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ORIGINAL PAPER

# Do mature pine plantations resemble deciduous natural forests regarding understory plant diversity and canopy structure in historically modified landscapes?

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**Abstract** We compared the structure of the arboreal layer and the diversity and species composition of the understory vegetation of three types of mature forest communities: oak (*Quercus pyrenaica*) and beech (*Fagus sylvatica*) forests and Scots pine (*Pinus sylvestris*) plantations. Our main aim was to determine whether differences in these variables existed and were due to the identity of the dominant tree species. We selected four stands or replicates per forest type located geographically close and with relatively similar conditions. We found no differences in the arboreal structure of oak and beech forests, which were characterised by great variability in tree size, while in case of plantations, this variability was lower at both the intra-stand (estimated by the coefficient of variation) and inter-stand (i.e. the four replicates harboured trees of similar sizes) scales. However, the highest variability in the canopy layer of natural forests was not consistently linked to greater understory species richness. Indeed, the lowest plant species richness was found in beech forests, while oak forests harboured the highest value at either the sampling unit (per $m^2$) or stand scales. The greatest negative correlation between plant diversity and the environmental variables measured was found for litter depth, which was the highest in beech forests. The results obtained by the CCA indicated that the four replicates of each forest type clustered together, due to the presence of characteristic species. We concluded that pine plantations did not approach the environmental conditions of native forests, as plantations were characterised by singular understory species composition and low arboreal layer variability, compared to natural woodlands.

**Keywords** *Fagus sylvatica* · *Pinus sylvestris* · Plant species composition · Plantations · *Quercus pyrenaica* · Species richness · Understory · Woodlands

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## Introduction

In general, compared to native mature forests, conifer plantations established in hardwood naturally occupied areas are considered low-diversity communities (Peterken 1996). One of the main criticisms to the plantation of fast-growth conifer species has been addressed to the resulting tree spatial pattern, traditionally characterised by high densities of even-aged individuals planted at regular distances. Consequently, many conifer plantations harbour very low structural diversity, both horizontal (spatial heterogeneity) and vertical (stratification), fundamental components of forest biodiversity (Magurran 1989; Kint 2005). However, the initial uniform distribution of the planted trees can evolve, progressively leading to a random or aggregated spatial pattern, depending on the natural population dynamics or the management regimes (Kint 2005; Marcos et al. 2007). Similarly, the diversification of the even-aged structure of the planted trees (by either selective logging or natural regeneration) can increase the variability in tree height (i.e. greater canopy stratification) and crown size. This may result in an arboreal structure similar to that of natural woodlands, characterised by structurally more diverse canopy layers, including trees of various ages and sizes. On the other hand, different human management practices can also influence the spatial structure in semi-natural deciduous forests (Rozas et al. 2009). Several authors have compared the stand structure of plantations and natural forests (Summers et al. 1999; Kint et al. 2006) and the effects of the overstory features, mainly associated to management practices, on the understory plant species (Tárrega et al. 2006; Deal 2007; Gracia et al. 2007; Marcos et al. 2007). In a review article, Barbier et al. (2008) stated that the assumption of lower diversity under conifer species may not always be correct and considered that it is very difficult to generalise about the effects of tree species structure and composition on the understory diversity. Therefore, in order to improve management planning and forestry practices, more studies are needed on comparing tree canopy structure and its effects on the understory vegetation between plantations and natural forests, especially in stands with similar maturity level. Nonetheless, despite the relevance of the overstory structure, there are other important factors related to the identity of the dominant tree species that can affect the understory vegetation, such as the physical and chemical features of the litter layer, the edaphic characteristics or the leaf area index determining the amount of light in the understory (Augusto et al. 2003; North et al. 2005; Estevan et al. 2007; Barbier et al. 2008). Therefore, these factors can as well determine differences between conifer stands and hardwoods and even between several types of hardwoods.

In Spain, extensive reforestation with conifers and other fast-growing species started in the 1940s to provide wood for industrial purposes and to compensate for the effects of past deforestation (Luis-Calabuig et al. 2000). Nowadays, reforestation continues in order to increase the total forested area and to improve soil conditions and vegetation structure in degraded shrub and grasslands (Ministerio de Medio Ambiente 2002). Moreover, mature stages of conifer plantations are expected to approach the environmental conditions (e.g. arboreal structure and understory diversity) of natural woodlands and, thus, to facilitate the natural establishment of native deciduous forests in historically deforested areas.

In this study, we aimed at comparing the arboreal structure and the diversity of the understory vegetation in *Pinus sylvestris* plantations (aged between 40 and 80 years since planting) and mature beech (*Fagus sylvatica*) and oak (dominated by *Quercus pyrenaica*, with presence of *Quercus petraea* and their hybrids) natural forests, located geographically close and with relatively similar conditions. Specifically, we intended to determine whether there were differences between forest communities due to the identity of the dominant tree species, regarding: (1) mean distance between adjacent trees (as an estimator of tree density), and tree size, their variability (both at the intra- and inter-stand scales) and, thus, the degree of canopy heterogeneity, (2) plant species composition of the understory, (3) plant species diversity at both small (at the sampling unit of 1 $m^2$ scale or alpha diversity) and larger (at the stand scale or gamma diversity) scales and (4) the possible relation between the canopy structure and the understory plant species composition and diversity.

