Plant  $\beta$ -diversity in human-altered forest ecosystems: The importance of the structural, spatial, and topographical characteristics of stands in patterning plant species assemblages

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### Abstract

An understanding of spatial patterns of plant species diversity and the factors that drive those patterns is critical for the development of appropriate biodiversity management in forest ecosystems. We studied the spatial organization of plants species in human-modified and managed oak forests (primarily, Quercus faginea) in the Central Pre-Pyrenees, Spain. To test whether plant community assemblages varied non-randomly across the spatial scales, we used multiplicative diversity partitioning based on a nested hierarchical design of three increasingly coarser spatial scales (transect, stand, region). To quantify the importance of the structural, spatial, and topographical characteristics of stands in patterning plant species assemblages and identify the determinants of plant diversity patterns, we used canonical ordination. We observed a high contribution of  $\beta$ -diversity to total  $\gamma$ diversity and found  $\beta$ -diversity to be higher and  $\alpha$ -diversity to be lower than expected by random distributions of individuals at different spatial scales. Results, however, partly depended on the weighting of rare and abundant species. Variables expressing the historical management intensities of the stand such as mean stand age, the abundance of the dominant tree species (O. faginea), age structure of the stand, and stand size were the main factors that explained the compositional variation in plant communities. The results indicate that (1) the structural, spatial, and topographical characteristics of the forest stands have the greatest effect on diversity patterns, (2) forests in landscapes that have different land use histories are environmentally heterogeneous and, therefore, can experience high levels of compositional differentiation, even at local scales (e.g., within the same stand).

- 1 Maintaining habitat heterogeneity at multiple spatial scales should be considered in
- 2 the development of management plans for enhancing plant diversity and related
- 3 functions in human-altered forests.
- **Key words**: secondary forests; community assembly; forest structure;
- 5 compositional dissimilarity; beta diversity; species turnover.

### Introduction

Most studies of forest ecosystems focused on  $\alpha$ -diversity, i.e., the diversity within a specific site; however, recent studies that have partitioned diversity into hierarchical components have shown that much of the plant diversity is due to differentiation in species composition among sites ( $\beta$ -diversity; Arroyo-Rodríguez et al., 2013; Chandy, Gibson, & Robertson, 2006; Gossner et al., 2013). Particularly in human-altered forests, the assessment of plant diversity patterns across multiple spatial scales and the identification of the factors that drive those patterns is required to accurately evaluate the impact of historical man-induced disturbances on the spatial dissimilarities in species composition ( $\beta$ -diversity) and to gain a better understanding of the mechanisms that contribute to the maintenance of species diversity in this type of forests (Arroyo-Rodríguez et al., 2013).

In human-altered forests, the structural, spatial, and topographical characteristics of the stand, which are strongly influenced by historical land use-type and intensity, might have a significant role in shaping plant diversity patterns (Flinn and Vellend 2005; Hermy and Verheyen 2007; Berhane et al. 2013). Recent studies have found that forest stands in landscapes that have different land use histories manifest a high environmental heterogeneity, which can lead to high levels of compositional differentiation (i.e.,  $\beta$ -diversity) even at fine scales (e.g. Arroyo-Rodríguez et al. 2013). The floristic differentiation can drive successional trajectories and potentially affect the maintenance of biodiversity in such altered forests (Chazdon 2008; Chazdon et al. 2009; Melo et al. 2013; Arroyo-Rodríguez et

1 al. 2013).

For centuries, the oak forests (mainly, *Quercus faginea*) in the western Mediterranean region have been harvested intensively for timber and firewood, and clearcut for agriculture (Sancho et al. 1998), which has reduced them to coppice stands that have different management histories; i.e., different coppicing intensities and time since coppicing ceased (Sancho et al. 1998). In the late 19th and 20th centuries, however, changes in socioeconomic structures and production systems resulted in the abandonment of the poorest arable lands and their subsequent afforestation (Sciama et al. 2009). In particular, in the Central Pyrenees, Spain, the encroachment of some abandoned farmlands by Q. faginea has led to new, secondary growth Q. faginea-dominated stands (Kouba et al. 2012). Although most of these forests (i.e., either the formerly managed or the new secondary growth forests) are deprived of any conservation status, they provide habitats for a wide diversity of plant and animal communities (Kouba and Alados 2011), which enables them to recover many components of the original biodiversity, and provide important ecosystem services such as control of climate and erosion. The management of these forests for biodiversity conservation and ecologically sustainable services is, therefore, of great interest (Kouba and Alados 2011).

In this study, we used multiplicative diversity partitioning to understand how plant species diversity changes across three spatial scales (transect, stand, and region) as well as to identify the spatial scales at which nonrandom processes have had the greatest effect. In addition, we used constrained ordination analysis to

identify the forest structural and environmental factors that might have patterned plant species diversity in human-modified and managed oak forests. We hypothesized that (H1) plant community assemblages vary non-randomly across the spatial scales, (H2)  $\beta$ -diversity components contribute more to  $\gamma$ -diversity than do  $\alpha$ -diversity components because of high habitat heterogeneity, and (H3) the structural properties, spatial attributes, and topographical conditions of the forest stands are the main factors that structure the compositional variation in plant communities in these human-modified and managed forests.

### Methods

12 Study area

The study was conducted within a 1363-km² area in the Central Pre-Pyrenees, Spain (between 42.32 N to 42.11 N, and 0.31 W to 0.04 W) (Fig. 1). The lithology is mostly conglomerate, limestone, marl, and sandstone developed on Eocene flysch sedimentary formations (Kouba and Alados 2011). The climate is transitional sub-Mediterranean; i.e., influenced by continental effects from the Pyrenees to the north and by milder Mediterranean conditions that prevail from the south (i.e., the Ebro Basin). In the study area, mean annual precipitation is  $1317 \pm 302$  mm (1915-2005) (Kouba et al. 2012) and mean annual air temperature is  $11.5 \pm 2.8^{\circ}$  C (1910-2005) (Kouba et al. 2012).

