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Relationship between vegetation diversity and soil functional diversity in native mixed-oak forests

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Abstract

Most studies on the interactions between aboveground vegetation and belowground soil diversity have been carried out in microcosms or manipulated field plots. In the current study, we investigated the relationship between forest vegetation diversity and soil functional diversity (calculated from the activity of soil enzymes) in naturally developed plant communities of native mixed-oak forests without imposing any disturbances to already existing plant–soil relationships. In order to do so, five different vegetation types, i.e., herbaceous plants, climbing plants, trees, shrubs, and ferns, were considered. Correlations between plant diversity, soil physicochemical properties, and soil enzyme activities were determined. Soil physicochemical parameters appeared strongly correlated with both enzyme activities (e.g., pH was positively correlated with amidase and arylsulphatase, and negatively with acid phosphatase; OM content was positively correlated with β-glucosidase, acid and alkaline phosphatase and urease, and negatively with amidase; total N was positively correlated with β-glucosidase, and acid and alkaline phosphatase, and negatively with amidase) and soil functional diversity. For ferns, strong correlations between enzyme activities and plant diversity indexes were found (i.e., dehydrogenase was positively correlated with species richness and Shannon's diversity; acid and alkaline phosphatase were negatively correlated with Shannon's diversity; acid phosphatase was also negatively correlated with species richness). Most interestingly, herbaceous plants and ferns showed a strong positive correlation between Shannon's plant diversity and soil functional diversity. Furthermore, herbaceous plants showed a strong positive correlation between species richness and soil functional diversity. Although these correlations between plant diversity and soil functional diversity might possibly be due to the fact that higher values of plant richness and diversity result in a greater habitat heterogeneity in the soil, current knowledge on the topic is mixed and very incomplete and, then, one must be extremely cautious when interpreting such correlations.

Keywords: Aboveground; Belowground; Functional diversity; Mixed-oak forest; Plant diversity; Soil enzymes

1. Introduction

Until recently, those scientists involved in the study of the vast diversity of organisms that live on Earth have had an almost exclusively aboveground focus, with little effort being put into characterizing and understanding the significance of belowground biodiversity (Wardle, 2002; Bardgett, 2005). But aboveground and belowground components of terrestrial ecosystems are closely related, with soil organisms being intimately linked to plant communities (Bardgett, 2005). Indeed, plants provide a source of C and other nutrients for the soil decomposer community in the form of plant litter and root exudates and, in turn, the soil biota, particularly its microbiota, decomposes soil organic matter, stabilizes soil structure and, through its essential role in the cycling of elements, releases nutrients for plant growth (Porazinska et al., 2003). In addition, although abiotic factors have traditionally been interpreted as the drivers of the vegetation patterns observed in terrestrial ecosystems, more recently, biotic interactions in the soil have also been reported as

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major drivers of the composition of plant communities (Hooper et al., 2000; Wardle, 2005). Therefore, in order to understand the complex patterns of biodiversity in terrestrial ecosystems and, above all, their relationship to ecosystem function, a combined aboveground–belowground approach is required.

Biodiversity in soil is extremely high, particularly at the microbial scale (Torsvik et al., 1994), and, additionally, there are a large number of trophically equivalent organisms. In this respect, it has been suggested that most species in soil must be functionally redundant (Bardgett, 2005; O'Donnell et al., 2005). For that reason, measurements of functional diversity in soil communities are likely to provide information more relevant to the functioning of soil than species diversity (Zak et al., 1994). Besides, belowground, for microorganisms, a species approach is not always practical since the traditional species concept is difficult to apply (Hooper et al., 2000). In this regard, soil enzyme measurements are very useful for the assessment of the status or the condition of the soil environment (Naseby and Lynch, 2002). Certainly, soil enzyme activities (i) control rates of nutrient cycling processes, (ii) are crucial to the availability of nutrients to both soil microbiota and plants, and (iii) can be valuable indicators of soil functional diversity (Bending et al., 2002; Naseby and Lynch, 2002). But soil functional diversity depends on numerous metabolic reactions and interactions of biota, and hence it is certainly unrealistic to assume that a simple relationship might exist between a single enzyme activity and soil functional diversity (Nannipieri et al., 2002). Consequently, it is always crucial to measure simultaneously a range of enzyme activities.

The most important problem in interpreting data of soil enzyme activities is to discriminate among many components contributing to the overall activity. After all, the activity of any particular enzyme depends on enzymes that can have different locations such as (i) in resting or dead cells, (ii) in cell debris, (iii) intracellularly in living cells, (iv) extracellularly in the soil solution, (v) absorbed by inorganic colloids and (vi) associated with humic molecules (Nannipieri et al., 2002). Although intracellular enzymes are present in plant, animal, and microbial cells, enzyme activities are usually determined after removal of visible animals and plant debris and on sieved soil samples under laboratory conditions. Accordingly, and since those enzymes that have been released from lysed cells are rapidly degraded by microorganisms, the most important intracellular enzymes of soil are probably those in living microbial cells (Nannipieri et al., 2002).