## Methods

A total of twelve forest stands were selected (therefore, four replicates or stands per forest type), located geographically close to minimise variability (situated in León province, NW Spain, 42° 36′–43° 4′ N, 4° 52′–5° 16′ W), at 1,000–1,400 m of altitude. Climatic conditions are similar in all the stands, characterised by 900–1,200 mm of annual rainfall, mean temperatures between 8 and 11°C, with a mean minimum temperature of −3°C in the coldest month and a mean maximum of 25°C in the warmest month. The frost-free period lasts 4 months and there is a short summer dry period in July (Instituto Tecnológico Geominero de España 1995). Stands are located on siliceous substrate, and the soil types are humic cambisol and ranker (Forteza et al. 1987). A more detailed description of the topsoil features of each forest type is in Marcos et al. (2010).

Oak and beech stands are well-developed forests with similar environmental characteristics and have been subjected to traditional management practices, such as grazing, timber and firewood exploitation, nowadays abandoned. Pine plantation stands age between 40 and 80 years since planting; two of them are located in areas where beech forests are the naturally developing forests and the other two in areas of naturally developing oak forests. Pine plantations have not been subjected to large-scale harvesting. There are no detailed records on the specific management practices developed in these plantations; probably, only scarce and haphazard forestry practices have been applied (e.g. selective thinning).

Since the objective was not to characterise the stands exhaustively but to compare them, a similar surface was studied, located in the centre of each stand, using a systematic sampling method. For the tree layer, two perpendicular transects of about 40 m were studied in each stand and five points 8 m apart were sampled in each transect (Fig. 1). At each point, the distance to the nearest tree was measured in the four quadrants (point-centred-quarter PCQ method, Cottam and Curtis 1956). As the distance estimation by the PCQ method is biased in opposite form when the tree spatial distribution pattern is aggregated and when it is uniform (Bryant et al. 2004), we measured distances between the central point and the four nearest trees in the case of natural forests (aggregated or random pattern was expected) and between trees in case of plantations (uniform

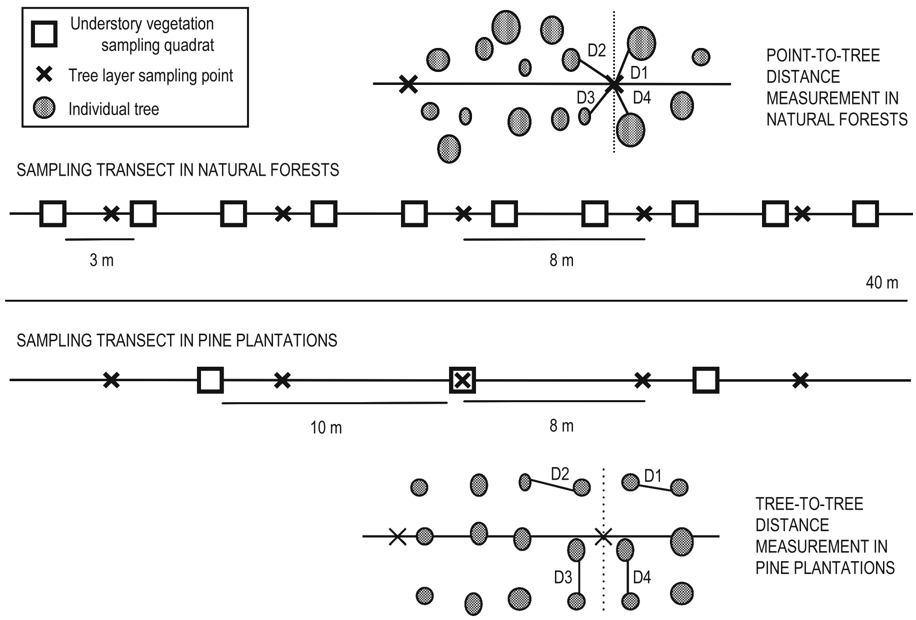


**Fig. 1** Sampling scheme for tree layer and understory vegetation in natural forests and pine plantations

or random pattern was expected) in order to minimise the bias. Therefore, in case of pine plantations, for each of the four quadrants, we measured the distance between the nearest tree to each sampling point and its closer neighbour tree (Fig. 1). Thus, in any case, 40 distance measurements were available in each stand (i.e. 4 trees per sampling point × 5 sampling points per transect × 2 transects per stand). Distance measurements were used to compare the horizontal heterogeneity of the tree layer. To determine tree dimensions, the trunk perimeter (at breast height) and two crown diameters (one in the transect direction and the other perpendicularly) were measured in the same 40 trees used for distance estimation. In addition, tree height (up to the top of the crown) was calculated as the mean of the visual estimation, always by the same researchers (so that the bias, if it existed, was similar in all the stands). Therefore, 40 trees per stand were measured, using the mean values and coefficients of variation of the studied variables for further analyses.