The area has a variety of land use types including natural forests of *Pinus* sylvestris, P. nigra, Fagus sylvatica, Q. ilex, and Q. faginea, shrublands of Q. coccifera and Buxus sempervirens, artificial plantations of P. sylvestris and P. nigra, arable farmland, pastures (xeric pastures and subalpine pastures), urban areas, and abandoned farmland. In the second half of the twentieth century, major changes in land use occurred in the area (Lasanta et al. 2005) because of agricultural mechanization and intensification, the introduction of pine plantations, and the abandonment of croplands and pastures, which has led to forest regrowth (Lasanta et al. 2005; Vicente-Serrano et al. 2010). In the area, Q. faginea is one of the most abundant naturally occurring species and the communities in which it occurs constitute a transition zone between Mediterranean forests in which Q. ilex ssp. ballota or P. halepensis are predominant, and mountain continental or mesic forests of P. sylvestris, P. nigra ssp. salzmannii, and F. sylvatica (Loidi and Herrera 1998; Sancho et al. 1998). The overstorey canopy of those semi-deciduous oak stands is dominated by *Q. faginea* interspersed with some scattered pines (*Pinus sylvestris* and *P. nigra*) and evergreen oak (*Q. ilex* subsp. ballota). The understory is composed of shrubs (*Q. coccifera*, *B. sempervirens*, *Genista scorpius*, *Juniperus communis*), forbs (Aphyllanthes monspeliensis, Arenaria montana, Achillea millefolium), graminoids (Brachypodium pinnatum, Carex halleriana, Festuca rubra, Carex flacca, Bromus erectus).

Stand selection and data collection

Based on the distribution maps of *Q. faginea* in the study area in 1957 and 2006 (Kouba and Alados 2011) and dendrochronological data that reflect the historical dynamics of Q. faginea stands in the study area (Kouba et al. 2012), ten Q. faginea-dominated stands that differed in their structural, spatial, and topographical characteristics were selected within the study area (see Table 1, Fig. 1). Primarily, the stands were surrounded by farmland, pine plantations, abandoned land, and grassland (see Fig. 1). In 2009 and 2010, during the period of peak growth (May and June), the vascular plant species were surveyed in the ten stands. Within each stand, three 500-m linear transects (30 transects in total) were established (hereafter, floristic transects). To estimate plant abundance and richness within each transect, we used the Point-Intercept Method (Goodall 1952), which involves recording, at 40-cm intervals, the identity of all individuals that are in contact with a vertical nail (Alados et al. 2009). We recorded all of the vascular plants that touched the nail and any overstorey species (including *Q. faginea*) that were above the nail. The abundance of each species in each transect was estimated as the number of its individuals recorded along the transect. Plant species that could not be identified with certainty in the field were collected, pressed, and brought to the laboratory for identification by botanical experts. Species that have traits that make them difficult to distinguish were only identified to the genera level. Plant nomenclature followed "Flora Ibérica" (Castroviejo et al. 1986-2012). Plant growth forms represent broad patterns of variation among correlated plant traits that are more related to ecosystem functions, e.g. nutrient use efficiency,

protection against abiotic and biotic hazards, and competitive strength (Lavorel et al. 1997; Dorrepaal 2007), and, therefore, are expected to differ in their responses to forest structural and environmental factors. Accordingly, plant species were grouped based on growth forms: woody (tree and shrubs), graminoids, or forbs. In this study, the relative abundance of Q. faginea (QFAB) in each floristic transect was included in the analyses as surrogate for the amount of canopy cover (%). To quantify the structural properties of each stand (Table 1) a 500-m linear transect (hereafter, forest structure transect) was established within each stand (n =10) and the forest was sampled using the Point-quarter Method (Cottam and Curtis 1956). Each forest structure transect was placed close to the central floristic transect within each stand. Sampling points (n = 20) were at 25-m intervals along each of the transects. At each sampling point, we identified the closest adult Q. faginea tree in each of the four cardinal directions within a maximum distance of 5 m from the sampling point (Kouba et al. 2012). Adult trees were defined as those > 2 m high or that had a stem diameter at breast height (DBH)  $\geq$  4 cm. The following measurements were recorded: diameter at breast height (DBH) (cm), tree height (m), and age (for details about age estimation, see Kouba et al. 2012). Those data were used to estimate the following variables for each stand: density (DENSITY), mean diameter at breast height (DBH), mean tree height (TREHEIGHT), mean age (AGE), and coefficient of variation of tree age (CVAGE). Furthermore, forest type (FORTYPE; secondary growth stands vs. abandoned coppice stands) was recorded for each stand based on visual observation on the field (see Table 1).

To quantify the spatial attributes of each stand (Table 1), we measured stand size

- 1 (STSIZE) and shape complexity (SHPCOMP) using a digitized *Q. faginea* distribution
- 2 map, the 'Patch Analyst' extension in ArcGIS 10.1 (ESRI 2013), the Third National
- 3 Forest Inventory map (IFN3; MAGMARA, 2013), and orthorectified aerial
- 4 photographs taken in 2006 (CINTA 2013). In addition, the mean elevation
- 5 (ELEVAT), mean slope (SLOP), and orientation (ORIENT) of each stand were derived
- 6 from a Digital Elevation Model (CINTA 2013).

Partitioning of biodiversity

 To assess plant diversity patterns across multiple spatial scales, we used multiplicative partitioning because of the advantages of the Hill Number ( ${}^qD$ ) and q-metric (see below):  ${}^qD_{\gamma} = {}^qD_{\beta} \times {}^qD_{\alpha}$  (Whittaker 1972; Jost 2006, 2007, 2010). Diversity is quantified using the Hill Number ( ${}^qD$ ), which has the property to be invariant to changes in absolute numbers; if all species double in abundance,  ${}^qD$  remains unchanged. It measures variation in relative, rather than absolute abundance, and it follows the replication principle: Combining two sets of non-overlapping species that have the same abundance distributions doubles the value of  ${}^qD$  (Jost 2006; Scheiner 2012). To quantify diversity patterns based on various weightings for rare and abundant species, we used the q-metric, which reflects the sensitivity of the diversity index to the relative frequencies of species. The analyses included two q-values: (1) q = 0 reflects species richness, which is not sensitive to species abundance and, therefore, assigns disproportionate weight to rare species (Jost 2006), and (2) q = 0.999 (and not q = 1, which would require division by zero)

is equivalent to the exponential of Shannon entropy; here, species are weighted in proportion to their frequency in the sampled community and, therefore, it can be

3 interpreted as the number of 'typical species' in the community (Chao et al. 2012).

We used a nested hierarchical design of three increasingly coarser spatial scales: individual assemblages at the transect level, pooled assemblages within a stand, and a single, pooled assemblage across the entire region (Fig. 2). The design allowed  ${}^qD_{\gamma}$  diversity to be decomposed into within transect ( ${}^qD_{\alpha\_transects}$ ), among transects ( ${}^qD_{\beta\_transects}$ ), within stand ( ${}^qD_{\alpha\_stands}$ ), and among stands ( ${}^qD_{\beta\_stands}$ ) components (Fig. 2). To test for significant differences in the spatial partitioning of diversity, the expected values of the measures of diversity were calculated using individual-based randomizations ( $10^4$  permutations; Crist et al. 2003), which evaluated whether the  $\alpha$  and  $\beta$  components of diversity differed significantly from a random distribution of individuals among samples (Crist et al. 2003). Those analyses were performed using the 'vegan' package (Oksanen et al. 2013) implemented in the R software (R

To test whether differences in species richness might have biased the observed spatial diversity pattern, we additively partitioned  $\beta$ -diversity into the two components of spatial turnover and nestedness using the method suggested by Baselga (2010). We performed this analysis using the 'betapart' package (function 'beta.sample') (Baselga and Orme 2012) within the R software (R Development Core Team 2013).