Finally, it has been reported that both plant species identity and diversity are major factors affecting the abundance and diversity of soil organisms (Johnson et al., 2003; Wardle, 2005). But the mechanisms through which plant composition and diversity affect soil communities and trophic levels in soil food webs remain essentially unexplored (Wardle et al., 2003). Furthermore, the few studies that have so far dealt with the interactions between vegetation structure and soil diversity have been restricted largely to a few ecosystem types and a few taxonomic groups of organisms within them (Bardgett, 2005). Most importantly, these studies on the interactions between aboveground and belowground communities have predominantly been carried out in microcosms or manipulated field plots (Porazinska et al., 2003; Van der Putten, 2005). To avoid the disturbances inherently associated with these two approaches, in the current study, the interactions between vegetation diversity and soil functional diversity have been investigated in naturally developed plant communities of native mixed-oak forests without imposing any disturbances to already existing plant–soil relationships.

The major objective of the current work was to study the relationship between vegetation diversity (species richness, diversity, evenness) and soil functional diversity (calculated from the activity of soil enzymes which have a key function in the cycling of C, N, P and S) in native mixed-oak forests. Additionally, correlations between soil physicochemical properties and plant community diversity or soil enzyme activities were determined.

2. Materials and methods

2.1. Study area

This study was carried out in the Urdaibai Biosphere Reserve (220 km^2) located in the north of the Iberian Peninsula (43°19′N, 02°40′W). Apart from the coastal landscape, within the Urdaibai Reserve, the potential vegetation in most of the territory consists of mixed-oak forests, dominated by *Quercus robur* L. with *Fraxinus excelsior* L. and *Castanea sativa* Miller (Onaindia et al., 2004). Throughout the 20th century, these native mixed-oak forests were heavily fragmented and, as a result, nowadays they only cover around 6% of the total area of the Urdaibai Reserve (Rodríguez-Loinaz et al., 2007). In fact, most of the area initially covered by those mixed-oak forests is now occupied by forest plantations (*Pinus radiata* and *Eucalyptus* sp.) together with grasslands and crops.

2.2. Analysis of vegetation samples

For this study, 23 different stands (average size: 12 ha) of native mixed-oak forest located at an altitude of 50–300 m above sea level, and distributed throughout the Urdaibai Reserve, were selected. In order to avoid a possible edge effect, square sampling plots (25 × 25 m^2) were demarcated approximately in the centre of each stand (i.e., one sampling plot per stand). In each sampling plot, five different smaller (2 × 1 m) sub-plots, 12 m apart from each other, were delimited according to the method of the species/area curve (Kent and Coker, 1992). In each of the 115 sub-plots (23 stands × 5 sub-plots per stand), plant species identification, according to Flora del País Vasco (Aizpuru et al., 2000), and percentage cover for each plant species, calculated through visual estimation, were

determined. Then, the following diversity indexes were calculated (Magurran, 2004): species richness (S), Shannon's diversity (H') and Shannon's evenness (J'). These three indexes were calculated for both (i) all the plant species present in the sampling plots considered as a whole and (ii) each of the five different growth forms here considered (i.e., herbaceous plants, climbing plants, trees, shrubs, and ferns).

2.3. Analysis of soil samples

After removing plant litter, soil samples were taken at the centre of each sub-plot (i.e., one core per sub-plot was taken from 0 to 15 cm depth using a 4.0 cm auger). The five soil samples corresponding to each sampling plot were pooled to get a composite sample. Since soil samples were taken 12 m apart from each other, the lack of spatial correlation between them was warranted (Boerner et al., 2005).

For soil chemical analysis, soils were air-dried at 30 °C for 48 h, sieved to <2 mm, and stored at room temperature. Soil pH was measured in the 1:2.5 (w v^{-1}) suspension of soil and water. Soil organic matter content, total N, C/N ratio, particle size distribution, exchangeable P (bicarbonate) and exchangeable K^+, Ca^{2+}, Mg^{2+} (ammonium nitrate) were determined following standard methods (MAPA, 1994). Table 1 summarizes the data obtained during the physicochemical characterization of the soils collected from the 23 studied stands.

For analysis of enzyme activities, soils were air-dried at 30 °C for 48 h, sieved to <2 mm and stored at 4 °C. Dehydrogenase, β-glucosidase, acid and alkaline phosphatase, and arylsulphatase activity were determined according to Dick et al. (1996) and Taylor et al. (2002). Urease and amidase activity were determined according to Kandeler and Gerber (1988) and Acosta-Martínez and Tabatabai (2000), respectively.