For the understory vegetation, sampling was carried out following the same transects as for the tree layer, using a 1-m$^2$ sampling unit (quadrat). In the natural forests, 10 quadrats, each 3 m apart, were sampled in each transect (Fig. 1). Therefore, data on 20 quadrats per stand were available for oak and beech forests. In the plantations, 3 equidistant quadrats were sampled in each transect, so only 6 quadrats per pine stand were sampled, because higher homogeneity was presupposed. All the species present in each quadrat were recorded, quantifying their abundance as cover percentage (visually estimated always by the same researchers). Plant nomenclature follows Tutin et al. (1964–1980). In order to determine the effects of litter depth on the understory plants, five measurements were taken in each stand, along the same perpendicular transects.

Species richness (S, number of species) was used as diversity measure. Alpha diversity (Whittaker 1972; Magurran 1989) was estimated as the mean species richness per square metre (quadrat) in each stand. Gamma diversity was considered as the total species richness in each stand (from the joint consideration of the samples carried out in the quadrats). Since diversity is a parameter highly dependent on surface (Magurran 1989), to allow comparison between oak and beech forests with pine plantations, and because of the different sampling sizes, rarefaction (by means of randomised curves extrapolation) was used to estimate gamma (stand) diversity. Computation requires Monte Carlo re-sampling, in which samples are randomly accumulated in many iterations (Gotelli and Colwell 2001). The curves traced in this way were adjusted to parametric functions in order to estimate total species richness (gamma diversity) as the asymptote value (Colwell and Coddington 1994; Jiménez-Valverde and Hortal 2003). The software used was EstimateS725 (Colwell 2005). The obtained $R^2$ value was higher than 0.99 for all the stands. Beta diversity or spatial heterogeneity was also estimated by the Whittaker formula (in Magurran 1989) as: S beta = (S gamma/mean S alpha) − 1.

An analysis of variance (ANOVA) was carried out to determine whether there were significant differences in distance between trees and tree dimensions (both for mean values and coefficients of variation in each stand, as a measure of intra-stand heterogeneity) between forest types. Analysis of variance was also used to compare litter depth, alpha, rarefied gamma and beta diversity in the understory.

In all cases, four replicates were considered. The Scheffe test was applied for the *post hoc* comparisons when ANOVA was significant ($P < 0.05$). Sample normality had been checked beforehand using the Kolmogorov–Smirnov test and homogeneity of variances with the Cochran test.

For the joint comparison of the tree measures, a principal components analysis (PCA) was carried out, using the Statistica 6.0 program. Tree height and distance between trees were not included in the PCA, but we included their coefficients of variation. Understory plant species composition was analysed by a detrended correspondence analysis (DCA). Only 47 species were included in this analysis, excluding the species appearing in only one or two stands (54 species). The correlation among tree features (mean values and coefficients of variation), alpha and gamma species diversity and the first two DCA axes was analysed using the Pearson's coefficient, in order to determine whether the canopy structure and the intra-stand variability affected the understory plant diversity and composition. Then, a canonical correspondence analysis (CCA) was performed, including the same 47 species and only those environmental variables significantly correlated with the DCA axes. CANOCO program (Ter Braak 1991) was used for DCA and CCA (only CCA figure is shown).

## Results

Contrary to what we expected, the coefficients of variation of distance between trees were similar for plantations and natural woodlands (Table 1). Regarding tree dimensions, there were only differences between forest types in terms of tree height that was significantly higher in plantations (Table 1). However, variability in tree size at the intra-stand scale was significantly higher in the two types of natural forests (i.e. higher coefficients of variation) than in plantations, which were characterised by greater evenness in the size of the planted trees. In addition to low intra-stand variability, plantations were also characterised by lower tree size inter-stand variability than natural forests. The results obtained in the joint comparison of all variables by a principal components analysis (Fig. 2) indicated that the four pine replicates clustered together and quite far apart from the natural woodland stands along the axis I. The PCA analysis also showed less evident differences in the characteristics of the arboreal layer between oak and beech stands, which clustered together and were characterised by higher values of both intra-stand (i.e. higher coefficients of variation) and inter-stand variability (e.g. differences in tree size between stands, with the greatest values in B1 and the smallest in O3) than plantations. However, differences between the two types of natural forests were found in terms of the litter depth (Table 1). Litter depth was significantly higher in beech forests (mean litter depth value: 8.6 cm) than in pine plantations and oak forests (4.9 and 3.8 cm, respectively).