Development Core Team 2013).

Partitioning the variation in plant communities in response to forest structural and

### environmental factors

To identify the variables that explained a significant amount of the variation in species composition, we used Canonical Redundancy Analyses (RDA). The matrices of species abundance were Hellinger transformed prior to analysis (Legendre and Gallagher 2001). After this transformation, RDA is based on the Hellinger distance, which is appropriate for community composition data, instead of being based on the inappropriate Euclidean distance (Legendre and Gallagher 2001). The explanatory variables included in the finale RDA models were selected based on forward stepwise procedure, which provided an estimate of the best set of non-redundant variables for predicting species composition and a ranking of the relative importance of the individual explanatory variables. The spatial autocorrelation of the residuals of the RDA models was tested using a multi-scale ordination (MSO; Borcard et al. 2011; Legendre and Legendre 2012). Initial analyses indicated significant spatial autocorrelation in the residuals of the RDA models and a scale-dependent relationship between the species data and the explanatory variables. To address those problems, the following three steps were followed: (i) the Hellinger-transformed species data matrices and the explanatory variables were detrended along the Y Cartesian geographic coordinates (i.e., the coordinates of transect-central points), which supported the assumption of stationarity in the computation of confidence intervals in the MSO variograms (Legendre and Legendre 2012). (ii) The sampling design was spatially nested; therefore, the function 'create.MEM.model' (Borcard et al. 2011; Declerck et al. 2011) was used to construct a staggered spatial matrix of Moran's eigenvector maps

(MEM), and (iii) partial canonical redundancy analyses (partial RDAs) were

performed using the detrended data and included the computed MEMs as

covariables, which controlled for the effects of spatial structure (i.e., excluded the

compositional variation caused by spatial structure; Borcard et al. 2011; Legendre

### Results

and Legendre 2012).

In the survey of the 10 oak stands in the Central Pre-Pyrenees, Spain, we identified 238 vascular plant species. On average, the floristic transects contained 64 species (range = 43-98). Twenty-one (9%) of the species contributed 80% of the total plant coverage by abundance, and *B. sempervirens* was the most abundant species in all of the stands (Fig. 3). Most of the species were forbs (159 species), followed by woody plants (54 species) and graminoids (25 species). Among rare species (i.e., species that had a relative abundance <0.01% and occurred in <5% of the transects; see Appendix 1), 75 % were forbs, 7 % were graminoids, and 18 % were woody species.

### Patterns of diversity across spatial scales

In general,  $\beta$ -diversity components ( ${}^qD_{\beta\_transects}$  and  ${}^qD_{\beta\_stands}$ ) made up a large proportion of overall diversity (Fig. 4). At all spatial scales, and independently of the value of q,  $\beta$ -diversity was significantly higher, and alpha diversity was significantly

- 1 lower than expected based on a random distribution of individuals (Table 2). β-
- 2 diversity and the deviations from random distributions were higher among stands
- 3 than among transects for the two values of q (0 and 1). The two components of  $\beta$ -
- 4 diversity ( ${}^{q}D_{\beta\_transects}$  and  ${}^{q}D_{\beta\_stands}$ ) declined with increasing values of q (Table 2),
- 5 which reflected the lower emphasis given to rare species as *q* increases.
- β The partitioning of β-diversity into two components, spatial turnover and
- nestedness, revealed that overall spatial turnover accounted for > 96% of total β-
- 8 diversity, which suggests that bias caused by differences in species richness among
- 9 transects was negligible.
- 11 Partitioning the variation in plant communities in response to forest structural and
- 12 environmental factors
- 14 The explanatory variables selected by the RDA explained a significant amount of the
- variation in the composition of forbs and woody species (Table 3), but not the
- 16 composition of graminoids. Collectively, AGE (10.6%), QFAB (8.9), CVAGE (13.3),
- and SLOP (11.4) explained 44.2% of the variation in the composition of forbs
- 18 species (Table 3). Most of the forbs were common in young and uneven-aged stands,
- 19 although there were some exceptions, such as Aphyllanthes monspeliensis
- 20 (APHMON) and Bupleurum rigidum (BUGRA), which were related to lower Q. faginea
- abundance and higher stand age, respectively, and the perennial species *Hepatica*
- *nobilis* (HEPAT) and *Q. faginea* abundance were correlated (Fig. 5).
- 23 For woody species, STSIZE (11.7%), QFAB (11.4), AGE (11.5), and CVAGE (9.2)

explained 43.8% of the variation in species composition (Table 3). The long-lived shrub *B. sempervirens* (BUXSEM) was positively correlated with *Q. faginea* abundance, Genista scorpius (GENSCO), Thymus vulgaris (THYVUL), and Echinospartum horridum (ECHIOR) were prevalent in uneven-aged stands, and others, i.e., Juniperus oxycedrus (JUNOXY) and P. sylvestris (PINSIL), were related to lower Q. faginea abundance. Cytisophyllum sessilifolium (CYTSES), Amelanchier ovalis (AMEOVA), and Arctostaphylos uva-ursi (ARCUVA) predominated in old stands (Fig. 5).

## Discussion

Our study is one of the first to assess plant spatial diversity patterns and identify the factors that drive the structuring of plant species composition in human-modified and managed forests. The high contribution of  $\beta$ -diversity to total  $\gamma$ -diversity with  $\beta$ -diversity being significantly higher than expected by chance at all spatial scales, independent of the value of q, suggests that changes in species composition, rather than variation in species abundances, are primarily responsible for the spatial diversity patterns, which has been observed elsewhere (Devictor et al. 2010; Gossner et al. 2013). In addition, the fact that  $\beta$ -diversity was largely due to spatial turnover rather than nestedness, indicates that assemblages in species-poor transects are not a subset of assemblages of species-rich transects.

weighted equally (q = 0), which corresponds to a stronger influence of rare species

In our study, among stands β-diversity was highest when all species were

(i.e., species with small populations). Thus, rare species appeared to have a heterogeneous distribution in the human-modified and managed oak forests; probably, because their habitats had a clumped distribution (Chávez and Macdonald 2012; Gossner et al. 2013, Arroyo-Rodríguez et al. 2013). It should be noted that although the rare species were not really rare (with a conservation status); some of them were forest specialists (with great conservation value). High structural and environmental heterogeneities caused by differences in stand history and successional stage might have led to the high level of compositional differentiation among stands observed in our study. Indeed, the constrained ordination showed that the structural, spatial, and topographical characteristics of the forest stands explained a high proportion of the compositional variation. Stand age, the age structure distribution, *Q. faginea* abundance, stand size, and site conditions (i.e., slope) explained most of the spatial variation in composition, particularly, of forbs and woody species. Other studies have shown that forest structure (e.g., stand age, canopy cover), forest spatial attributes (e.g., patch size), and topographical conditions can have important roles in structuring the composition of plant communities in many types of forests worldwide (e.g., Aavik et al. 2009; Vockenhuber et al. 2011; Lomba et al. 2011), mainly, by controlling the availability of resources, particularly light and soil nutrients, and habitat conditions, particularly substrate, temperature, and pH (Härdtle et al. 2003; Aubert et al. 2004; Hart and Chen 2006). 