Dehydrogenase (EC 1.1) activity is an intracellular process that occurs in every viable microbial cell and is measured to determine overall microbiological activity of soil (Nannipieri et al., 2002). β-Glucosidase (EC 3.2.1.21), a glycosidase important in the C cycle, hydrolyses carbohydrates with a β-D-glycoside bond by splitting off the terminal β-D-glucose (Schinner et al., 1996) and then plays a central role in the hydrolysis of polymers of plant residues, such as cellobiose, releasing glucose as an important energy source for soil heterotrophic organisms. Phosphatases (alkaline: orthophosphoric monoester phosphohydrolase, EC 3.1.3.1; acid: orthophosphoric monoester phosphohydrolase, EC 3.1.3.2) are important in the P cycle because they provide P for plant uptake by releasing PO_4 from organic P (Eivazi and Tabatabai, 1977). Arylsulphatase (arylsulphatase sulphohydrolase, EC 3.1.6.1) is the enzyme that catalyses the hydrolysis of organic sulphate ester ($R^{\bullet}O^{\bullet}SO_3^{\bullet} + H_2O \rightarrow R^{\bullet}OH + H^+ + SO_4^{2-}$) releasing sulphate ($SO_4^{2-}$), the plant available form of S. Urease (urea amidohydrolase, EC 3.5.1.5) is an important enzyme in the N cycle that catalyses the hydrolysis of urea to CO_2 and NH_3 (Tabatabai and Bremner, 1972). Amidase (acylamide amidohydrolase, EC 3.5.1.4) is another important enzyme in the N cycle that releases phytoavailable NH_4^+ from linear amides by acting on C–N bonds other than peptide bonds (Frankenberger and Tabatabai, 1981).

For the determination of dehydrogenase activity, 1 g of soil (wet weight) was mixed with 0.4 ml of 100 mM Tris (hydroxymethyl) aminomethane buffer-THAM, pH 7.0, and 0.5 ml of iodonitrotetrazolium chloride-INT (0.5% w v^{-1}). The mixture was then incubated at 25 °C for 4 h and the reaction stopped with 8 ml of methanol. After centrifugation (1250g, 5 min), the absorbance value of the samples was read at 490 nm.

For β-glucosidase, acid and alkaline phosphatase, and arylsulphatase, 1 g of soil (dry weight) was mixed with 1.6 ml of buffer (i.e., 20 mM modified universal buffer-MUB, pH 6.0, for β-glucosidase; 20 mM MUB, pH 6.5, for acid phosphatase; 20 mM MUB, pH 11, for alkaline phosphatase; 500 mM acetate buffer, pH 5.8, for arylsulphatase) and 0.4 ml of substrate (i.e., 4-nitrophenyl-β-D-glucopyranoside (1.5% w v^{-1}) for β-glucosidase; 4-nitrophenyl phosphate disodium salt (1.85% w v^{-1}) for acid and alkaline phosphatase; potassium 4-nitrophenyl sulphate (1.3% w v^{-1}) for arylsulphatase). The mixture was incubated at 37 °C for 45 min and the reaction stopped with 0.4 ml of 500 mM $CaCl_2$ and 1.6 ml of 500 mM NaOH. After centrifugation (1250g, 5 min), the absorbance value of the samples was read at 410 nm.

For urease activity, 1 g of soil (dry weight) was mixed with 1.75 ml of 100 mM borate buffer (pH 10.0) and 0.25 ml of 820 mM urea. The mixture was then incubated at 37 °C for 1 h and the reaction stopped with 6 ml of acidified 2 M KCl. After centrifugation (1250g, 5 min), 0.25 ml of the supernatant fraction was mixed with 3.75 ml of distilled water and 2 ml of a reagent composed of a sodium salicylate/sodium nitroprusiate mixture (17% and 0.12% w v^{-1}, respectively), 0.3 M NaOH and distilled water (1:1:1

Table 1
Physicochemical properties of the 23 studied soils

	Mean ± SEM	Interval
pH	4.9 ± 0.1	4.1–5.6
Organic matter (%)	5.87 ± 0.35	3.25–10.14
Total N (%)	0.23 ± 0.01	0.15–0.37
C/N ratio	14.8 ± 0.3	11.8–17.5
Coarse sand (%)	9.2 ± 1.7	0.7–34.7
Fine sand (%)	34.2 ± 2.1	16.7–52.1
Silt (%)	27.2 ± 1.4	15.6–41.0
Clay (%)	29.4 ± 1.7	17.6–49.1
P (mg kg^{-1})	3.6 ± 0.3	2.0–6.0
K^+ (mg kg^{-1})	95 ± 5	54–166
Ca^{2+} (mg kg^{-1})	707 ± 124	160–1940
Mg^{2+} (mg kg^{-1})	231 ± 73	44–1241

Mean ± SEM ($n = 23$). Interval: maximum and minimum values.

v/v/v). Finally, 0.8 ml of sodium dichloroisocyanurate was added to the reaction mixture. After 30 min, the absorbance value of the samples was read at 670 nm.