Concerning the understory plant species composition, we recorded 101 species in total in the twelve forest stands (76 species in oak forests, 38 in beech forests and 37 in pine plantations). Besides, there were 43 oak "exclusive" species (i.e. species either characteristic or not of this forest community, but that did not occur in the other two forest types in this study), of which 11 species were shared by more than two stands. In case of pine plantations, there

**Table 1** Mean and standard deviation (SD) values for distance between trees, tree height, trunk perimeter and crown diameter, and for their coefficients of variation (cv). Litter depth values are also included

| | PINE | | OAK | | BEECH | | ANOVA results | |
|---|---|---|---|---|---|---|---|---|
| | Mean | SD | Mean | SD | Mean | SD | *F* test | *P* value |
| Distance (m) | 3.82 | 0.74 | 2.80 | 0.56 | 3.21 | 1.50 | 1.00 | 0.404 |
| Tree height (m) | 17.28 | 1.19 | 12.44 | 2.64 | 12.84 | 1.61 | 7.87 | **0.011** |
| Trunk perimeter (cm) | 86.52 | 7.65 | 61.16 | 16.18 | 67.27 | 30.29 | 1.70 | 0.237 |
| Crown diameter (m) | 4.23 | 0.47 | 4.57 | 1.12 | 5.56 | 1.29 | 1.83 | 0.215 |
| cv Distance (%) | 49.42 | 11.23 | 45.95 | 4.54 | 54.47 | 3.63 | 1.38 | 0.301 |
| cv Tree height (%) | 13.22 | 3.57 | 34.50 | 15.21 | 44.04 | 9.38 | 8.99 | **0.007** |
| cv Trunk perimeter (%) | 27.33 | 9.67 | 85.81 | 20.48 | 77.33 | 12.37 | 17.99 | **0.001** |
| cv Crown diameter (%) | 31.68 | 11.38 | 53.67 | 9.58 | 54.15 | 6.66 | 7.45 | **0.012** |
| Litter depth (cm) | 4.94 | 1.35 | 3.77 | 1.37 | 8.57 | 1.82 | 10.67 | **0.004** |

Results of the analyses of variance (*F* test and *P* value) are indicated. Significant differences ($P < 0.05$; bold face) in tree variables were always found between pine plantations vs. oak and beech forests. Significant differences in litter depth were found between beech forests and the other two types of forest communities

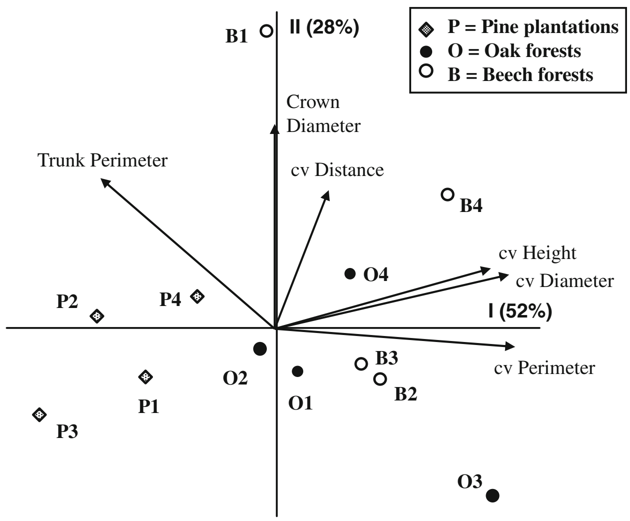


**Fig. 2** Location of tree variables, their coefficients of variation (cv) and the study stands in the plane defined by the first two axes of the principal components analysis (explained variance and eigenvalues: axis I = 52% and 3.10, axis II = 28% and 1.66)

were only 11 pine "exclusive" species of which none was shared by more than two stands. Finally, there were 13 beech "exclusive" species, of which only 2 were found in more than two stands. The most frequent species were *Agrostis capillaris* and *Carex* gr. *muricata*, which were recorded in nine of the twelve studied stands (see Table 3). Besides, *Arenaria montana, Avenula marginata, Cruciata glabra, Deschampsia flexuosa, Festuca* gr. *rubra, Stellaria holostea, Teucrium scorodonia* and *Viola riviniana* were found in eight of the twelve forest stands (see Table 3). Most of the stands were characterised by high understory cover values, except beech forests that showed great variability (Table 2).

At the sampling unit scale, the understory alpha diversity (estimated as species richness) was significantly higher in oak forests than in beech forests, with intermediate values and no significant differences in pine plantations (Fig. 3). Similar results were obtained at the stand scale with significantly higher values of gamma diversity (i.e. total number of species per stand) in oak forests than in beech forests and pine plantations, either before or after rarefaction (Table 2, Fig. 3). The highest mean value of beta diversity was found in beech forests, although no significant differences with oak forests and pine plantations were detected, due to the great inter-stand variability that characterised beech forests.