At the finest spatial scale, among transects, the compositional differentiation was higher than expected, based on either rare or typical species, which reflects a degree

of microhabitat heterogeneity within the same stand (Chávez and Macdonald 2012).

2 The within-stand dissimilarity in canopy cover (i.e. differences in Q. faginea

3 abundance among the transects) might be responsible for the microhabitat

heterogeneity; i.e., heterogeneity can result from the creation of gaps in the canopy,

which might increase the resources available at forest floor and, therefore, provide

conditions for the development of species with different niches (Hart and Chen

2006; Fahey and Puettmann 2007; Chávez and Macdonald 2012), which can lead to

relatively high rates of species turnover within the same stand (Sabatini et al. 2014).

Implications for management and conservation

Our results clearly demonstrate the importance of  $\beta$ -diversity components; i.e.,

among-transects and among-stands  $\beta\text{-diversity,}$  for overall diversity, which

underscores the need to consider  $\beta$ -diversity at all spatial levels including smaller

spatial scales when making management plans designed to enhance plant diversity

and related functions in human-altered forests. In addition, the high spatial turnover

in relation to nestedness suggests that conservation efforts should be concentrated

on a large number of not necessarily the richest sites and this is also supported by

other studies (e.g. Gossner et al. 2013).

Furthermore, this study has highlighted the importance of stand characteristics

in structuring β-diversity. Keeping a mixture of stands of different structural

properties, spatial attributes, and topographical conditions could, therefore, help to

enhance plant diversity in these oak forests, and in turn supporting conservation of

associated faunal communities. Finally, our study points to the importance of maintaining micro-environmental heterogeneity within oak stands (e.g. by creating canopy gaps), to conserve and restore understory plant species richness and diversity.

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**Table 1** Characteristics of ten oak stands within a 1363-km<sup>2</sup> area in the Central Pre-Pyrenees, Spain. Values are mean elevation, ORIENT = orientation (S = South, SE = South East, SW = South West, E = East), SLOP = slope, STSIZE = st complexity, DENSITY = density, QFAB = *Q. faginea* abundance, DBH = diameter at breast height, TREHEIGHT = tree height CVAGE = Coefficient of Variation of age of stand, FORTYPE = Forest type (SF = secondary forest, CS = abandoned coppice states)

Stand characteristics/stand							
locations	Rasal (RA)	Belsué (BE)	Abena (AB)	Ara (AR)	Lucera (LU)	Ibort (IB)	Ipies (IP)
Topography							
ELEVAT (m a.s.l.)	868.3 ± 4.8	1158.5 ± 1.20	970.3 ± 1.50	971.1 ± 2.00	1198.0 ± 7.70	950.8 ± 2.60	852.5 ±2.30
ORIENT	S	S	S	SE	SE	S	Е
SLOP (º)	$9.3 \pm 0.50$	30.5 ± 0.40	11.7 ± 0.50	19.6 ± 0.50	16.8 ± 1.20	14.8 ± 1.10	$7.8 \pm 0.60$
Spatial attributes							
STSIZE (ha)a	114	94	73	244	1115	40	146
SHPCOMP (perimeter/area) <sup>a</sup>	126.41	119.60	77.49	164.23	244.28	103.17	268.11
Forest structure							
DENSITY (stems ha-1)	$607 \pm 0.20$	$1100 \pm 0.10$	999 ± 0.10	$503 \pm 0.30$	867 ± 0.10	1088 ± 0.10	812 ± 0.10
QFAB (Tree/Transect)	239±43	362±15	339±18	133±32	173±14	426±7	193±8
DBH (cm)	14.00 ± 1.40	$9.0 \pm 0.70$	13.3 ± 1.30	7.2 ± 0.50	12.0 ± 0.80	13.3 ± 0.80	11.4 ± 0.70
TREHEIGHT (m)	5.10 ± 0.40	4.8 ± 0.30	5.1 ± 0.30	$3.4 \pm 0.20$	5.5 ± 0.30	6.1 ± 0.20	4.3 ± 0.30
AGE (years)	31 ± 3	40 ± 4	50 ± 2	35 ± 1	39 ± 1	63 ± 2	64 ± 2
CVAGE (%)d	31	43	19	17	12	17	15
FORTYPE	SF	CS	SF	CS	CS	CS	CS

<sup>&</sup>lt;sup>a</sup> Calculated based on the distribution map of *Q. faginea* forests in the study area (for more details, see Kouba et al. 2011)

**Table 2** Hierarchical multiplicative partitioning of the alpha  $({}^qD_\alpha)$  and beta  $({}^qD_\beta)$  components of overall diversity  $({}^qD_\gamma)$  in ten *Q. faginea* forest stands in the Central Pre-Pyrenees, Spain. Diversity was quantified using the Hill Index  $({}^qD)$ , with q=0 (all species are given equal weight) or q=1 (greater weight is given to common species). Deviations from null distributions (numbers within brackets) are expressed by dividing the observed values by the expected values. The p-values were obtained by comparing the observed values with the values generated by  $10^4$  randomizations

	q = 0			q = 1			
	Observed	Expected	p-value	Observed	Expected	p-value	
$^qD_{\alpha\_{transects}}$	62.88 (0.52)	120.09	< 0.01	17.31 (0.57)	30.27	<0.01	
$^qD_{lpha\_{ m stands}}$	93.70 (0.58)	159.73	< 0.01	20.58 (0.65)	31.49	< 0.01	
$^qD_{eta_{ ext{transects}}}$	1.49 (1.12)	1.33	< 0.01	1.18 (1.13)	1.04	< 0.01	
$^qD_{eta\_stands}$	2.54 (1.82)	1.39	< 0.01	1.56 (1.52)	1.02	< 0.01	
$^qD_{\gamma\_ ext{study area}}$	238	238	-	32.12	32.12	-	