For amidase activity, 1 g of soil (dry weight) was mixed with 1.5 ml of 100 mM THAM buffer, pH 8.0, and 0.5 ml of 8 mM L-leucine-β-naphthylamide. The mixture was then incubated at 37 °C for 45 min and the reaction stopped with 3 ml of 95% ethanol. After centrifugation (1250g, 5 min), the absorbance of the samples was read at 540 nm.

From the values of these seven enzyme activities, soil functional diversity was determined using the Shannon's diversity index ($H' = -\Sigma p_i \log_2 p_i$), as indicated by Bending et al. (2004), where p_i is the ratio of the activity of a particular enzyme to the sum of activities of all enzymes. Since the seven enzymes here tested did show activity in all the analysed samples, then, in this work, Shannon's diversity index reflects only the "evenness" or distribution of the enzyme activities (Bending et al., 2004). The order of magnitude of the values obtained for the different enzyme activities varied considerably depending on the specific activity being determined, thus leading to some enzyme activities having more weight than others during the calculation of the Shannon's diversity index. To resolve this problem, prior to the calculation of this index, a simple mathematical transformation was applied so that all enzyme activities had the same weight/relevance during such calculation, i.e. the value obtained for each enzyme activity was divided by the highest value found for that specific activity in the whole set of samples, and then multiplied by 100. In other words, for each enzyme activity, the percentage of the maximum value found for that specific activity in the whole set of samples was calculated.

2.4. Statistical analysis

Statistical analyses were performed using SPSS Programme (Inso Corporation, 1999). Pearson's correlations were calculated between soil physicochemical parameters, enzyme activities and vegetation data. When data did not adjust to a normal distribution, they were normalized using $\log_{10}$. When data could not be normalized, the Spearman's non-parametric correlation test was used.

3. Results

3.1. Vegetation structure

Table 2 shows the composition and percentage cover of those plant species found in the 23 stands of native mixed-oak forest here studied. Although altogether 110 different species of vascular plants were found in the studied stands, i.e., 53 herbaceous plants, 5 climbing plants, 18 trees, 23 shrubs, and 11 ferns, only those species appearing in at least more than one stand have been included in Table 2. At the time of sampling, gramineae were not flowered and then their identification was problematic. Consequently, all gramineae present in each sampling plot were identified

Table 2
Plant species composition and percentage cover (mean ± SEM; $n = 23$) of the plant species found in the 23 studied stands of native mixed-oak forest

Plant species	% Cover (Mean ± SEM)
Herbaceous plants	
Ajuga reptans L.	1.45 ± 0.44
Anemone nemorosa L.	0.45 ± 0.39
Angelica sylvestris L.	1.18 ± 0.89
Arum italicum Miller	0.24 ± 0.14
Cardamine pratensis L.	0.42 ± 0.34
Cardamine raphanifolia Pourret	0.25 ± 0.19
Carex pendula Hudson	0.82 ± 0.52
Cirsium sp.	0.09 ± 0.06
Eupatorium cannabinum L.	0.07 ± 0.06
Euphorbia amygdaloides L.	1.82 ± 0.84
Euphorbia dulcis L.	0.61 ± 0.44
Geranium robertianum L.	0.56 ± 0.24
Glechoma hederacea L.	0.33 ± 0.19
Helleborus viridis L.	0.12 ± 0.09
Hypericum pulchrum L.	0.34 ± 0.13
Lamiastrum galeobdolon (L.) Ehrend. & Polatschek	4.13 ± 1.79
Lathyrus linifolius (Reichard) Bässler	0.49 ± 0.16
Mercurialis perennis L.	0.07 ± 0.06
Oxalis acetosella L.	0.73 ± 0.45
Picris sp.	0.04 ± 0.03
Poaceae Barnhart (Gramineae Juss.)	42.36 ± 6.09
Potentilla erecta (L.) Raeuschel	1.01 ± 0.60
Potentilla sterilis (L.) Garcke	0.68 ± 0.33
Pulmonaria longifolia (Bast) Boreau	0.55 ± 0.38
Ranunculus tuberosus Lapeyr.	1.19 ± 0.50
Rubia peregrina L.	3.04 ± 0.99
Rumex sp.	0.19 ± 0.13
Saxifraga hirsuta L.	0.58 ± 0.41
Solidago virgaurea L.	0.82 ± 0.37
Stachys officinalis (L.) Trevisan	4.86 ± 1.44
Stellaria holostea L.	0.67 ± 0.51
Symphytum tuberosum L.	1.36 ± 0.63
Teucrium scorodonia L.	6.77 ± 1.84
Vicia sepium L.	0.97 ± 0.45
Viola riviniana Reichenb.	3.20 ± 0.99
Climbing plants	
Clematis vitalba L.	3.24 ± 3.09
Hedera helix L.	52.67 ± 5.42
Lonicera periclymenum L.	19.30 ± 3.04
Smilax aspera L.	20.62 ± 4.88
Tamus communis L.	4.84 ± 1.30
Trees	
Acer campestre L.	2.78 ± 1.61
Alnus glutinosa (L.) Gaertner	1.94 ± 1.52
Arbutus unedo L.	1.39 ± 0.79
Betula alba L.	3.42 ± 1.98
Castanea sativa Miller	24.70 ± 5.77
Fagus sylvatica L.	0.52 ± 0.43
Fraxinus excelsior L.	10.49 ± 3.07
Laurus nobilis L.	15.55 ± 7.39
Prunus avium L.	1.79 ± 0.91
Quercus ilex L.	2.18 ± 1.46
Quercus robur L.	98.11 ± 5.12
Salix atrocinerea Brot.	8.64 ± 3.65
Shrubs	
Calluna vulgaris (L.) Hull	0.79 ± 0.59
Cornus sanguinea L.	9.22 ± 3.40