Results obtained from the Pearson's correlation analyses showed that none of the tree feature variables and coefficients of variation considered was significantly correlated with any of the measures of the understory plant diversity. However, there was a significantly negative correlation between litter depth and diversity at both the sampling unit (S alpha, $r = -0.59$) and stand (S gamma, $r = -0.67$) scales. Regarding the complex environmental gradient represented by the two first axes of the DCA (associated with understory plant species composition), we found that the only significant correlations were with litter depth ($r = 0.59$), understory plant diversity (S alpha, $r = -0.81$; and S gamma, $r = -0.89$), trunk perimeter ($r = 0.58$) and coefficients of variation of tree size (height, $r = -0.58$; and perimeter, $r = -0.69$).

The joint comparison by the CCA differentiated the three types of forest communities (Fig. 4). Oak forests were associated with the highest diversity values and with several plant species that did not occur in the other two forest types, such as *Anthoxanthum odoratum, Luzula forsteri, Ornithogalum umbellatum, Silene nutans* and *Physospermum cornubiense,* and with sprouts of *Quercus pyrenaica*, which were also less abundantly found in the understory of pine plantations and beech forests (see Table 3). Beech forests were characterised by the highest litter depth and species as *Anemone nemorosa, Helleborus foetidus* (also present in oak forests) and sprouts of *Fagus sylvatica*. Pine plantations were characterised by high cover values of *Vaccinium myrtillus, Cytisus scoparius, Rubus* sp., *Luzula lactea, Veronica officinalis* and *Viola riviniana*, although these species also appeared in the other two forest communities. The highest variability of tree size (coefficients of variation of trunk perimeter and tree height) was associated with the two natural forests.

**Table 2** Total understory cover (sum of all species cover), number of understory species (gamma species richness before rarefaction) and rarefaction results in the studied stands (P = Pine plantations, O = Oak forests, B = Beech forests)

| | P1 | P2 | P3 | P4 | O1 | O2 | O3 | O4 | B1 | B2 | B3 | B4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Total understory cover (%) | 104 | 138 | 131 | 124 | 181 | 190 | 152 | 96 | 116 | 7 | 5 | 79 |
| Total number of species (S) | 8 | 24 | 22 | 24 | 41 | 44 | 46 | 43 | 28 | 7 | 10 | 17 |
| S after rarefaction | 12 | 30 | 37 | 36 | 46 | 49 | 52 | 51 | 33 | 10 | 24 | 18 |
| Rarefaction var. expl. | 99.4 | 99.6 | 99.8 | 99.9 | 99.3 | 99.1 | 98.5 | 99.1 | 99.4 | 99.9 | 99.9 | 97.0 |

**Table 3** Mean percentage cover value of the most frequent, abundant or representative annual, perennial herbaceous and woody species sampled in the studied stands (P = Pine plantations, O = Oak forests, B = Beech forests)

