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Plant and carabid beetle species diversity in relation to forest type and structural heterogeneity

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Abstract The aim of this study was to evaluate the influence of forest structure (mainly resulting from human uses) and forest type (the identity of the dominant tree species) on biodiversity. We determined the diversity of two taxonomical groups: the understory vegetation and the edaphic carabid beetle fauna. We selected eight types of forest ecosystems (five replicates or stands per forest type): pine (*Pinus sylvestris*) plantations of three age classes (10, 40 and 80 years since reforestation), an old-growth relict natural pine forest, and four types of oak (*Quercus pyrenaica*) stands: mature forests with livestock grazing and firewood extraction, mature forests where uses have been abandoned, "dehesa" ecosystems and shrubby oak ecosystems. The results obtained by a global PCA analysis indicated that both tree size and dominant species influenced the ordination of the 40 forest stands. In general, carabids were more sensitive to changes in forest heterogeneity and responded more clearly to the analysed structural variables than the understory vegetation, although the species richness of both groups was significantly correlated and higher in case of oak forests. Pine forest ecosystems were characterised by the lowest species richness for both taxonomical groups, the lowest plant diversity and by the lowest coefficients of variation and, consequently, low structural heterogeneity. As a result, it was very difficult to discriminate the effects of the spatial heterogeneity and the dominant tree species on biodiversity.

Keywords Biodiversity · Carabid beetles · Heterogeneity · Oak forests · Pine plantations · Understory vegetation

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Introduction

The relevant role of spatial heterogeneity, either horizontal or vertical, in determining forest biodiversity has been previously pointed out in the literature (Magurran 1989; Summers et al. 1999; Gracia et al. 2007). Consequently, the main criticisms of traditional reforestation strategies refer to the resulting even structure of plantations (Peterken 1996; Kint 2005; Barbier et al. 2008), apart from the often negative effects of planting non-native fast-growing species in natural deciduous tree areas. In general, conifer plantations are considered low-diversity ecosystems (Peterken 1996; Cannell 1999) as compared to native mature forests (e.g. for carabid beetles: Fahy and Gormally 1998; Elek et al. 2001; Magura et al. 2002). However, the low structural heterogeneity of plantations can evolve due to the ageing process or management practices, progressively leading to a more diversified structure of the planted trees (Kint 2005), resembling that of natural deciduous forests, and, consequently, increasing variability of tree characteristics and the forest diversity (see Barbier et al. 2008). Indeed, the results obtained by several authors have pointed out that it is not possible to make generalisations regarding the influence of the dominant conifer or deciduous tree species on biodiversity (for vegetation: Augusto et al.

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2003; Estevan et al. 2007; Barbier et al. 2008; for carabid beetles: Desender et al. 1999; Koivula 2001; du Bus de Warnaffe and Lebrun 2004).

On the other hand, either forest exploitation or the abandonment of management practices usually cause changes in the structure of the arboreal layer that affect biodiversity in very different ways and in any type of forest ecosystem (Luis-Calabuig et al. 2000; Hartley 2002; Onaindía et al. 2004; Montes et al. 2005). Most of the studies assessing the effects of human uses and changes in forest structure on biodiversity usually analyse the understory vegetation (Brunet et al. 1996; Onaindía et al. 2004; Barbier et al. 2008). However, recent studies have showed that the evaluation of changes in the diversity of several groups of insects, such as carabid beetles (e.g. Fahy and Gormally 1998; Humphrey et al. 1999; Werner and Raffa 2000; Jukes et al. 2001), can improve the information obtained from vegetation diversity, because of their sensitive response to habitat alteration (Lövei and Sunderland 1996; Rainio and Niemelä 2003; Pearce and Vernier 2006). In previous studies, we analysed the effects of forest structure on the diversity of the understory vegetation in oak forests (Tárrega et al. 2006) and pine plantations (Marcos et al. 2007), as well as on the diversity of the edaphic carabid beetle fauna (Taboada et al. 2006b, 2008) in the two types of forest ecosystems. However, the global analysis of all these factors has never been done. Actually, there is no consensus in the literature on whether the understory vegetation and the carabid fauna respond in a similar way to changes in the structural heterogeneity created by either the forest ageing process or the management practices developed (see Fahy and Gormally 1998; Humphrey et al. 1999; Werner and Raffa 2000; Taboada et al. 2008). Furthermore, it has been suggested that the carabid fauna may be affected not only by the shrub and herb cover (e.g. impeding its movement but protecting it from predation) (Brose 2003; Thomas et al. 2006; Taboada et al. 2008; see also Koivula et al. 2003) but also by diversity (i.e. increasing the availability of food resources) (e.g. Halme and Niemelä, 1993; but see Koricheva et al. 2000).

It is generally assumed that great environmental heterogeneity may support high species richness (Huston 1994), although, at the small-scale level, the field evidence on this relationship is scarce and contradictory in case of vegetation (Moora et al. 2007). For carabid beetles, several authors have confirmed the importance of high small-scale heterogeneity in increasing species richness in forest ecosystems (Niemelä et al. 1996; Koivula et al. 1999; Koivula 2001). Moreover, alternative management practices have been suggested in order to increase the forest structural heterogeneity and, thus, to preserve carabid diversity (Koivula 2002; Koivula and Niemelä 2003).

Therefore, our aim was to evaluate the influence of forest structure (mainly resulting from human uses) and forest type (the identity of the dominant tree species) on the diversity of two taxonomical groups at a small-spatial scale: the understory vegetation (defined as number of species/m^2) and the edaphic carabid beetle fauna (total number of species collected per stand).