Table 2 (*continued*)

Plant species	% Cover (Mean±SEM)
Corylus avellana L.	42.15±8.73
Crataegus monogyna Jacq.	3.14±1.74
Daboecia cantabrica (Hudson) C. Koch	1.13±0.51
Erica vagans L.	0.25±0.14
Euonymus europaeus L.	1.06±0.66
Frangula alnus Miller	2.65±0.97
Hypericum androsaemum L.	1.95±0.61
Ilex aquifolium L.	2.06±1.46
Ligustrum vulgare L.	1.97±1.68
Prunus spinosa L.	0.97±0.94
Rosa sp.	8.41±2.07
Rubus sp.	54.37±5.88
Ruscus aculeatus L.	3.70±1.48
Ulex sp.	1.39±0.65
Ferns	
Asplenium adiantum-nigrum L.	0.67±0.30
Asplenium scolopendrium L.	0.27±0.15
Athyrium filix-femina (L.) Roth	8.49±3.06
Blechnum spicant (L.) Roth	11.95±3.04
Dryopteris affinis (Lowe) Fraser-Jenkins	9.54±2.81
Dryopteris carthusiana (Vill.) H. P. Fuchs	0.15±0.12
Polystichum setiferum (Forsskål) Woynar	7.48±2.46
Pteridium aquilinum (L.) Kuhn	22.24±4.89

Only those species found in at least more than one stand have been included in this table.

only at the family level as Poaceae and quantified as one species. In any case, in our region, only two species of Poaceae (*Brachypodium sylvaticum* and *Bromus ramosus*) are usually found in this type of forests (Aseginolaza et al., 1988). Hence, the fact that gramineae were not identified to species level in this study should have only a minor effect on diversity values.

In relation to herbaceous plants, gramineae showed a value of percentage cover of 42.36%. *Hedera helix* (52.67% cover) was the most frequent climbing plant found in our study area. As expected, the most common tree species found were *Q. robur* (98.11% cover), *C. sativa* (24.70% cover), *Laurus nobilis* (15.55% cover) and *F. excelsior* (10.49% cover). In turn, the two most common shrubs were *Rubus* sp. (54.37% cover) and *Corylus avellana* (42.15% cover). Finally, the two dominant fern species were *Pteridium aquilinum* (22.24% cover) and *Blechnum spicant* (11.95% cover).

Table 3 shows the values of the different diversity indexes calculated for all the plant species considered as a whole and also according to growth forms (i.e., herbaceous plants, climbing plants, trees, shrubs, and ferns) in the 23 studied stands. The number of species per stand (S) ranged from 14 to 33. On average, there were 7.43, 3.17, 4.26, 5.52, and 3.43 species of herbaceous plants, climbing plants, trees, shrubs, and ferns, respectively, per stand. The highest

Table 3
Diversity indexes calculated for all the plant species considered as a whole (total) and also according to growth forms (i.e., herbaceous plants, climbing plants, trees, shrubs, and ferns) in the 23 studied stands of native mixed-oak forest

Growth form	S (Mean±SEM)	H' (Mean±SEM)	J' (Mean±SEM)
Herbaceous plants	7.43±0.82	1.76±0.17	0.64±0.03
Climbing plants	3.17±0.16	1.16±0.11	0.69±0.05
Trees	4.26±0.28	1.29±0.11	0.64±0.03
Shrubs	5.52±0.28	1.66±0.08	0.69±0.03
Ferns	3.43±0.39	1.28±0.15	0.80±0.03
Total	23.83±1.16	3.59±0.06	0.79±0.01

S: species richness; H': Shannon's diversity; J': Shannon's evenness.

mean values of S and H' corresponded to herbaceous plants. Finally, according to Shannon's evenness index, ferns were the plants more uniformly distributed.