| | | P1 | P2 | P3 | P4 | O1 | O2 | O3 | O4 | B1 | B2 | B3 | B4 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Annual herb species | | | | | | | | | | | | | |
| *Galium aparine* | GAAP | 0.0 | 0.0 | 0.0 | 0.0 | 2.4 | 0.6 | 6.9 | 0.3 | 1.4 | 0.0 | 0.0 | 0.0 |
| *Melampyrum pratense* | MEPR | 0.0 | 0.0 | 0.0 | 10.2 | 6.5 | 6.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Perennial herb species | | | | | | | | | | | | | |
| *Agrostis capillaris* | AGCA | 0.0 | 3.6 | 3.3 | 2.0 | 3.0 | 0.0 | 5.2 | 0.0 | 2.0 | 0.8 | 0.2 | 1.7 |
| *Anemone nemorosa* | ANNE | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.5 | 2.7 |
| *Anthoxanthum odoratum* | ANOD | 0.0 | 0.0 | 0.0 | 0.0 | 3.2 | 0.3 | 0.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Arenaria montana* | ARMO | 2.5 | 0.3 | 2.2 | 0.5 | 5.6 | 9.0 | 3.7 | 5.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Avenula marginata* | AVMA | 1.7 | 8.3 | 14.7 | 9.2 | 0.0 | 1.0 | 6.5 | 2.6 | 14.5 | 0.0 | 0.0 | 0.0 |
| *Brachypodium pinnatum* | BRPI | 0.0 | 0.0 | 0.0 | 0.0 | 4.2 | 11.0 | 13.0 | 0.0 | 1.5 | 0.0 | 0.0 | 0.0 |
| *Carex* gr. *muricata* | CAMU | 0.0 | 1.1 | 0.0 | 4.2 | 0.6 | 2.9 | 3.8 | 1.5 | 2.8 | 0.0 | 0.1 | 0.2 |
| *Clinopodium vulgare* | CLVU | 0.0 | 0.0 | 0.0 | 0.0 | 7.0 | 4.7 | 1.0 | 0.4 | 5.7 | 0.0 | 0.0 | 0.0 |
| *Conopodium majus* | COMA | 0.0 | 0.0 | 0.2 | 0.0 | 0.4 | 0.0 | 0.5 | 5.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Cruciata glabra* | | 0.0 | 1.1 | 1.7 | 0.7 | 0.3 | 1.1 | 12.7 | 1.7 | 0.8 | 0.0 | 0.0 | 0.0 |
| *Deschampsia flexuosa* | DEFL | 25.8 | 22.6 | 12.2 | 6.7 | 0.0 | 0.0 | 0.0 | 2.4 | 24.5 | 0.0 | 0.4 | 10.2 |
| *Dryopteris filix-mas* | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.8 | 2.5 | 0.0 |
| *Festuca* gr. *rubra* | FERU | 0.0 | 3.3 | 15.8 | 11.3 | 8.4 | 9.9 | 10.3 | 21.5 | 4.3 | 0.0 | 0.0 | 0.0 |
| *Galium rotundifolium* | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 4.5 | 3.3 | 0.0 | 0.0 |
| *Helleborus foetidus* | HEFO | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.0 | 0.0 | 1.8 | 0.6 | 0.0 | 0.0 |
| *Hieracium* gr. *pilosella* | HIPI | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.4 | 4.0 | 0.0 | 0.0 | 0.0 |
| *Holcus mollis* | HOMO | 0.0 | 3.8 | 0.0 | 4.7 | 28.0 | 15.2 | 3.3 | 15.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Lathyrus niger* | LANI | 0.0 | 0.0 | 0.0 | 0.0 | 1.0 | 0.1 | 0.0 | 1.2 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Luzula forsteri* | LUFO | 0.0 | 0.0 | 0.0 | 0.0 | 3.7 | 0.3 | 3.3 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Luzula lactea* | LULA | 13.3 | 6.7 | 10.8 | 4.2 | 0.0 | 0.0 | 0.0 | 4.8 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Ornithogalum umbellatum* | ORUM | 0.0 | 0.0 | 0.0 | 0.0 | 0.1 | 0.1 | 0.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Physospermum cornubiense* | PHCO | 0.0 | 0.0 | 0.0 | 0.0 | 2.4 | 0.9 | 0.1 | 1.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Pteridium aquilinum* | PTAQ | 0.0 | 0.0 | 0.0 | 0.0 | 6.3 | 16.5 | 0.0 | 0.4 | 17.3 | 0.0 | 0.0 | 2.5 |
| *Silene nutans* | SINU | 0.0 | 0.0 | 0.0 | 0.0 | 3.8 | 3.9 | 0.9 | 3.1 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Stellaria holostea* | STHO | 0.0 | 0.0 | 0.0 | 1.3 | 11.2 | 4.4 | 0.0 | 5.1 | 0.4 | 0.5 | 0.5 | 3.1 |
| *Teucrium scorodonia* | TESC | 0.0 | 2.9 | 3.3 | 10.8 | 7.1 | 13.8 | 0.0 | 2.3 | 4.7 | 0.0 | 0.0 | 0.6 |
| *Veronica officinalis* | VEOF | 0.0 | 5.8 | 0.0 | 0.0 | 0.0 | 0.0 | 0.4 | 1.7 | 0.0 | 0.0 | 0.0 | 0.3 |
| *Viola riviniana* | VIRI | 0.0 | 2.8 | 3.8 | 4.7 | 1.0 | 1.0 | 1.6 | 0.6 | 0.7 | 0.0 | 0.0 | 0.0 |
| Woody species | | | | | | | | | | | | | |
| *Cytisus scoparius* | CYSC | 1.7 | 5.6 | 11.2 | 0.5 | 0.0 | 1.2 | 0.0 | 0.3 | 3.6 | 0.0 | 0.0 | 0.1 |
| *Erica arborea* | ERAR | 0.0 | 10.1 | 0.0 | 0.0 | 13.3 | 8.3 | 2.5 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Fagus sylvatica* | FASY | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 10.0 | 1.0 | 0.3 | 17.2 |
| *Genista florida* | GEFL | 1.7 | 8.9 | 0.0 | 0.0 | 3.3 | 2.2 | 0.0 | 4.9 | 0.0 | 0.0 | 0.2 | 0.0 |
| *Ilex aquifolium* | | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 1.7 |
| *Lithodora diffussa* | LIDI | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 3.7 | 7.2 | 0.7 | 8.1 | 0.0 | 0.0 | 0.0 |
| *Quercus pyrenaica* | QUPY | 0.0 | 1.9 | 2.5 | 0.0 | 34.2 | 25.7 | 35.5 | 4.5 | 0.5 | 0.0 | 0.0 | 0.0 |
| *Rubus* sp. | RUBU | 0.0 | 1.0 | 0.2 | 7.5 | 0.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| *Vaccinium myrtillus* | VAMY | 56.7 | 41.0 | 2.5 | 26.7 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.2 | 0.0 | 29.6 |