**Table 3** Redundancy analysis of the forest structural and environmental factors that explained a significant amount of the variation in species composition of forbs and woody species (significant relationships are shown). " $R^2_{adj}Cum$ " is the cumulative adjusted  $R^2$  of the model; the values within brackets indicate the variance (%) explained by each explanatory variable, " $R^2_{adj}$ " is the total explained variance (%) in each model. AGE = Mean stand age, CVAGE = Coefficient of variation of tree age, STSIZE = Stand size, SLOP = slope, QFAB = Q. faginea abundance

Species group	Variables	$R^2_{adj}Cum$	F	p-value
Forbs ( $R^{2}_{adj} = 44.2$ )	AGE	0.10 (10.6)	2.65	0.01
	QFAB	0.19 (08.9)	2.41	0.02
	CVAGE	0.33 (13.3)	3.28	0.00
	SLOP	0.44 (11.4)	3.11	0.01
Woody ( $R^2_{adj} = 43.8$ )	STSIZE	0.12 (11.7)	2.65	0.01
	QFAB	0.23 (11.4)	2.67	0.01
	AGE	0.34 (11.5)	2.77	0.01
	CVAGE	0.44 (9.2)	2.46	0.02

### Figure legends

**Fig. 1** Location of the study area within Europe (upper right panel), and the locations of the ten *Q. faginea* forest stands sampled in the Central Pre-Pyrenees, Spain (left panel). The location of the three floristic transects (FT) and the forest structural transect (ST) within each stand (lower right panel). AB = Abena, AG = Arguis, AR = Ara, BE = Belsué, IB = Ibort, IP = Ipies, LU = Lucera, NO = Nocito, RA = Rasal, RP = Rapun

**Fig. 2** Hierarchical levels in the multiplicative partitioning of plant species diversity in ten oak forest stands in the Central Pre-Pyrenees, Spain

**Fig. 3** The abundances of common species (expressed as median values) in ten Q. faginea forest stands (n = 30 transects) in the Central Pre-Pyrenees, Spain. Boxes indicate the 25th and 75th percentiles, and whiskers indicate the 5th and 95th percentiles

**Fig. 4** The contributions of the alpha and beta components of diversity to total gamma diversity for two values of q (0 and 1) assessed using multiplicative diversity partitioning of plant species within ten oak forest stands in the Central Pre-Pyrenees, Spain. Apha-transect = within-transect diversity ( ${}^{q}D_{\alpha\_transects}$ ), Beta-transect = among-transects β-diversity ( ${}^{q}D_{\beta\_transects}$ ), and Beta-stand = among-stands β-diversity ( ${}^{q}D_{\beta\_stands}$ )

**Fig. 5** Ordination plots of the significant forest structural and environmental factors and the composition of forbs and woody species within ten oak forest stands in the Central Pre-Pyrenees, Spain. Arrows indicate the direction of increasing values of significant forest structural and environmental variables. AGE = mean stand tree age, CVAGE = coefficient of variation of stand age, STSIZE = stand size, SLOP = slope, QFAB = Q. faginea abundance. The letter codes indicate the locations of plant species that had a correlation of  $\geq 0.25$  to the ordination axes. Species presented are: Forbs (APHMON: Aphyllanthes monspeliensis, GLOBNU: Globularia nudicaulis, THALIC:

Thalictrum alpinum, LINOSUB: Linum suffruticosum, TEUPY: Teucrium pyrenaicum, BUGRA: Bupleurum rigidum, CORIS: Coris monspeliensis, POTE: Polygala monspeliaca, GLOBVU: Globularia vulgaris, EPIPAC: Epipactis sp., MEDICA: Medicago minima, HIERACI: Hieracium pilosella, TRIPRA: Trifolium pretense, HEPAT: Hepatica nobilis, THALTUB: Thalictrum tuberosum, SANCHA: Santolina chamaecyparissus, HEDERA: Hedera helix, AQUIMIL: Achillea millefolium, SEDUAL: Sedum album, COREME: Coronilla emerus, TEUCHA: Teucrium chamaedrys, MEDILUP: Medicago lupulina, LATHCIC: Lathyrus cicero, GALUCI: Galium lucidum, VICSAT: Vicia sativa, ERYNCAM: Eryngium campestre, THAPSIA: Thapsia villosa); Woody (THYVUL: Thymus vulgaris, GENSCO: Genista scorpius, JUNOXY: Juniperus oxycedrus, PINSIL: Pinus sylvestris, HELIMA: Helianthemum marifolium, ARGYZA: Argyrolobium zanonii, FUMAPRO: Fumana procumbens, ECHIOR: Echinospartum horridum, FUMERI: Fumana ericifolia, STADUB: Staehelina dubia, QUEILE: Quercus ilex, ONOFRU: Ononis fruticosa, GENHIS. Genista hispanica, DORPEN: Dorycnium pentaphyllum, THYMELEA: Thymelaea pubescens, VIBLAN: Viburnum lantana, ACEMON: Acer monpessulanum, JUNCOM: Juniperus communis, LONXYL: Lonicera xylosteum, ARCUVA: Arctostaphylos uva-ursi, LONETRU: Lonicera etrusca, AMEOVA: Amelanchier ovalis, CYTSES: Cytisophyllum sessilifolium, BUXSEM. Buxus sempervirens).

Fig. 1

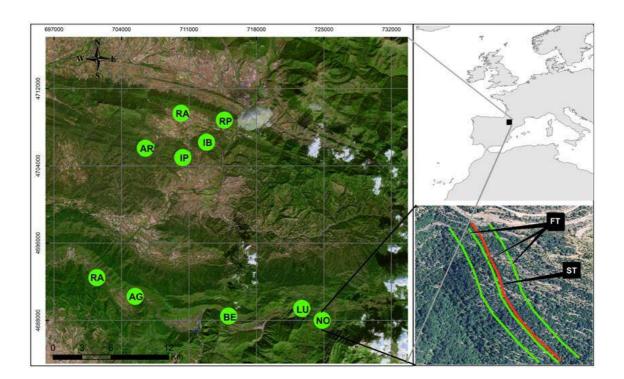


Fig. 2

# **Landscape level:** Total area = $1363 \text{ km}^2$

 $^qD_{\gamma_{-\text{study area}}}$ :
Within-study area diversity
Average within-study area
diversity

### Stand level:

10 stands (40 - 294 ha) Distances between stands ranged from 3 to 25 km  $^{y}D_{\alpha_{\_stands}}$ :
Within-stand diversity
Average within-stand
diversity

X

×

 $D_{eta\_stands}$ :
Among-stands diversity
Average variability among-stands
diversity

### Transect level:

30 500-m transects (n = 3 per stand)
Distances between transects ranged
from 0.05 to 25 km

 $^qD_{a\_{
m transects}}$ :
Within-transect diversity
Average within-transect
diversity