Materials and methods

We selected two tree species, *Pinus sylvestris* and *Quercus pyrenaica*, and eight types of forest stands, four of each species, with varied arboreal structure: (1) 10-year-old pine plantations (P10), (2) 40-year-old pine plantations (P40), (3) 80-year-old pine plantations (P80), (4) an old-growth relict natural pine forest located in Puebla de Lillo (PL), which allows the analysis of the effect of tree species, taking out the influence of the homogeneity of plantations, (5) mature oak forests with livestock grazing and firewood extraction and, therefore, characterised by low abundance of plant woody species in the understory (i.e. with open understory, OMO), (6) mature oak forests whose uses have been abandoned and woody species have invaded the understory (i.e. with closed understory, OMC), (7) oak "dehesa" ecosystems (ODE), with livestock grazing and characterised by low density of trees, which have been pruned to favour crown development at the expense of height growth and (8) young shrubby oak ecosystems (OSH), with great density of small-size specimens resulting from vegetative resprouting after repeated disturbance, such as fire, or because of secondary succession after grazing abandonment.

In total, we sampled 40 forest stands (i.e. eight forest structural types and five replicates per type) located in the northeast of León province (NW Spain, 42°36′–43°4′N, 4°53′–5°16′W). Stands were characterised by similar conditions, such as siliceous soil type, except dominant tree species and type of human use. Mean annual rainfall in the area is 920–1,200 mm and mean annual temperature 8–11°C (Ministerio de Agricultura 1980). The surrounding landscape is characterised by a mosaic of agricultural and pastoral lands, natural forests (oak and beech) and recently established conifer plantations. A more detailed description of the forest stands can be found in Tárrega et al. (2006) and Marcos et al. (2007).

In the centre of each stand, we placed two perpendicular transects of about 40 m length and determined the arboreal layer characteristics at five sampling points (8 m apart) per transect. In each sampling point, we measured the distance to the nearest tree in the four quadrats (40 measurements per stand in total; point-centre-quarter method (Cottam and Curtis 1956)) to estimate tree density based on the measurement of the mean tree distance (density = 1/(mean distance)^2). In the same tree individuals, we also measured the trunk perimeter (1 m above ground level) and two crown diameters, each in the direction of the two perpendicular transects, (mean crown diameter was calculated by the average value). Besides, tree height (up to the top of the crown) was visually estimated always by the same researchers, so that the bias, if it existed, was similar in all the forest stands. Trunk perimeter and tree height were used as suitable measures of tree size to allow comparison between the eight forest types considered (see Taboada et al. 2006a, b; Tárrega et al. 2006; Marcos et al. 2007). For each variable and in order to compare the different forest stands, we calculated the mean value and the coefficient of variation of the 40 measurements per stand. The understory vegetation was sampled by using a 1 m^2 unit and following the same perpendicular transects. We obtained a total of 20 vegetation samples for each oak forest stand and three samples for each pine plantation stand. We recorded all the plant species present in each sampling unit, and we visually estimated their percentage of cover (see "Appendix 1"). In this study, we analysed the herb and shrub cover (quantified as the sum of the percentage cover of all the herbaceous and woody species recorded in each sampling unit, respectively). We also calculated the mean value and coefficient of variation of the herb and shrub cover for later analyses. The measures of diversity were carried out with two indexes: species richness (S) and the Shannon diversity index (H′, Shannon and Weaver 1949). To allow comparison between vegetation samples from oak forests and pine plantations, we used the mean values per square metre to estimate plant diversity, as we obtained different number of samples from each forest type.

Plastic pitfall traps (depth 86 mm, diameter 60 mm) covered by 10 cm × 10 cm roofs and partly filled with 25% propylene glycol were used to collect the beetles. In order to account for small-scale spatial heterogeneity that influences carabid catches (Niemelä et al. 1996), several independent sampling points were placed within each stand (see Digweed et al. 1995). We placed 15 traps per stand (300 in total), following the same perpendicular transects used for vegetation sampling. Traps were active from May to October and were emptied each 20–25 days (Taboada et al. 2006b, 2008). Pitfall trapping is an invaluable and generally applied sampling method for studying surface dwelling arthropods, and especially carabid beetles (Spence and Niemelä 1994; Koivula et al. 2003). Beetles were identified using standard keys (Jeannel 1941–1942; Lindroth 1974; Trautner and Geigenmüller 1987), and follow the nomenclature in Serrano (2003). For the analysis of carabid diversity, we considered the total number of species captured in each stand for the whole period.

One-way analyses of variance (ANOVA) were carried out to determine whether there were significant differences between oak and pine forest ecosystems in terms of the structural variables measured (mean tree distance, trunk perimeter, crown diameter, tree height and herb and shrub cover), their coefficients of variation, plant and carabid species richness and diversity and the percentages of carabid species of different ecological groups (i.e. flight ability and habitat association; see "Appendix 2"). Sample normality was checked beforehand using the Kolmogorov–Smirnov test and homogeneity of variances with the Cochran test. For the joint comparison of all the results we performed a principal components analysis (PCA) considering 12 variables: mean tree distance, trunk perimeter, crown diameter, tree height, herb and shrub cover and their coefficients of variation. We used the Pearson's coefficient to analyse the correlation between the structural variables measured (mean tree distance, trunk perimeter, crown diameter, tree height and herb and shrub cover), their coefficients of variation and the two-first axes of the PCA, with the plant and carabid species richness and diversity, independently for the two forest types studied (oak and pine) and for all the data together. We used Statistica 6.0 for the analyses.

Results

A total of 172 plant and 76 carabid species were sampled for the 40 forest stands ("Appendices 1 and 2"). In case of carabid beetles, a significantly higher number of brachypterous ($F = 108.60$, $P < 0.001$) and forest specialist species ($F = 14.10$, $P = 0.009$) were collected in the pine stands as compared to the oak forest ones. Furthermore, a significantly greater number of macropterous species ($F = 103.20$, $P < 0.001$) was captured in the oak forest stands.