## Discussion

Our results indicated that differences in the characteristics of the arboreal layer between pine plantations and natural woodlands were mainly found in terms of the vertical heterogeneity of the canopy layer. The two deciduous forest types were characterised by higher variability in the dimension of trees, probably related to the natural

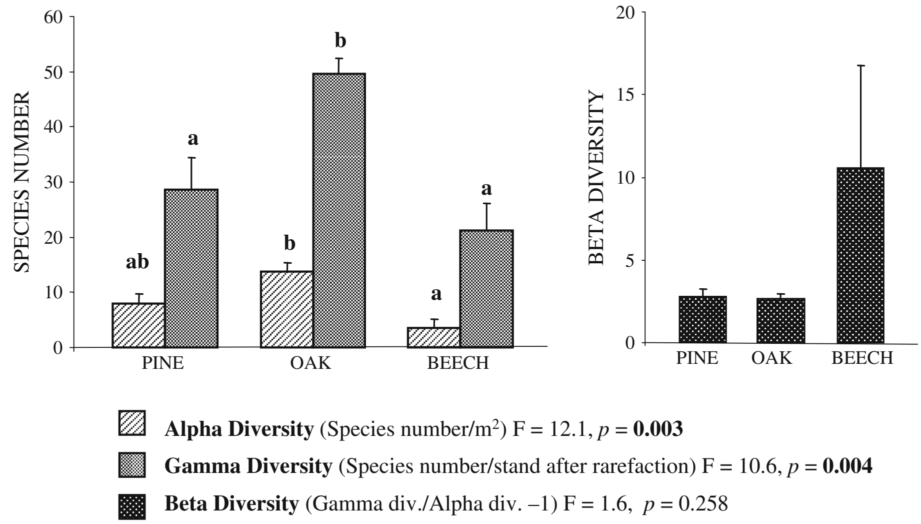


**Fig. 3** Mean values and standard error bars of alpha, gamma and beta diversity in the three types of forest communities studied. Results of ANOVAs (*F* test and *P* value) and *post hoc* comparisons are also included (different letters indicate significant differences between forest types)

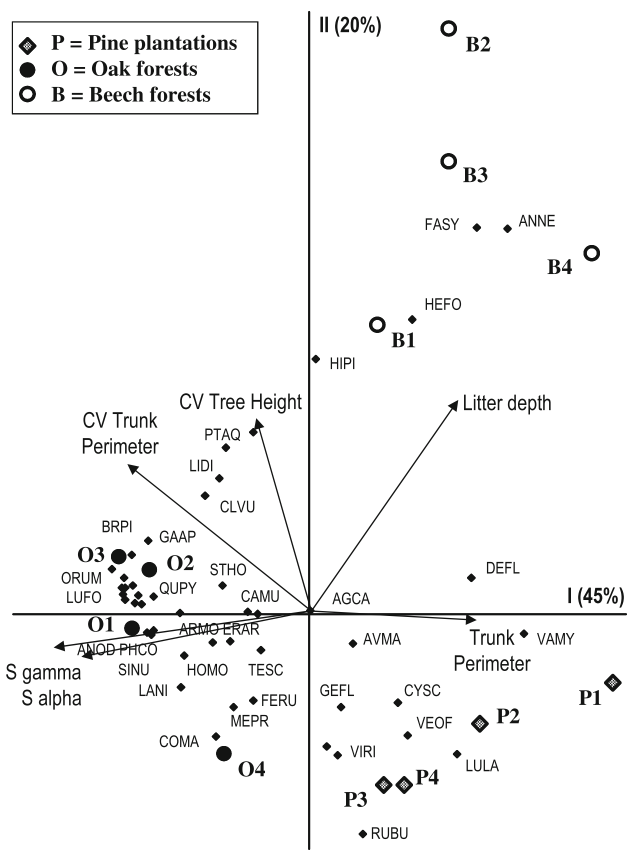


**Fig. 4** Location of plant species, environmental variables and study stands in the plane defined by the first two axes of the canonical correspondence analysis (explained variance and eigenvalues: axis I = 45% and 0.60, axis II = 20% and 0.27). (Summary of the Monte Carlo test of significance: *F* ratio = 2.32, *P* value = 0.002). For species name abbreviations, see Table 3

regeneration dynamics of the oak and beech tree species. On the contrary, the planted trees showed greater size evenness and pine plantations were characterised by the practically total absence of *Pinus sylvestris* seedlings in the understory, indicating difficulties in tree regeneration. Greater diversity in tree age and size of natural forests compared to plantations was also observed in other studies (Summers et al. 1999; Kint 2005; Marcos et al. 2007). However, no differences were detected regarding the horizontal heterogeneity of the three forest types. Similar values of the coefficient of variation of distance between adjacent trees were obtained for the three forest communities considered. On the other hand, the lowest inter-stand variability of the characteristics of the arboreal layer (i.e. highest similarity of the four replicates) was found in pine plantations as shown by the PCA. Similar results were obtained when studying the topsoil features of the same forest stands, meaning that the greatest homogeneity of the edaphic properties was found in the four plantation replicates compared to natural forests (Marcos et al. 2010).