3.2. Vegetation and soil physicochemical parameters

Table 4 shows the Pearson's correlation values obtained between some soil physicochemical parameters (pH, OM, total N, K^+, Ca^{2+}) and diversity indexes for all the plant species considered as a whole and also according to growth forms. Since no correlations were found between the other physicochemical properties here determined (i.e., C/N ratio, particle size distribution, and P and Mg^{2+} contents) and plant diversity indexes, their data have not been included in Table 4. Similarly, no significant correlations ($^*P<0.05$ or $^{**}P<0.01$) were found between soil physicochemical parameters and diversity indexes for climbing plants, trees or shrubs, and then their data have not been included either in Table 4. Although some significant correlations ($P<0.05$) were indeed found between physicochemical parameters and diversity indexes for all three categories included in Table 4 (all the plant species considered as a whole, ferns, and herbaceous plants), strong significant correlations ($P<0.01$) were only detected for herbaceous plants (a strong positive correlation between soil pH and both species richness and Shannon's diversity) and when all the plant species were considered as a whole (a strong positive correlation between soil pH and species richness). Ferns also showed a significant, though not strong, positive correlation between soil pH and species richness and Shannon's diversity. In addition, for ferns, a significant, though not strong, negative correlation was found between species richness and OM, total N and K^+ content (in turn, ferns also showed a significant, though not strong, negative correlation between Shannon's diversity and OM and total N content). There was a strong positive correlation between Ca^{2+} content and richness of herbaceous plants. Calcium content was also positively (not strongly) correlated with Shannon's diversity for herbaceous plants and with species richness when all the plant

Table 4
Pearson's correlations between soil physicochemical parameters and diversity indexes for all the plant species considered as a whole (total) and also according to growth forms (i.e., herbaceous plants and ferns)

	Total			Herbaceous plants			Ferns		
	S	*H′*	*J′*	*S*	H′	*J′*	*S*	H′	*J′*
pH									
R	0.732**	0.519*	−0.311	0.772**	0.672**	0.201	0.446*	0.419*	0.047
P	<0.001	0.011	0.148	0.000	0.000	0.370	0.033	0.046	0.839
OM (%)									
R	−0.451*	−0.469	−0.135	−0.256	−0.095	0.100	−0.479*	−0.522*	−0.321
P	0.031	0.024	0.538	0.238	0.667	0.659	0.021	0.011	0.157
Total N (%)									
R	−0.394	−0.409	−0.167	−0.217	−0.038	0.130	−0.427*	−0.466*	−0.235
P	0.063	0.053	0.446	0.321	0.863	0.564	0.042	0.025	0.305
K^+ (mg kg^{-1})									
R	−0.191	−0.203	−0.162	0.052	0.094	0.097	−0.415*	−0.300	−0.065
P	0.393	0.352	0.461	0.815	0.669	0.667	0.049	0.164	0.780
Ca^{2+} (mg kg^{-1})									
R	0.434*	0.336	−0.139	0.574**	0.419*	0.073	0.076	−0.004	−0.261
P	0.039	0.117	0.528	0.004	0.047	0.748	0.729	0.985	0.253

S: species richness; *H′*: Shannon's diversity; *J′*: Shannon's evenness. *R*: Pearson's coefficient of correlation; *P*: significance; $*P<0.05$; $**P<0.01$.

species were considered as a whole. Finally, a significant, not strong, correlation was found between soil pH and Shannon's diversity (positive) and between OM content and species richness (negative) when all the plant species were considered as a whole (Table 4).

3.3. Soil enzyme activities and physicochemical parameters

Table 5 shows the Pearson's correlation values obtained between some soil physicochemical parameters (pH, OM, total N, C/N ratio, and P, Ca^{2+} and Mg^{2+} contents) and soil enzyme activities and functional diversity (calculated through the application of Shannon's diversity index to the seven enzyme activities here determined). Since no correlations were found between the other soil physicochemical properties here determined (i.e., particle size distribution and K^+ content) and soil enzyme activities or functional diversity, their data have not been included in Table 5. Soil pH appeared strongly correlated with three enzyme activities (i.e., amidase and arylsulphatase were positively correlated with soil pH; acid phosphatase was negatively correlated with soil pH) and soil functional diversity. Similarly, soil OM content was strongly and positively correlated with β-glucosidase, acid and alkaline phosphatase, and urease, and negatively with amidase and functional diversity. Total N was also strongly and positively correlated with β-glucosidase, and acid and alkaline phosphatase, and negatively with amidase. C/N ratio was strongly and positively correlated with acid phosphatase (and also correlated, though not strongly, with β-glucosidase and alkaline phosphatase). A strong positive correlation was found between P content and β-glucosidase and alkaline phosphatase. Finally, Ca^{2+} and Mg^{2+} contents were strongly and positively correlated with amidase and arylsulphatase, respectively.