 $^qD_{eta_{ ext{transects}}}$ :

Among-transects diversity

Average variability among-transects
diversity

Fig. 3

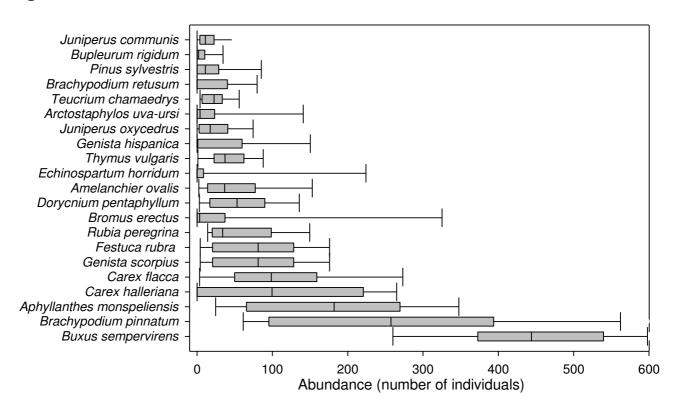


Fig. 4

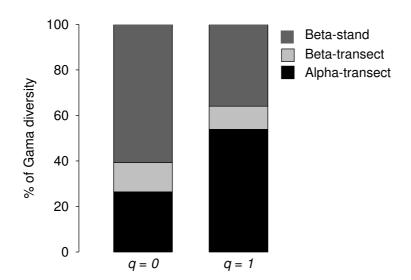
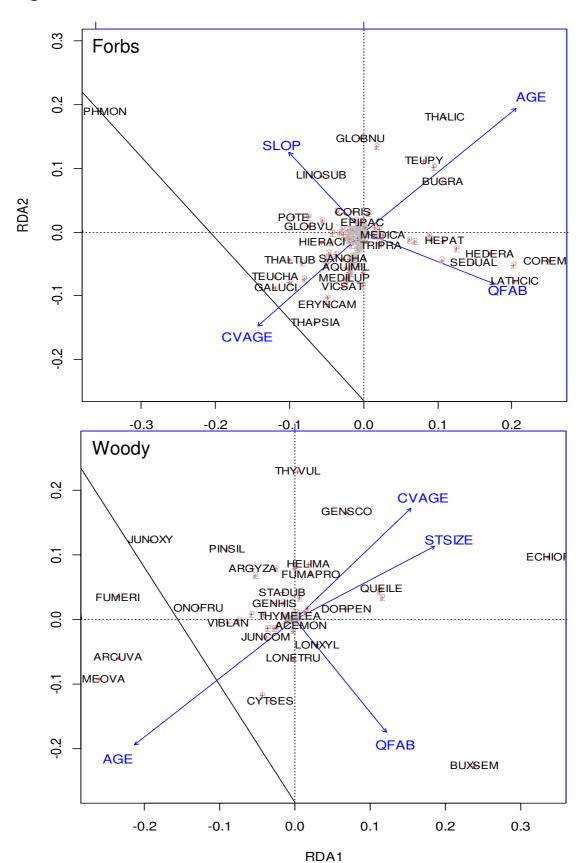


Fig. 5



**Appendix 1:** The codes, scientific names, growth forms, abundance, and frequency (i.e., number of transects in which the species occurred) of the documented plant species in ten *Q. faginea* forest stands in the Central Pre-Pyrenees, Spain. Species are listed based on their abundance (lowest to highest)

Code	Species scientific name	Growth form		Frequency (nº of
			Abundance (%)	transects)
ANVUL	Anthyllis vulneraria	Forb	0.001	1
ARATUR ASPERULA	Arabis turrita Asperula aristata	Forb Forb	0.001 0.001	1 1
BROTEC	Asperuia aristata Bromus tectorum	Graminoid	0.001	1
CEPHARUB	Cephalanthera rubra	Forb	0.001	1
CLEVIT	Clematis vitalba	Woody	0.001	1
CROCNEV	Crocus nevadensis	Forb	0.001	1
DIANTPUN	Dianthus pungens	Forb	0.001	1
ECHIUM	Echium vulgare	Forb	0.001	1
ERYSIRUS	Erysimum ruscinonense	Forb	0.001	1
HELHAPE	Helianthemum apenninum	Forb	0.001	1
HIPCOM	Hippocrepis comosa	Woody	0.001	1
HYACINHIS LATHSPHA	Hyacinthoides hispanica	Forb Forb	0.001 0.001	1 1
LATHYSAX	Lathyrus sphaericus Lathyrus saxatilis	Forb	0.001	1
NARCISS	Narcissus sp.	Forb	0.001	1
OPHRYS	Ophrys sp.	Forb	0.001	1
ORCHUS	Orchis ustulata	Forb	0.001	1
PLAMED	Plantago media	Forb	0.001	1
PRUNVU	Prunella vulgaris	Forb	0.001	1
RESEDA	Reseda lutea	Forb	0.001	1
SALVER	Salvia verbenaca	Forb	0.001	1
TAMUCOM	Tamus communis	Forb	0.001	1
VALERI VULUNI	Valerianella sp.	Forb Graminoid	0.001 0.001	1 1
ALLIUM1	Vulpia unilateralis Allium sp.	Forb	0.001	1
AVENBRO	Avenula bromoides	Graminoid	0.003	1
CENTNIG	Centaurea nigra	Forb	0.003	1
LINUCAM	Linum campanulatum	Forb	0.003	1
PRUMA	Prunus mahaleb	Woody	0.003	1
SORARI	Sorbus aria	Woody	0.003	1
ARENAR	Arenaria leptoclados	Forb	0.003	2
CAMPANULA	Campanula sp.	Forb	0.003	2
CONOPOD	Conopodium sp.	Forb	0.003	2
HELLFOE LONPERI	Helleborus foetidus	Forb	0.003	2 2
PLATBIF	Lonicera periclymenum Platanthera bifolia	Woody Forb	0.003 0.003	2
GENIS	Genista cinerea	Woody	0.003	1
GEUSYLV	Geum sylvaticum	Forb	0.004	1
LATHAPH	Lathyrus aphaca	Forb	0.004	1
MEREMON	Merendera montana	Forb	0.004	1
VERBA	Verbascum lychnitis	Forb	0.004	1
BISCUTE	Biscutella valentina	Forb	0.004	2
LINVIS	Linum viscosum	Forb	0.004	2
VERORSI	Veronica orsiniana	Forb	0.004	2
THYMPUB	Thymelaea pubescens Cephalaria leucantha	Woody Forb	0.004 0.006	3 1
CEPHALEU CRUCAN	Crucianella angustifolia	Forb	0.006	1
PRUNHYS	Prunella hyssopifolia	Forb	0.006	1
ALYSALY	Alyssum alyssoides	Forb	0.006	2
BRASYL	Brachypodium sylvaticum	Graminoid	0.006	2
GERAROB	Geranium robertianum	Forb	0.006	2
ORCHY	Orchis sp.	Forb	0.006	3
TARAXA	Taraxacum sp.	Forb	0.006	3
BERVU	Berberis vulgaris	Woody	0.007	2
SORBUS	Sorbus sp.	Woody	0.007	2
ORIVUL	Origanum vulgare	Forb	0.007	3
ARRHENATALB	Arrhenatherum album	Graminoid Forb	0.009	2 2
DIGIPUR PRUNELLA	Digitalis purpurea Prunella sp.	Forb	0.009 0.009	2
SIBERHIR	Sideritis hirsuta	Woody	0.009	2
TRIPRA	Trifolium pratense	Forb	0.009	2
	) F			