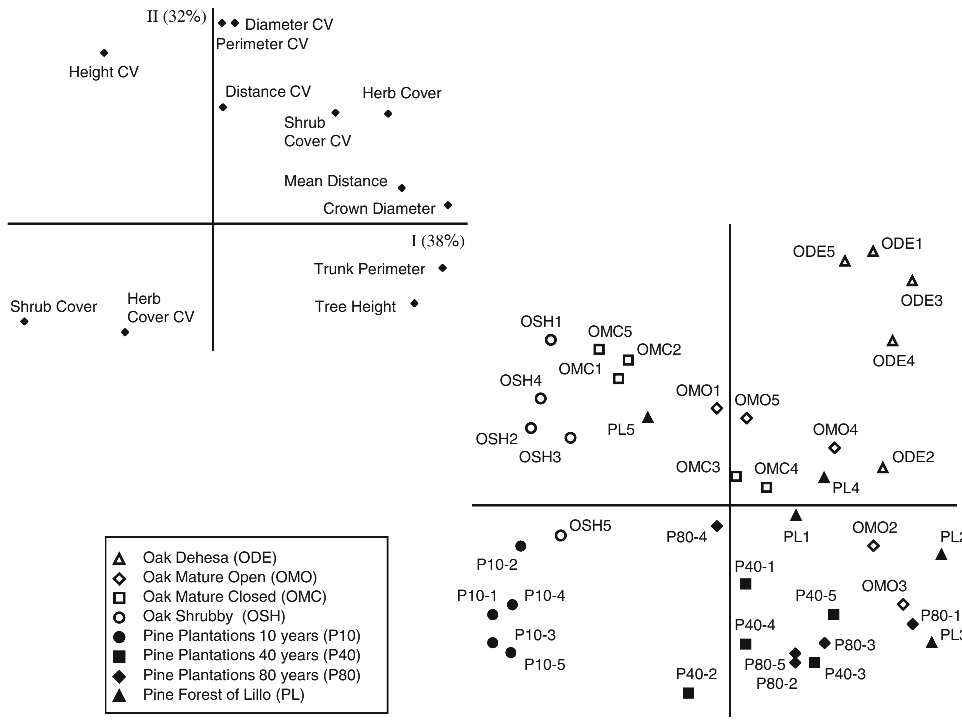
Our results indicated that there were several differences in terms of the structural tree characteristics among forest stands (Table 1). In general, tree size was higher in "dehesa" ecosystems and mature oak forests, the older (40 and 80 year-old) stages of the pine plantations and the natural pine forest. The lowest tree size was found in young shrubby oak forests and 10-year-old pine plantations. Mean tree distance (the inverse of tree density) was higher in "dehesa" ecosystems and the natural pine forest, but differences between oak and pine forest stands were not statistically significant. The greatest value for woody species cover was found in 10-year-old plantations

Table 1 Mean and standard deviation (SD) (five replicates in all cases) of the structural variables measured, their coefficients of variation (CV) and the species richness and diversity (H′) of the understory vegetation and the edaphic carabid beetle fauna

	ODE		OMO		OMC		OSH		P10		P40		P80		PL		*F*	*P*
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD		
Tree height (m)	10.7	2.0	14.4	3.1	11.2	3.0	4.9	0.9	2.6	1.0	17.3	1.6	17.8	1.1	15.9	2.8	3.14	ns
Trunk perimeter (cm)	93.9	18.8	89.5	37.9	49.9	16.0	22.5	3.2	16.1	5.2	86.7	13.5	91.9	18.6	122.0	38.1	1.38	ns
Crown diameter (m)	6.7	0.5	6.1	1.7	3.9	0.9	1.8	0.2	1.1	0.3	4.5	0.5	4.2	0.9	6.3	1.8	0.78	ns
Mean tree distance (m)	7.5	1.5	4.1	1.0	2.9	0.5	2.3	0.9	3.0	0.3	3.9	0.6	4.4	1.8	6.4	1.1	0.14	ns
Shrub cover (%)	8.6	7.1	27.7	16.8	56.8	6.2	79.1	20.2	127.8	30.4	57.8	19.6	39.3	21.3	63.2	17.4	6.63	0.014
Herb cover (%)	183.4	27.4	110.8	43.2	96.1	30.6	75.0	26.0	19.9	13.7	64.1	27.6	95.3	27.4	93.1	32.3	11.08	0.002
CV tree height	39.9	14.9	28.8	11.0	41.5	18.2	48.1	10.5	30.0	2.7	13.4	5.7	9.4	2.2	34.5	17.7	15.30	<0.001
CV trunk perimeter	90.5	20.1	54.3	20.0	87.1	16.0	54.4	16.7	29.7	8.6	24.8	5.9	20.1	8.2	49.5	13.9	40.90	<0.001
CV crown diameter	64.0	10.6	42.3	12.0	51.9	8.0	45.2	15.0	25.6	5.7	28.1	3.7	29.9	15.5	45.4	14.3	19.57	<0.001
CV mean tree distance	57.8	7.8	51.9	3.5	56.0	16.2	69.6	15.9	28.8	3.9	49.0	5.1	47.4	26.3	53.3	5.5	9.47	0.004
CV shrub cover	139.6	43.0	86.2	79.6	47.1	10.5	32.0	4.1	22.0	12.7	46.2	33.9	32.2	26.2	47.4	38.7	6.97	0.012
CV herb cover	21.3	3.4	25.1	7.9	28.7	6.4	35.5	11.7	77.9	28.5	76.8	65.5	33.6	23.7	44.7	22.5	10.50	0.002
No. of plant species/m^2	15.9	2.0	12.8	3.4	13.6	1.3	13.1	4.1	8.3	3.5	6.7	3.7	8.5	1.2	7.3	2.1	46.20	<0.001
Plant species H'/m^2	2.38	0.16	2.21	0.32	2.22	0.14	1.94	0.29	1.45	0.31	1.29	0.56	1.74	0.13	1.59	0.15	45.18	<0.001
Total no. of carabid species	22.2	4.6	15.4	3.8	13.4	2.8	11.4	3.4	9.8	2.9	7.6	0.9	11.2	1.3	13.4	2.6	13.92	<0.001
Carabid species H′	2.20	0.41	1.44	0.26	1.33	0.15	1.45	0.44	1.05	0.74	1.40	0.14	1.21	0.26	2.05	0.08	1.18	ns