3.4. Soil enzyme activities and vegetation

Table 6 shows the Pearson's correlation values obtained between soil enzyme activities and diversity indexes for all the plant species considered as a whole and also according to growth forms (i.e., herbaceous plants and ferns). Again, no significant correlations ($*P<0.05$ or $**P<0.01$) were found between soil enzyme activities and diversity indexes for climbing plants, trees, or shrubs, and their data have not been included in Table 6. In the case of herbaceous plants, no strong significant correlations were found. By contrast, some strong significant correlations ($P<0.01$) were found between enzyme activities and diversity indexes for ferns (acid and alkaline phosphatase were negatively correlated with Shannon's diversity; dehydrogenase was positively correlated with species richness and Shannon's diversity; acid phosphatase was negatively correlated with species richness) and when all the plant species were considered as a whole (dehydrogenase activity was positively correlated with species richness; amidase was positively correlated with Shannon's diversity).

3.5. Soil functional diversity and vegetation

Table 7 shows the Pearson's correlation values obtained between soil functional diversity (calculated through the application of Shannon's diversity index to the seven enzyme activities here determined) and diversity indexes for all the plant species considered as a whole and also according to growth forms (i.e., herbaceous plants and

Table 5
Pearson's correlations between soil physicochemical parameters and soil enzyme activities and soil functional diversity (soil H')

	β-Glucosidase	Acid phosphatase	Alkaline phosphatase	Urease	Amidase	Dehydrogenase	Arylsulphatase	Soil H'
pH								
R	−0.030	−0.630**	−0.315	−0.075	0.577**	0.479*	0.553**	0.706**
P	0.890	0.001	0.143	0.735	0.004	0.021	0.006	0.000
OM (%)								
R	0.723**	0.762**	0.944**	0.532**	−0.670**	−0.300	−0.022	−0.570**
P	0.000	0.000	0.000	0.009	0.000	0.165	0.919	0.005
Total N (%)								
R	0.658**	0.647**	0.861**	0.464*	−0.584**	−0.308	0.063	−0.442*
P	0.001	0.001	0.000	0.026	0.003	0.153	0.776	0.035
C/N								
R	0.439*	0.530**	0.474*	0.334	−0.346	−0.105	−0.087	−0.386
P	0.036	0.009	0.022	0.120	0.106	0.634	0.693	0.069
P ($mg\,kg^{-1}$)								
R	0.620**	0.487*	0.705**	0.449*	−0.526*	−0.285	0.141	−0.323
P	0.002	0.018	0.000	0.032	0.010	0.188	0.521	0.133
Ca^{2+} ($mg\,kg^{-1}$)								
R	0.167	−0.417*	−0.126	−0.067	0.565**	0.098	0.504*	0.479*
P	0.446	0.048	0.565	0.760	0.005	0.658	0.014	0.021
Mg^{2+} ($mg\,kg^{-1}$)								
R	0.433*	−0.160	0.242	0.122	0.272	0.066	0.648**	0.396
P	0.039	0.465	0.265	0.581	0.209	0.767	0.001	0.062

R: Pearson's coefficient of correlation; *P*: significance; $*P<0.05$; $**P<0.01$.

Table 6
Pearson's correlations between soil enzyme activities and diversity indexes for all the plant species considered as a whole (total) and also according to growth forms (i.e., herbaceous plants and ferns)