	MELICI	Melica ciliata	Graminoid	0.009	3
1	CENTALB	Centaurea alba	Forb	0.010	2
1	HELVIO	Helianthemum violaceum	Forb	0.010	2
2	CIRSITUB	Cirsium tuberosum	Forb	0.010	3
3	BLAKPER	Blakstonia perfoliata	Forb	0.010	6
4	DIANT	Dianthus benearnensis	Forb	0.010	6
5	POLYMONS	Polygala monspeliaca	Forb	0.012	2
	ARENASER	Arenaria serpyllifolia	Forb	0.012	4
6	LEUCA	Leucanthemum pallens	Forb	0.012	4
7	LEUCANTEMUN	Leucanthemun sp.	Forb	0.012	4
8	EUCHA	Euphorbia characias	Forb	0.012	5
9	CREPVIS	Crepis vesicaria	Forb	0.013	2
	PINNIG	Pinus nigra	Woody	0.013	2
10	SORAUC	Sorbus aucuparia	Woody	0.013	3
11	SILEVU	Silene vulgaris	Forb	0.013	4
12	ARABIS	Arabis sp.	Forb	0.013	5
13	RANUREP	Ranunculus repens	Forb	0.015	2
14	CHEIRINT	Cheirolophus intybaceus	Woody	0.015	4
	PAROKAP	Paronychia kapela	Forb	0.015	4
15	HELISTO	Helichrysum stoechas	Woody	0.015	5
16	PRUNLAC	Prunella laciniata	Forb	0.015	5
17	FI	Festuca indigesta	Graminoid	0.016	2
18	INUMON	Inula montana	Forb	0.016	3
	EPIPAC	Epipactis sp.	Forb	0.016	7
19	GERADIS	Geranium dissectum	Forb	0.018	3
20	ONOSP	Ononis spinosa	Forb	0.018	3
21	SCABAT	Scabiosa atropurpurea	Forb	0.018	4
22	CLINOVU	Clinopodium vulgare	Forb	0.018	5
23	BRIZA	Briza media	Graminoid	0.018	6
	HIEMURO	Hieracium murorum	Forb	0.018	6
24	PHLEPRA	Phleum pratense	Forb	0.019	2
25	THYFONT	Thymus fontqueri	Forb	0.019	2
26	CEPHALARIS	Cephalaria sp.	Forb	0.019	4
27	TRAPOG	Tragopogon sp.	Forb	0.019	4
	VICSEPI	Vicia sepium	Forb	0.019	7
28	BRADIS	Brachypodium distachyon	Graminoid	0.021	3
29	CORSCO	Coronilla scorpioides	Forb	0.021	3
30	TRINIGLA	Trinia glauca	Forb	0.021	6
31	ACEMON	Acer monpessulanum	Woody	0.021	3
32	HYPEPER	Hypericum perforatum	Forb	0.022	4
	TRIFOL	Trifolium sp.	Forb	0.022	5
33	ONONIS	Ononis sp.	Forb	0.022	5
34	HELINUM	Helianthemum nummularium	Woody	0.024	7
35	SCABIOSA	Scabiosa columbaria	Forb	0.024	7
36	TEUCAP	Teucrium capitatum	Forb	0.024	11
	AGROCA	Agrostis capillaris	Graminoid	0.024	1
37	LATHYLIN	Lathyrus linifolius	Forb		2
38	LONETRU	Lonicera etrusca	Woody	0.025 0.025	2
39	VICILATH		Forb	0.025	2
40		Vicia lathyroides			
	VICCRA	Vicia cracca Medicago sativa	Forb	0.027	3
41	MEDI	0	Forb	0.027	4
42	STIPERIO	Stipa eriocaulis	Graminoid	0.027	4
43	AREMON	Arenaria montana	Forb	0.027	6
44	QUECO	Quercus coccifera Cephalanthera alba	Woody	0.028 0.028	4 5
45	CEPHALB		Forb		
	ERYGIU	Eryngium bourgatii	Forb	0.028	6
46	PRIMULA	Primula sp.	Forb	0.028	6
47	ASTRAMON	Astragalus monspessulanus	Forb	0.028	7
48	ACHMIL	Achillea millefolium	Forb	0.030	1
49	PLANTAG	Plantago sp.	Forb	0.030	2
	XERINA	Xeranthemum inapertum	Forb	0.030	3
50	CORSAN	Cornus sanguinea	Woody	0.031	4
51	STACHREC	Stachys recta	Forb	0.031	4
52	RANUNC	Ranunculus sp.	Forb	0.031	5
53	SANCHA	Santolina chamaecyparissus	Forb	0.031	7
54	ASPCY	Asperula cynanchica	Forb	0.031	8
	ASTRA	Astragalus sp.	Forb	0.033	5
55	PLANLAN	Plantago lanceolata	Forb	0.034	3
56	GALVER	Galium verum	Forb	0.036	4
57	HELHIR	Helianthemum hirtum	Woody	0.036	5
58	LOTUSCOR	Lotus corniculatus	Forb	0.036	6
	CONVCANT	Convolvulus cantabrica	Forb	0.039	6
59	ARISTOPIS	Aristolochia pistolochia	Forb	0.039	13
60	COLUTARB	Colutea arborescens	Woody	0.040	3
61			-		
62					