The results of the ANOVA tests (*F* test and *P* value) between oak and pine forest types (20 replicates) are also included (*n. s.* no significant). Shrub and herb cover values higher than 100% are due to layer superposition. For abbreviations see text

Fig. 1 Location of the forest stands and the structural variables measured in the plane defined by the first two axes of the principal components analysis



and the lowest in "dehesa" ecosystems. Although we detected great variability among all the forest stands, shrub cover was significantly higher in pine plantations than in oak forests, while opposite results were found for herb cover. There were statistically significant differences between oak and pine plantations in terms of the coefficients of variation of all the structural variables measured, with the lowest values found in case of plantations, except for herb cover. Species richness for both the understory vegetation and the edaphic carabid fauna and plant diversity were significantly higher in oak forests than in pine plantations.

The joint comparison of all variables by a principal components analysis showed that to a certain degree both forest structure and the identity of the dominant tree species were relevant to the ordination of the forest stands (Fig. 1). The first axis (explained variance 38%) ordered the forest stands according to the greatest tree size (positive part of axis I) and the highest values for shrub cover (negative part of axis I). Axis II variables were high values for the coefficients of variation at the positive end, except for herb cover CV that was located in the negative part of axis II, with the highest tree height and shrub cover at the negative end. As a result, the second axis (explained variance 32%) differentiated oak forests and pine plantations. The clearest groups of forest stands that clustered together (i.e. more similar to each other) in the diagram were, 10-year-old pine plantations, young oak shrubby forests and the older stages (40- and 80-year-old) of the plantations. "Dehesa" ecosystems were located at the positive end of both axes. Open and closed mature oak forests showed intermediate characteristics between "dehesa" ecosystems and oak shrubby forests. The natural pine forest was characterised by great variability, with most of the stands related to mature oak forests and one stand located near the older stages of pine plantations.

We detected a significant positive correlation ($r = 0.46$, $P < 0.05$) between plant and carabid beetle species richness, but not in case of diversity ($r = 0.20$, $P > 0.05$). Furthermore, we also found that plant richness and the coefficients of variation of the tree size variables (height, trunk perimeter and crown diameter) were significantly and positively correlated (Table 2). No such correlation was found for the tree size variables. H′ was also positively correlated with the coefficients of variation of the tree size variables, and also with the crown diameter. Regarding the understory, we found a negative correlation between plant species richness and diversity with shrub cover and the coefficient of variation of herb cover, while a positive correlation was found with herb cover and the coefficient of variation of shrub cover. Carabid species richness and diversity were correlated with several variables: positively with tree size variables and their coefficients of variation. Regarding the understory vegetation, similar results were found for carabid species richness and diversity (Table 2). Nevertheless, for carabid beetles, more significant correlations were found for species richness than for species

Table 2 Results for the Pearson's correlation analyses between the structural variables measured, their coefficients of variation (CV) and the two-first axes of the PCA, with the species richness (S) and diversity (H′) of the understory vegetation (plant species/m^2) and the edaphic carabid beetle fauna (total number of species collected per stand for the whole period), independently for the two forest types studied (oak and pine) and for all the data together

	Total				Oak				Pine			
	Plant S	Carabid S	Plant H′	Carabid H′	Plant S	Carabid S	Plant H′	Carabid H′	Plant S	Carabid S	Plant H′	Carabid H′
Tree height (m)	−0.19	0.00	−0.03	0.19	−0.02	0.25	0.35	0.09	0.04	0.14	0.23	0.35
Trunk perimeter (cm)	−0.08	0.28	0.08	**0.46***	0.10	**0.56***	0.37	**0.46***	0.10	0.37	0.30	**0.54***
Crown diameter (m)	0.18	**0.52***	**0.33***	**0.56***	0.15	**0.63***	**0.45***	**0.50***	0.06	0.38	0.24	**0.60***
Mean tree distance (m)	0.12	**0.51***	0.20	**0.57***	0.32	**0.71***	0.39	**0.61***	0.14	0.43	0.37	**0.61***
Shrub cover (%)	−0.28	**−0.50***	**−0.41***	−0.27	−0.14	**−0.69***	−0.37	**−0.55***	0.12	−0.03	−0.11	−0.02
Herb cover (%)	**0.66***	**0.65***	**0.74***	**0.43***	**0.62***	**0.61***	**0.76***	**0.47***	0.37	0.38	**0.58***	0.33
CV tree height	**0.33***	**0.32***	0.27	0.20	−0.01	−0.03	−0.24	−0.10	−0.25	0.22	−0.22	0.34
CV trunk perimeter	**0.56***	**0.59***	**0.57***	0.29	0.29	0.36	0.34	0.21	−0.35	0.37	−0.23	0.34
CV crown diameter	**0.49***	**0.55***	**0.49***	0.31	0.40	0.40	0.28	0.25	−0.24	0.33	−0.03	0.26
CV mean tree distance	0.26	0.13	0.23	0.19	−0.20	−0.38	**−0.54***	−0.06	−0.06	0.21	0.08	0.26
CV shrub cover	0.29	**0.64***	**0.34***	**0.43***	−0.05	**0.67***	0.08	**0.58***	0.08	0.14	0.10	0.17
CV herb cover	**−0.54***	**−0.40***	**−0.71***	−0.13	**−0.48***	**−0.47***	**−0.70***	−0.31	−0.37	−0.26	**−0.67***	−0.01
Axis I PCA	0.06	**0.42***	0.22	**0.47***	0.14	**0.67***	0.41	**0.54***	0.07	0.27	0.28	0.43
Axis II PCA	**0.53***	**0.58***	**0.51***	**0.32***	0.19	0.37	0.06	0.29	−0.29	0.31	−0.14	0.28

