (meq/100 g)	0.29	0.06	0.44	0.09	0.39	0.18	0.56	0.19	3.19	0.052
Na (meq/100 g)	0.02	0.01 <b>a</b>	0.02	0.01 <b>a</b>	0.02	0.01 <b>a</b>	0.04	0.01 <b>b</b>	4.87	<b>0.014</b>

SL: oak shrublands, DE: dehesas, FS: oak forests with shrubby understory, FO: oak forests with open understory. Results of analysis of variance are also included (when  $p < 0.05$ , different letters within a row indicate significant differences by Scheffe test).



- |  |                                     |                                       |
|--|-------------------------------------|---------------------------------------|
| AICA = <i>Aira caryophyllea</i>          | ERAR = <i>Erica arborea</i>         | LOPE = <i>Lolium perenne</i>          |
| ANAR = <i>Anthemis arvensis</i>          | ERTE = <i>Erica tetralix</i>        | LOPR = <i>Lonicera periclymenum</i>   |
| ANNE = <i>Anemone nemorosa</i>           | ERUM = <i>Erica umbellata</i>       | MEPR = <i>Melampyrum pratense</i>     |
| ANOD = <i>Anthoxanthum odoratum</i>      | FEPa = <i>Festuca paniculata</i>    | MEME = <i>Melittis melissophyllum</i> |
| ARMI = <i>Arnoseria minima</i>           | FILU = <i>Filago lutescens</i>      | PEPR = <i>Petrorhagia prolifera</i>   |
| BEPE = <i>Bellis perennis</i>            | GEFL = <i>Genista florida</i>       | PHCO = <i>Phytolacca cornubiense</i>  |
| BROR = <i>Bromus hordeaceus</i>          | GEPU = <i>Geranium pusillum</i>     | PRSP = <i>Prunus spinosa</i>          |
| BRST = <i>Bromus sterilis</i>            | HAAL = <i>Halimium alyssoides</i>   | PTAQ = <i>Pteridium aquilinum</i>     |
| CANI = <i>Carex nigra</i>                | HEFO = <i>Helleborus foetidus</i>   | QUPY = <i>Quercus pyrenaica</i>       |
| CAPL = <i>Caucalis platycarpus</i>       | HEGL = <i>Herniaria glabra</i>      | RABU = <i>Ranunculus bulbosus</i>     |
| CEGL = <i>Cerastium glomeratum</i>       | HICA = <i>Hieracium castellanum</i> | RUAC = <i>Rumex acetosella</i>        |
| CHSA = <i>Chamaespartium sagittale</i>   | HIMU = <i>Hieracium murorum</i>     | SCAN = <i>Scleranthus annuus</i>      |
| CHTR = <i>Chamaespartium tridentatum</i> | HICO = <i>Hippocrepis comosa</i>    | STHO = <i>Stellaria holostea</i>      |
| COMA = <i>Conopodium majus</i>           | HYPE = <i>Hypericum perforatum</i>  | TENU = <i>Teesdalia nudicaulis</i>    |
| CRLA = <i>Crepis lampanoides</i>         | HYRA = <i>Hypochoeris radicata</i>  | TRAR = <i>Trifolium arvense</i>       |
| CRVE = <i>Crepis vesicaria</i>           | JAMO = <i>Jasione montana</i>       | TRCA = <i>Trifolium campestre</i>     |
| CYEC = <i>Cynosurus echinatus</i>        | LANI = <i>Lathyrus niger</i>        | TUGU = <i>Tuberaria guttata</i>       |
| CYSC = <i>Cytisus scoparius</i>          | LIDI = <i>Lithodoradiffusa</i>      | VECH = <i>Veronica chamaedrys</i>     |
| DEFL = <i>Deschampsia flexuosa</i>       | LOMI = <i>Logfia minima</i>         | VUBR = <i>Vulpia bromoides</i>        |

Fig. 2. (a) Location of study sites and soil variables in the plane defined by the first two axes in the canonical correspondence analysis (SL: oak shrublands, DE: dehesas, FS: oak forests with shrubby understory, FO: oak forests with open understory). (b) Location of species in the plane defined by the first two axes in the canonical correspondence analysis.



were also associated with exclusive herb species, like *Crepis lampanoides*, *Veronica chamaedrys* and *Anemone nemorosa*. There were other herb species (*Helleborus foetidus*, *Physospermum cornubiense*, *Anthoxanthum odoratum*, *Lathyrus niger*, *Pteridium aquilinum*, *Hieracium murorum*, *Melittis melissophyllum* and *Lonicera periclymenum*), and shrubs like *Cytisus scoparius*, *Genista florida* and *Prunus spinosa*, associated with the two types of mature forests. The forests with shrubby understory occupied an intermediate situation, because they also had deeper litter, like the oak shrublands, and greater woody cover in the understory, above all of *Q. pyrenaica* sprouts, as well as *Erica arborea*, which was only found in the forests with shrubby understory. *Q. pyrenaica* sprouts appeared at all the sites but were much more abundant in the oak shrublands and the forests with shrubby understory. *Melampyrum pratense* was recorded in all the community types except the dehesas.

#### 4. Discussion

Of all the species found, 45% were only recorded in one community type and the proportion increased to 51% if the 11 species only appearing in mature forests, although common to forests with shrubby understory and open forests, were included. However, when we eliminated the 52 species that only appeared in one site, the percentage of exclusive species would be reduced to 32%. That is, there were 68% common species in these *Q. pyrenaica* communities which did not seem to be affected by the type of management, based on presence/absence data. Other studies found similar results. For example, Schumann et al. (2003), recorded great superposition between species found in harvest-created gaps and unharvested controls. However, the similarity was more qualitative than quantitative in our study communities. Many of these common species presented changes in their relative abundance, as in the case of the grasses *Aira caryophyllea* or *Agrostis capillaris*, appearing very frequently in all the sites, but with higher cover in the dehesas, or much more abundance of woody species, both chamaephytes and young sprouts of phanerophytes, in the understory of oak shrublands and mature forests with shrubby understory.