Although the three types of forest communities had several plant species in common, the results of the multivariate analyses indicated that they harboured distinct and characteristic plant species compositions in the understory, as the four replicates of each forest type formed separate clusters. Consequently, we found no clear indication that understory plant species composition of mature pine plantations may be approaching that of the surrounding native deciduous forests. Moreover, very few oak and none beech sprouts were found in the understory of pine plantations. Therefore, according to our results, mature pine plantations may not facilitate the natural establishment of native deciduous forests in the studied historically deforested areas.

On the other hand, we found that plant species diversity of the understory was higher in oak forests than in pine plantations. This finding is in accordance with the general idea that coniferous species are less favourable to understory diversity than deciduous trees (Barbier et al. 2008). Contrary to this, beech forests showed the lowest understory plant diversity. Several authors have found great variability when comparing the plant diversity values under different hardwood species, although generally there was higher vascular species richness in *Quercus* stands than in *Fagus* ones (Brunet et al. 1996; Barbier et al. 2008). This may be partly due to greater topsoil acidity in beech forests than in oak forests (see Barbier et al. 2008), also found in our study areas (Marcos et al. 2010). Furthermore, also the litter layer may have negative physical effects on the understory vegetation, obstructing seed germination or seedling emergence (Sayer 2006), supporting the negative correlation we found between litter depth and species richness. Some authors have suggested that the effects of the identity of the dominant tree species on understory diversity (either increasing or decreasing its value) may result from differences in litter layer thickness among different tree species (Augusto et al. 2003; North et al. 2005; Barbier et al. 2008). In general, there is higher litter mass under conifer tree species than under hardwood species (Barbier et al. 2008), although great variability when comparing different deciduous tree species (Archibold 1995; Costa et al. 1998). In our study, no significant differences in litter depth were detected between oak and pine forests, while the highest value corresponded to beech forests. Great litter accumulation on the beech forest ground may be due to its slow leaf litter decomposition rates (Archibold 1995; Costa et al. 1998). According to Costa et al. (1998), beech forests are characterised by great acidity of topsoil layers, which decreases microorganisms activity and slows down mineralisation rates.

Consequently, in beech forests, litter accumulation and the intense shade effect may limit vascular plant development, determining low understory diversity. Furthermore, the actual geographic distribution of beech forests in the study area (i.e. located at the periphery of their distribution range) may also negatively influence plant species richness. Indeed, most of the Iberian Peninsula beech forests are characterised by low species richness and cover of the herbaceous layer, and great variability and heterogeneity in plant species composition (Costa et al. 1998). In agreement with this, in our study, beech understory cover values were highly variable (values ranged from 5 to more than 100%), as well as species diversity. Indeed, we obtained the highest mean values and largest standard error bars for beech forest beta diversity (meaning high intra-stand heterogeneity and great variability among stands). On the other hand, the low understory plant diversity of beech forests does not mean low ecological value from the conservation point of view. Beech woodlands represent important forest ecosystems in the study area as they harbour characteristic plant species and act as valuable habitats for several endangered animal species, such as the Cantabrian capercaillie and the Cantabrian brown bear (Costa et al. 1998; Oria de Rueda 2003).

Finally, we detected differences in the arboreal layer structure and the understory plant species composition between the three forest types related to the identity of the dominant tree species. Nevertheless, it was not possible to assess the influence of the overstory on plant species diversity. In our study, differences in canopy structure between forest stands were mainly related to more or less amount of variability in tree size, but unrelated to differences in the horizontal heterogeneity (coefficients of variation of distance between adjacent trees). It is likely that horizontal heterogeneity has stronger effects on the understory, for example determining differences in light availability. Several authors have pointed out the negative effects of a homogeneous overstory cover on understory plant species richness and diversity, mainly due to the decrease in shade-intolerant species (Brosofske et al. 2001; Härdtle et al. 2003; Estevan et al. 2007; Gracia et al. 2007). But other studies have found no evident relationship between plant species diversity and the heterogeneity of the forest stand structure (Neumann and Starlinger 2001; Tárrega et al. 2006). On the other hand, the results obtained in this study also support the idea that studying changes in community plant species composition instead of determining plant diversity represents a more suitable method to evaluate the influence of management practices or the environmental conditions on the understory (Brosofske et al. 2001; Onaindía et al. 2004; Tárrega et al. 2007).

To conclude, mature pine plantations of the study area did not resemble native deciduous forests, regarding understory species composition and variability of the arboreal layer. Thus, they may not enable the natural establishment of these woodlands in this historically modified landscape.

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