Marked correlations (* and bold face) are significant at $P < 0.05$

diversity. However, when the analyses were performed independently for oak forests and pine plantations, we obtained slightly different results (Table 2). In case of plants, both for oak and pine forest types, fewer statistically significant correlations were found, being the strongest ones for herb cover (positive) and its coefficient of variation (negative). In case of carabids, oak carabid beetle species richness and diversity were also significantly correlated with several variables: positively with trunk perimeter, crown diameter, the mean distance between trees and herb cover, and negatively with shrub cover and the coefficient of variation of herb cover. No significant correlations were detected in case of pine carabid beetle species richness, while diversity was significantly and positively correlated with tree size variables. The complex environmental gradient represented by the first axis of the PCA was significantly and positively correlated with the number of carabid species and diversity when we considered all the forest stands together and oak forests alone. The second axis of the PCA was significantly and positively correlated with plant and carabid species richness and diversity only when analysing all the forest stands.

Discussion and conclusions

In this study, we reported that both the forest structure and the identity of the dominant tree species were important factors determining biodiversity, although it was not possible to discriminate their individual effects. Other authors have previously pointed out that it is not always possible to relate great structural heterogeneity and high species richness (Neumann and Starlinger 2001; Montes et al. 2005). At the small-scale considered (1 m^2), species richness and diversity of the understory vegetation were less dependent on the tree size variables measured than on their variability, estimated as the coefficients of variation. However, the positive relation between plant species richness and diversity with the spatial heterogeneity may be more related to the dominant tree species than to the structure of the arboreal layer itself, as this relation was not so clear when analysing oak and pine forest stands separately. In case of carabid species richness and diversity, our results pointed out a similar influence of the tree size variables and their coefficients of variation when considering all forest stands together. Nevertheless, when analysing each type of forest separately, there was a higher correlation with the tree size variables than with the structural variability. There is no doubt that both the arboreal characteristics and the structural heterogeneity of the vegetation strongly affect carabid beetle species richness (Humphrey et al. 1999; Ings and Hartley 1999; Jukes et al. 2001; Brose 2003; Taboada et al. 2006b, 2008), and most studies have related the development of the canopy layer along the forest cycle with a decrease in carabid diversity (e.g. Niemelä et al. 1996; Humphrey et al. 1999). Regarding the understory vegetation, carabid species richness and diversity were positively correlated with herb cover and negatively with its coefficient of variation, although this general trend was not significant in case of the pine forest type. In general, high herb cover may impede carabid movement, but also benefit large and brachypterous carabid species that prefer densely vegetated sites to avoid predation (Brose 2003). We found that variability in herb cover development did not favour carabid species richness, so the effects of vegetation density on the beetles may be more complex (e.g. mediated by changes in the microenvironment) and, therefore, may also be species-specific (Thomas et al. 2006).

Although we found that there was clearly less species richness for both taxonomical groups in pine plantations than in oak forests, we cannot confirm if this was either due to the low heterogeneity (resulting from traditional reforestation methods) that characterises plantations or due to the influence of the tree species itself. Conifer plantations are often considered poor wildlife ecosystems with reduced structural heterogeneity compared to natural forests (Peterken 1996; Cannell 1999; Moore and Allen 1999), although they constitute new habitats for generalist or colonizer species (e.g. refuge or feeding areas for insects; Brockerhoff et al. 2005; Taboada et al. 2008). Moreover, we found a higher proportion of carabid forest specialist species in the pine forest type than in the oak one. Thus, in the study area pine plantations may provide secondary habitats for forest specialists inhabiting adjacent deciduous forests (see Bonham et al. 2002; Brockerhoff et al. 2005). However, several authors have found that carabid species richness decreased after the establishment of non-indigenous conifer species in natural deciduous tree areas, including oak forests (Butterfield et al. 1995; Fahy and Gormally 1998; Magura et al. 2002, see also Wiezik et al. 2007). Regarding carabid diversity, there were no significant differences between oak and pine forest types, probably because, generally, the carabid community structure obtained by pitfall trapping is characterised by a few very abundant species and a large number of rare ones (Niemelä 1993), independently of the forest type or structural condition. For plant diversity, Barbier et al. (2008) indicated that understory species richness is often higher under hardwoods than under conifers; however, they concluded that it is very difficult to make generalisations on the effects of tree species on understory diversity. Other authors pointed out that forest management influenced the ground flora more than tree species did (Augusto et al. 2003). Nevertheless, to a certain degree plantation biodiversity can be enriched by the application of alternative management practices to improve their homogeneous structure (Lust et al. 1998; Koivula 2002, see also Bonham et al. 2002). On the other hand, the natural pine forest was characterised by great structural variability, which was associated to high carabid species richness and diversity, but not in case of the vegetation. This can be due to the scale used for analysing vegetation in this study (1 m^2). Moora et al. (2007) found that forest management resulted in spatially more heterogeneous understory vegetation, but did not influence small-scale species richness.