CCA is a quantitative ordination technique that takes into account differences in the relative importance of species. On comparing the two types of mature forest (FS and FO) there was great similarity in their species composition, since they did not separate in the qualitative cluster, although they did in the CCA. The main difference was the greater woody cover in the FS understory, partly due to shrub species typical of forests, like *Erica arborea*, but also to other species, like *Calluna vulgaris* or the oak sprouts which made them similar to the oak shrublands. Both types of forest shared many forest herb species, which were lacking in the other community types. Among them, some were typically nemoral and shade tolerant species, like *Anemone nemorosa* and *Melittis melissophyllum*, although others could also appear in other types of habitat. The oak shrublands also had species which were not found in the other community types, above all chamaephytes, like

*Chamaespartium tridentatum* or *Erica tetralix*, but also some herbs. However, the greatest difference regarding species composition was recorded in the dehesas, from a qualitative and a quantitative viewpoint. This was in accordance with Taboada et al. (2006) for carabid fauna of the same area. The dehesas presented less woody cover in the understory as well as greater annual species cover, which corresponded to the significantly higher number of annual species (Tárrega et al., 2006). The increase in richness or abundance of herb species as a result of grazing has been mentioned by several authors (Montalvo et al., 1993; Tybirk and Strandberg, 1999; Krzic et al., 2003; Onaindia et al., 2004; Strandberg et al., 2005). In addition, the lower tree density in dehesas allowed conditions of greater light availability, benefiting the development of ruderal shade-intolerant species, which coincided with what has been observed by many authors after canopy thinning (Brunet et al., 1996; Elliott et al., 1997; Fredericksen et al., 1999; Härdtle et al., 2003; Krzic et al., 2003; Götmark et al., 2005). This was also associated to the disappearance of nemoral species (Onaindia et al., 2004). However, other authors did not record any clear evidence of a negative effect of management on the species richness of the typical forest flora (Brunet et al., 1996; Götmark et al., 2005).

No clear relationship was found in the soil characteristics between the type of management and most of the edaphic variables, which coincided with the results of other research (Rubio et al., 1999; Krzic et al., 2003). Nevertheless, better soil conditions were observed in the open forests, associated with mature forests (Kimmins, 1987), like the high content in organic matter and total nitrogen, greater cation exchange capacity and higher nutrient content. These characteristics could be due to the combination of a series of factors like species composition (predominance of herbs in the understory) and microclimatic conditions (canopy closure), determining better soil conditions than in the dehesas and in the mature forests with shrubby understory, where both factors did not appear simultaneously.

The correlation between the C/N ratio and woody cover can be explained by the higher proportion of C in woody litter (Kimmins, 1987). Nevertheless, although there were differences between the different community types in woody abundance in the understory, the C/N ratio presented values relatively similar in all of them, so it is unlikely that it would have any effect on the functional characteristics of the ecosystem. The same could be said of the correlations between woody cover and K (–) and Ca (+). On the other hand, the lack of correlation between species richness and soil characteristics coincided with previously obtained results, according to which it was also not possible to show a clear relationship between diversity and management type (Tárrega et al., 2006). No unanimous trend in soil-richness relationships was observed when compared with other research. Some authors have found a relationship between species richness and litter depth (North et al., 2005) or soil pH (De Keersmaeker et al., 2004; Strandberg et al., 2005). Others mentioned that soil factors could have a different effect in terms of overstory properties (Brosfokske et al., 2001). Hutchinson et al. (1999) observed

greater richness in the most fertile plots; however, Pausas and Austin (2001) pointed out a general trend of decreasing species richness with nutrient enrichment, although they stated that this response was almost never linear due to the interactions among the various environmental parameters. On the other hand, Härdtle et al. (2003) did not find any significant correlation between the number of species and the chemical parameters of the soil.

In view of the results obtained, it seems clear that, in spite of differences in soil not being considerable and many species being common to all the types of *Q. pyrenaica* community, the type of use did determine changes in the understory species, as shown by the qualitative and quantitative multifactorial analyses. This coincided with the results of other researchers, which suggested that the differences in species composition seemed to function better than the diversity measures to detect the influence of management on vegetation (Fredericksen et al., 1999; Brososke et al., 2001; Nagaike et al., 2003; Onaindia et al., 2004). Given that all the community types presented some characteristic species that were not found in the other types, it was also clear that the greatest biodiversity would be obtained by preserving all of them. This involves conserving traditional uses like grazing and tree management in the dehesas, or obtaining firewood from the understory of mature oak forests, as well as preserving some intermediate succession stages in some communities, like oak shrublands, or more mature stages of recovery represented by forests with a shrubby understory. The last-mentioned management goal is not usually accepted by the administration forestry managers, who encourage the elimination of woody species in the understory because of the greater risk of forest fires (Vélez, 2000). However, the results of most studies (Tybirk and Strandberg, 1999; Farina, 2000; Magurran, 2004; Götmark et al., 2005; Strandberg et al., 2005) support the compatibility of different types of management with the maintenance of intermediate succession stages and unexploited mature communities as the most appropriate method for preserving maximum diversity at landscape scale, according with our conclusions.

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