	LINUNAR	Linum narbonense	Forb	0.043	10
1	POLYCAL	Polygala calcarea Viburnum lantana	Forb	0.045	6 6
2	VIBLAN CRUCIATA	Cruciata glabra	Woody Forb	0.046 0.048	4
3	LONXYL	Lonicera xylosteum	Woody	0.048	8
4	MEDILUP	Medicago lupulina	Forb	0.049	3
5	LATHYFIL	Lathyrus filiformis	Forb	0.051	7
6	CATACA	Catananche caerulea	Forb	0.052	7
7	THYMPRA	Thymus praecox	Forb	0.054	7
	LEUZEA RHAALA	Leuzea conifera Rhamnus alaternus	Forb Woody	0.054	12 3
8	LAVANG	Lavandula angustifolia	Woody	0.057 0.057	6
9	SCA	Scabiosa sp.	Forb	0.057	11
10	VICSAT	Vicia sativa	Forb	0.061	3
11	LAVAND	Lavandula latifolia	Woody	0.064	11
12	TANACOR	Tanacetum corymbosum	Forb	0.067	18
13	SEDUAL	Sedum album	Forb	0.070	5
14	SAPOCY SCORZO	Saponaria ocymoides Scorzonera aristata	Forb Forb	0.075 0.078	11 10
15	LITFRU	Lithodora fruticosa	Woody	0.076	8
16	ANTHELI	Anthericum liliago	Forb	0.087	6
17	KNAUTIA	Knautia arvensis	Forb	0.091	9
18	RHASAX	Rhamnus saxatilis	Woody	0.093	10
19	SANGUIMI	Sanguisorba minor	Forb	0.094	16
20	JUNPHO	Juniperus phoenicea	Woody	0.105	5
21	POTENEU SEDUSE	Potentilla neumanniana Sedum sediforme	Forb Forb	0.108 0.108	7 18
22	THESDIV	Thesium divaricatum	Forb	0.111	17
23	CORIS	Coris monspeliensis	Forb	0.115	16
24	POA	Poa angustifolia	Graminoid	0.118	12
	VIO	Viola sp.	Forb	0.120	7
25	HEDERA	Hedera helix	Forb	0.124	3
26	ERYNCAM	Eryngium campestre	Forb	0.127	7
27	STADUB	Staehelina dubia	Woody Forb	0.127	18 15
28	POLYGAL ARRHENAT	Polygala alpestris Arrhenatherum elatius	Graminoid	0.132 0.139	11
29	GLOBVU	Globularia vulgaris	Forb	0.141	10
30	LATHCIC	Lathyrus cicera	Forb	0.145	7
31	MEDICA	Medicago minima	Forb	0.145	10
32	THAPSIA	Thapsia villosa	Forb	0.156	8
33	GALIUM	Galium sp.	Forb	0.162	12
34	CERASPUM VICINCA	Cerastium pumilum Vicia incana	Forb Forb	0.165 0.166	2 8
35	ONONAT	Ononis natrix	Forb	0.178	o 11
36	LINOSUB	Linum suffruticosum	Forb	0.184	21
37	CYTSES	Cytisophyllum sessilifolium	Woody	0.185	10
38	HEPAT	Hepatica nobilis	Forb	0.191	11
39	EUPHSE	Euphorbia serrata	Forb	0.200	18
40	COREME	Coronilla emerus	Forb	0.206	10
41	BUPLE FUMAPRO	Bupleurum ranunculoides Fumana procumbens	Forb Woody	0.217 0.230	5 9
42	VIOLA	Viola alba	Forb	0.232	26
43	LIGVUL	Ligustrum vulgare	Woody	0.236	13
	FGL	Festuca glauca	Graminoid	0.262	3
44	DACT	Dactylis glomerata	Graminoid	0.271	13
45	HIERACI	Hieracium pilosella	Forb	0.271	25
46	ONOBRY POTE	Onobrychis viciifolia Potentilla sp.	Forb	0.278	17 23
47	THALTUB	Thalictrum tuberosum	Forb Forb	0.281 0.283	10
48	RUBUS	Rubus sp.	Woody	0.284	18
49	HIPPO	Hippocrepis ciliata	Forb	0.287	27
50	AVENULA	Avenula pratensis	Graminoid	0.319	14
51	PRUSPI	Prunus spinosa	Woody	0.347	15
52	QUEILE	Quercus ilex	Woody	0.350	13
53	ROSA	Rosa sp.	Woody	0.365	24
54	TEUPY	Teucrium pyrenaicum Galium lucidum	Forb	0.375	16 15
55	GALUCI ARGYZA	Argyrolobium zanonii	Forb Woody	0.407 0.407	24
56	HELIMA	Helianthemum marifolium	Woody	0.414	23
57	GALEST	Galium estebanii	Forb	0.437	21
58	FUMERI	Fumana ericifolia	Woody	0.459	13
59	BRAPH	Brachypodium phoenicoides	Graminoid	0.468	4
	PSBI	Psoralea bituminosa	Forb	0.470	22
60	CRAMON	Crataegus monogyna	Woody	0.471	27
61					
62			35		
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CORMIN	Coronilla minima	Woody	0.495	18	
KOELERVAL	Koeleria vallesiana	Graminoid	0.510	26	
ONOFRU	Ononis fruticosa	Woody	0.536	10	
THALIC	Thalictrum alpinum	Forb	0.540	20	
CARDUS	Carduus sp.	Forb	0.554	2	
GLOBNU	Globularia nudicaulis	Forb	0.576	14	
JUNCOM	Juniperus communis	Woody	0.706	26	
BUGRA	Bupleurum rigidum	Forb	0.742	17	
PINSIL	Pinus sylvestris	Woody	1.016	18	
BRARE	Brachypodium retusum	Graminoid	1.035	13	
TEUCHA	Teucrium chamaedrys	Forb	1.162	30	
ARCUVA	Arctostaphylos uva-ursi	Woody	1.200	16	
JUNOXY	Juniperus oxycedrus	Woody	1.248	25	
CAREX	Carex sp.	Graminoid	1.536	10	
GENHIS	Genista hispanica	Woody	1.750	17	
THYVUL	Thymus vulgaris	Woody	1.984	28	
ECHIOR	Echinospartum horridum	Woody	2.017	13	
AMEOVA	Amelanchier ovalis	Woody	2.338	29	
DORPEN	Dorycnium pentaphyllum	Woody	2.536	29	
BROMERE	Bromus erectus	Graminoid	2.557	17	
RUBPER	Rubia peregrina	Forb	3.424	30	
CAREXFLA	Carex flacca	Graminoid	3.539	19	
FR	Festuca rubra	Graminoid	3.673	30	
GENSCO	Genista scorpius	Woody	4.132	30	
CAREXHAL	Carex halleriana	Graminoid	5.215	19	
APHMON	Aphyllanthes monspeliensis	Forb	7.839	30	
BRAPIN	Brachypodium pinnatum	Graminoid	11.700	30	
BUXSEM	Buxus sempervirens	Woody	19.664	30	

**Appendix 2:** species richness (Hill Index with exponent q = 0) (A) and exponential of Shannon entropy (Hill index with exponent q = 1) (B) for plant ecological groups found in the *Q. faginea* forest stands in the Central Pre-Pyrenees, Spain. Boxes depict the 25th and 75th percentiles, and whiskers represent the 5th and 95th percentiles