According to our results, species richness was a better discriminator between forest types (oak and pine) for both taxonomical groups as compared with diversity. Besides, there was a clear correlation between plant and carabid species richness, but not in case of diversity. There is no consensus in the literature on the possible mechanisms that can be acting to support this positive relationship. For instance, it has been suggested that high vegetation species richness may increase food densities (prey and seeds) for the beetles favouring also great carabid species richness (Halme and Niemelä 1993), but other studies did not support this correlation (Koricheva et al. 2000). On the other hand, we can conclude that carabid beetles responded more clearly to the tree and understory characteristics than the vegetation at the small-scale considered here. Nevertheless, we also found that the vegetation can be more sensitive to the forest structural heterogeneity than carabid beetles. Therefore, at the small-spatial scale, our results suggest that the combination of the two taxonomical groups provided good information when assessing the effects of several tree species and the effects of changes in forest structure on biodiversity. Finally, it has been suggested that not only species richness or diversity but also other factors such as changes in species composition may be used as better indicators of the effects of human uses on biodiversity (Magurran 1989; du Bus de Warnaffe and Lebrun 2004; Onaindía et al. 2004). In fact, poorly diverse ecosystems, such as the natural pine forest of Lillo, can be relevant for conservation issues as they may host characteristic, geographically restricted, rare or endemic species.

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Appendix 1

See Table 3.

Table 3 Herbaceous and woody plant species sampled at the oak and pine forest types

	ODE	OMO	OMC	OSH	P10	P40	P80	PL
Herbaceous species								
Achillea millefolium	X	X	X	X		X	X	
Agrostis capillaris	X	X	X	X	X	X	X	X
Aira caryophyllea	X	X	X	X				X
Allium sp.	X							
Andryala integrifolia	X			X				
Anemone nemorosa		X			X			X
Anthemis arvensis	X							
Anthoxanthum odoratum	X	X	X	X				
Anthyllis vulneraria		X		X				
Arenaria montana	X	X	X	X	X	X	X	X
Arnoseris minima	X			X				
Arrhenatherum elatius subsp. *bulbosum*				X				
Asphodelus albus	X		X			X	X	X
Avenula marginata subsp. *sulcata*	X	X	X	X	X	X	X	X
Bellis perennis	X	X						
Biscutella laevigata				X				
Brachypodium pinnatum	X	X	X	X				
Brachypodium sylvaticum							X	
Briza media		X						
Bromus erectus	X			X				
Bromus hordeaceus subsp. *hordeaceus*	X							
Bromus sterilis	X							
Campanula rapunculus	X			X				
Carex divulsa	X							
Carex gr. *muricata*	X	X	X	X		X	X	X
Carex nigra			X	X				
Carex sylvatica				X				
Carlina vulgaris	X		X	X				
Catananche caerulea				X				
Caucalis platycarpos	X							
Centaurea cyanus	X	X	X	X				
Centaurea nigra		X					X	
Cerastium glomeratum	X			X				
Clinopodium vulgare	X	X	X	X				
Conopodium majus	X	X	X	X			X	X
Convolvulus arvensis			X					
Crepis lampsanoides		X						
Crepis vesicaria subsp. *haenseleri*	X							
Crucianella angustifolia	X			X				
Cruciata glabra	X	X	X	X		X	X	
Cynosurus echinatus	X			X				
Dactylis glomerata	X	X	X					
Danthonia decumbens		X						

Table 3 continued

	ODE	OMO	OMC	OSH	P10	P40	P80	PL
Daucus carota	X	X	X	X				
Deschampsia flexuosa	X	X			X	X	X	X
Digitalis parviflora			X	X				
Eleocharis palustres								X
Euphorbia amygdaloides	X	X		X				
Festuca paniculata				X				
Festuca rubra	X	X	X	X	X	X	X	
Filago lutescens	X							
Filago vulgaris	X							
Filipendula vulgaris				X				
Fragaria vesca		X				X		
Galium aparine	X	X	X	X		X	X	
Galium odoratum							X	
Galium saxatile								X
Galium verum	X	X	X	X				
Genciana lutea								X
Geranium pusillum	X							
Geranium sanguineum			X					
Geum sylvaticum	X	X	X	X				
Geum urbanum		X						
Helleborus foetidus		X	X					
Hepatica nobilis					X		X	
Herniaria glabra	X							
Hieracium castellanum	X							
Hieracium gr. *pilosella*	X	X	X	X	X			
Hieracium murorum		X	X			X	X	
Hippocrepis comosa	X	X	X	X				
Holcus lanatus			X					
Holcus mollis	X	X	X			X	X	
Hyacinthoides non-scripta		X	X					
Hypericum perforatum	X	X	X		X			
Hypochoeris radicata	X	X	X	X				
Jasione montana	X	X		X				X
Knautia arvensis		X	X	X				
Lathyrus niger		X	X					
Lathyrus sphaericus			X					
Leucanthemum vulgare			X	X				
Leuzea conifera				X				
Linaria triornithophora		X					X	
Linum suffruticosum				X				
Logfia minima	X		X					
Lolium perenne	X							
Lotus corniculatus	X	X	X	X			X	
Luzula campestris			X					
Luzula forsteri	X	X	X	X				X
Luzula lactea	X	X		X	X	X	X	X
Luzula multiflora						X		
Malva sylvestris	X							

Table 3 continued

	ODE	OMO	OMC	OSH	P10	P40	P80	PL
Melampyrum pratense		X	X	X			X	X
Melica uniflora		X						
Melittis melissophyllum		X	X					
Muscari comosum	X							
Ornithogalum umbellatum	X	X	X	X				
Petrorhagia prolifera	X							
Phleum pratense	X		X	X				
Physospermum cornubiense	X	X	X		X			
Pimpinella saxifraga	X	X	X	X				
Plantago holosteum				X				
Plantago lanceolata	X	X	X	X				
Polygala microphylla		X	X	X				
Potentilla erecta	X	X		X	X			X
Potentilla reptans	X				X			
Potentilla sterilis	X	X	X	X				
Primula vulgaris		X	X					
Prunella grandiflora	X	X	X	X	X			
Prunella laciniata	X							
Pteridium aquilinum		X	X				X	X
Ranunculus bulbosus	X	X			X			
Rumex gr. *acetosella*	X	X	X	X			X	X
Sanguisorba minor	X			X				
Saxifraga spathularis								X
Scilla verna							X	X
Scleranthus annuus	X							
Sedum album								X
Sedum forsteranum	X	X	X					
Senecio vulgaris	X							
Silene nutans	X	X	X	X		X		
Simethis planifolia				X				
Stachys officinalis	X	X	X	X				
Stellaria holostea	X	X	X				X	
Tanacetum corymbosum	X			X				
Teesdalia nudicaulis	X		X	X				
Teucrium scorodonia	X	X	X		X	X	X	
Thapsia villosa				X				
Thesium pyrenaicum		X		X	X		X	
Trifolium arvense	X							
Trifolium campestre	X	X	X					
Trifolium pratense	X	X	X	X				
Trisetum flavescens	X							
Tuberaria globularifolia	X							
Tuberaria guttata	X	X						
Valeriana tuberosa		X						
Veronica chamaedrys		X						
Veronica officinalis		X	X	X			X	
Vicia sativa subsp. *nigra*	X	X	X	X				
Vicia sepium		X						

Table 3 continued

	ODE	OMO	OMC	OSH	P10	P40	P80	PL
Viola riviniana	X	X	X	X	X	X	X	
Vulpia bromoides	X	X	X					
Woody species								
Adenocarpus complicatus		X						
Calluna vulgaris	X	X	X	X	X			X
Chamaespartium sagittale		X	X	X				
Chamaespartium tridentatum				X	X			
Corylus avellana		X						
Crataegus monogyna	X	X	X	X		X	X	
Cytisus scoparius		X	X			X	X	
Daboecia cantabrica					X			X
Erica arborea			X		X	X	X	X
Erica australis subsp. *aragonensis*			X		X	X		
Erica cinerea	X							
Erica tetralix				X				X
Erica umbellata	X	X		X				
Erica vagans		X						
Fraxinus excelsior						X	X	X
Genista florida subsp. *polygaliphylla*		X	X	X		X	X	
Genista micrantha	X		X	X	X			
Halimium alyssoides			X	X	X			
Halimium umbellatum	X		X	X	X			
Lavandula stoechas subsp. *pedunculata*				X				
Lithodora diffusa subsp. *diffusa*	X	X	X	X	X			
Lonicera periclymenum		X	X					
Pinus sylvestris					X		X	X
Prunus sp.		X	X					
Quercus pyrenaica	X	X	X	X		X	X	
Rosa sp.	X	X	X	X				
Rubus sp.		X	X			X	X	
Thymelaea ruizii	X			X				
Thymus serpyllum	X	X	X	X				
Thymus zygis				X				
Vaccinium myrtillus					X	X	X	X
Mean species number/m^2 stand 1	16	16	13	19	6	4	10	7
Mean species number/m^2 stand 2	19	17	12	9	6	2	8	11
Mean species number/m^2 stand 3	14	11	14	15	13	11	7	7
Mean species number/m^2 stand 4	14	9	14	11	11	6	9	7
Mean species number/m^2 stand 5	16	12	15	12	6	10	9	5

The mean number of species recorded per m^2 in each stand is also indicated. For abbreviations see text

Appendix 2

See Table 4.

Table 4 Carabid beetles collected at the oak and pine forest types

	ODE	OMO	OMC	OSH	P10	P40	P80	PL	W	H
Abax parallelepipedus parallelepipedus (Piller y Mitterpacher, 1783)		X							b	F
Amara (Amara) aenea (De Geer, 1774)	X							X	m	O
Amara (Amara) eurynota (Panzer, 1796)	X	X	X				X		m	O
Amara (Amara) famelica Zimmermann, 1832				X					m	O
Amara (Amara) familiaris (Duftschmid, 1812)	X		X						m	O
Amara (Amara) ovata (Fabricius, 1792)						X			m	O
Amara (Leironotus) glabrata Dejean, 1828		X		X					m	O
Amara (Percosia) equestris equestris (Duftschmid, 1812)				X					m	G
Anchomenidius astur (Sharp, 1873)								X	b	F
Badister (Badister) meridionalis Puel, 1925			X	X		X			m	G
Bembidion (Emphanes) normannum Dejean, 1831	X								m	O
Bembidion (Metallina) lampros (Herbst, 1784)		X							D	G
Bembidion (Phyla) tethys Netolitzky, 1926	X								m	G
Brachinus (Brachinoaptinus) bellicosus Dufour, 1820	X	X	X						b	O
Calathus (Calathus) fuscipes graecus Dejean, 1831	X	X	X	X			X		b	G
Calathus (Calathus) moralesi Nègre, 1966				X					b	F
Calathus (Calathus) uniseriatus Vuillefroy, 1866								X	b	O
Calathus (Neocalathus) asturiensis Vuillefroy, 1866					X				D	O
Calathus (Neocalathus) granatensis Vuillefroy, 1866	X	X	X	X			X		D	G
Calathus (Neocalathus) melanocephalus (Linnaeus, 1758)							X		D	O
Calathus (Neocalathus) mollis mollis (Marsham, 1802)	X								D	O
Calathus (Neocalathus) rotundicollis Dejean, 1828	X	X	X	X	X	X	X	X	D	F
Calosoma (Calosoma) inquisitor inquisitor (Linnaeus, 1758)	X	X	X						m	F
Carabus (Archicarabus) nemoralis prasinotinctus Heyden, 1880	X	X	X	X			X		b	G
Carabus (Chrysocarabus) lineatus lineatus Dejean, 1826		X		X	X	X	X	X	b	G
Carabus (Eucarabus) deyrollei Gory, 1839								X	b	G
Carabus (Mesocarabus) lusitanicus complanatus Dejean, 1826	X			X					b	F
Carabus (Mesocarabus) macrocephalus macrocephalus Dejean, 1826							X	X	b	G
Carabus (Oreocarabus) amplipennis getschmanni Lapouge, 1924	X	X	X	X	X	X	X	X	b	F
Cicindela (Cicindela) campestris campestris Linnaeus, 1758	X								m	O
Cryobius cantabricus cantabricus (Schaufuss, 1862)		X				X	X	X	b	G
Cychrus spinicollis spinicollis Dufour, 1857		X			X	X	X	X	b	F
Cymindis (Cymindis) coadunata kricheldorffi Puel, 1935					X				b	O
Cymindis (Menas) miliaris (Fabricius, 1801)					X				b	O
Dinodes (Dinodes) dives kricheldorffi (Wagner, 1932)	X								b	O
Dixus sphaerocephalus (Olivier, 1795)	X								m	G
Dromius (Dromius) agilis (Fabricius, 1787)		X						X	m	F
Harpalus (Harpalus) distinguendus distinguendus (Duftschmid, 1812)	X								m	G
Harpalus (Harpalus) ebeninus Heyden, 1870	X		X	X					m	O
Harpalus (Harpalus) latus (Linnaeus, 1758)				X				X	m	G
Harpalus (Harpalus) rubripes (Duftschmid, 1812)				X	X				m	O
Harpalus (Harpalus) rufipalpis rufipalpis Sturm, 1818	X				X			X	m	O
Harpalus (Harpalus) serripes serripes (Quensel, 1806)	X	X	X						m	G
Harpalus (Typsiharpalus) bonvouloiri Vuillefroy, 1866		X							m	G

Table 4 continued

	ODE	OMO	OMC	OSH	P10	P40	P80	PL	W	H
Laemostenus (Pristonychus) terricola terricola (Herbst, 1783)		X			X		X	X	b	F
Leistus (Leistus) barnevillei Chaudoir, 1867					X	X	X	X	b	F
Leistus (Leistus) nitidus (Duftschmid, 1812)								X	b	F
Leistus (Pogonophorus) spinibarbis spinibarbis (Fabricius, 1775)		X			X				m	F
Masoreus wetterhallii wetterhallii (Gyllenhal, 1813)	X		X	X					m	O
Microlestes corticalis (Dufour, 1820)	X								m	O
Microlestes negrita negrita Wollaston, 1854	X		X	X					D	O
Nebria (Nebria) asturiensis Bruneau de Miré, 1964		X				X		X	b	F
Nebria (Nebria) brevicollis (Fabricius, 1792)		X		X					m	G
Nebria (Nebria) salina Fairmaire and Laboulbène, 1856	X	X		X			X		m	O
Notiophilus biguttatus (Fabricius, 1779)	X	X	X	X		X	X	X	D	F
Ophonus (Hesperophonus) cribricollis (Dejean, 1829)	X								m	O
Ophonus (Metophonus) melletii (Heer, 1837)		X							m	O
Ophonus (Metophonus) rufibarbis (Fabricius, 1792)		X							m	O
Orthomus (Orthomus) hispanicus (Dejean, 1828)			X						b	O
Panagaeus bipustulatus (Fabricius, 1775)			X						m	O
Philorhizus notatus (Stephens, 1827)								X	D	O
Platyderus (Platyderus) quadricollis Chaudoir, 1866				X					b	F
Poecilus (Macropoecilus) kugelanni (Panzer, 1797)	X	X	X	X					m	O
Poecilus (Poecilus) versicolor (Sturm, 1824)				X					m	O
Pseudomasoreus canigoulensis (Fairmaire and Laboulbène, 1854)	X		X	X					m	F
Pseudoophonus (Pseudoophonus) rufipes (De Geer, 1774)	X								m	O
Pterostichus (Oreophilus) cantaber (Chaudoir, 1868)							X	X	b	F
Pterostichus (Phonias) strennus (Panzer, 1796)							X		b	G
Steropus (Sterocorax) globosus ebenus (Quensel, 1806)	X	X	X	X	X	X			b	G
Steropus (Steropidius) gallega (Fairmaire, 1859)	X	X	X	X	X	X	X	X	b	G
Syntomus foveatus (Geoffroy, 1785)	X				X				b	G
Syntomus obscuroguttatus (Duftschmid, 1812)							X		m	G
Synuchus vivalis vivalis (Illiger, 1798)	X	X	X	X					m	G
Trechus (Trechus) obtusus asturicus Jeannel, 1921	X	X	X					X	D	G
Trechus (Trechus) quadristriatus (Schrank, 1781)	X	X	X	X	X	X	X		m	G
Zabrus (Iberozabrus) silphoides asturiensis Heyden, 1880	X		X		X				b	O
Number of species stand 1	29	9	12	12	7	9	11	13		
Number of species stand 2	18	19	12	7	7	8	12	17		
Number of species stand 3	22	16	11	9	10	7	9	11		
Number of species stand 4	24	17	14	15	11	7	12	15		
Number of species stand 5	18	16	18	14	14	7	12	11		

For forest type abbreviations see text. Wings (W): wings morphology (*b* brachypterous, micropterous or flightless, i.e. unable to fly; *m* macropterous; *D* dimorphic). Habitat (H): habitat association of the species (*F* forest, *G* generalist, *O* open habitat species)

Literature used: Jeannel (1941–1942), Lindroth (1974), Vázquez (1990), Campos (2003), Ortuño and Marcos (2003) and Peláez (2004). The total number of species captured per stand is also indicated

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