	Total			Herbaceous plants			Ferns		
	S	H'	J'	S	H'	J'	*S*	H'	J'
β-Glucosidase									
R	−0.047	0.068	0.117	0.140	0.143	0.138	−0.406	−0.463*	−0.363
P	0.831	0.758	0.594	0.523	0.515	0.539	0.054	0.026	0.106
Acid phosphatase									
R	−0.487*	−0.377	0.058	−0.453*	−0.392	−0.266	−0.594**	−0.587**	−0.113
P	0.019	0.076	0.793	0.030	0.064	0.232	0.003	0.003	0.627
Alkaline phosphatase									
R	−0.324	−0.347	−0.141	−0.125	0.049	0.165	−0.492*	−0.534**	−0.374
P	0.131	0.105	0.522	0.570	0.826	0.464	0.017	0.009	0.095
Urease									
R	−0.012	−0.025	−0.113	0.006	−0.008	−0.115	−0.215	−0.239	−0.230
P	0.956	0.911	0.607	0.979	0.971	0.611	0.325	0.272	0.316
Amidase									
R	0.471*	0.606**	0.353	0.388	0.282	0.249	0.400	0.392	0.160
P	0.023	0.002	0.098	0.068	0.192	0.264	0.059	0.064	0.490
Dehydrogenase									
R	0.592**	0.325	−0.295	0.500*	0.431*	0.183	0.635**	0.628**	0.169
P	0.003	0.130	0.172	0.015	0.040	0.414	0.001	0.001	0.463
Arylsulphatase									
R	0.387	0.435*	0.100	0.441*	0.493*	0.449*	0.237	0.282	−0.061
P	0.068	0.038	0.649	0.035	0.017	0.036	0.276	0.193	0.794

S: species richness; H': Shannon's diversity; J': Shannon's evenness. *R*: Pearson's coefficient of correlation; *P*: significance; $*P<0.05$; $**P<0.01$.

Table 7
Pearson's correlations between soil functional diversity (soil H') and diversity indexes for all the plant species considered as a whole (total) and also according to growth forms (i.e., herbaceous plants and ferns)

	Total			Herbaceous plants			Ferns		
	S	*H′*	*J′*	*S*	*H′*	*J′*	*S*	*H′*	*J′*
Soil *H′*									
R	0.589**	0.630**	0.116	0.560**	0.545**	0.373	0.470*	0.554**	0.113
P	0.003	0.001	0.597	0.005	0.007	0.087	0.023	0.006	0.625

S: species richness; H': Shannon's diversity; J': Shannon's evenness. *R*: Pearson's coefficient of correlation; *P*: significance; $*P<0.05$; $**P<0.01$.

ferns). As above, no significant correlations ($*P<0.05$ or $**P<0.01$) were found between soil functional diversity and diversity indexes for climbing plants, trees or shrubs, and therefore their data have not been included in Table 7. Most interestingly, strong correlations were found between plant Shannon's diversity and soil functional diversity for all three categories (all the plant species considered as a whole, herbaceous plants, ferns). There was also a strong correlation between plant species richness and soil functional diversity for herbaceous plants and when all the plant species were considered as a whole. Finally, soil functional diversity was positively correlated, though not strongly, with ferns species richness.

4. Discussion

4.1. Vegetation structure

The specific plant species found in a forest have been reported to be good indicators of its conservation condition as well as of the effect of disturbances and management practices on such conservation (Ferris-Kaan et al., 1998; Kneeshaw et al., 2000). In the current study, most of the plant species found in the studied stands are characteristic of Atlantic mixed-oak forests (Aseginolaza et al., 1988; Aizpuru et al., 2000). Moreover, some of the species observed in the undergrowth, e.g. *Lamiastrum galeobdolon* and *Dryopteris affinis*, due to their having a small seed bank and being then difficult to maintain after certain management practices such as clear-cutting of undergrowth (Amezaga and Onaindia, 1997), can be considered good indicators of the degree of organization and naturalness of this kind of forests. In consequence, the stands here studied appear to be in a good condition of conservation and are thus suitable representatives of a mixed-oak forest ecosystem.

4.2. Vegetation and soil physicochemical parameters

In this study, for herbaceous plants, strong correlations ($P<0.01$) were found between soil physicochemical parameters and plant diversity (e.g., soil pH and Shannon's diversity). Ferns showed several positive and negative, not strong ($P<0.05$), correlations between soil physicochemical parameters and plant diversity. For the other three growth forms (climbing plants, trees and shrubs), no similar correlations were found. This is most likely due to ferns and herbaceous plants having their root systems within the area of the soil sampled in this study (upper 0–15 cm). After all, soil physicochemical and biological properties are known to change with soil depth (Agnelli et al., 2004). Trees, shrubs, and climbing plants have usually deeper root systems than ferns and herbaceous plants and, since plants are affected by the characteristics of the soil around their roots, then the lack of correlations between soil physicochemical parameters and plant diversity indexes for these three growth forms is not surprising.

Regarding pH, many authors have also reported higher values of plant diversity at higher soil pH values (Pärtel et al., 2004; Lenière and Houle, 2006). In addition, soil pH is known to affect many enzyme activities involved in the mineralization of essential nutrients such as N, S and P (Tabatabai and Bremner, 1970, 1972; Acosta-Martínez and Tabatabai, 2004). Finally, the fact that, in herbaceous plants, similar correlations were found between plant diversity indexes and both soil pH and Ca^{2+} content, is most likely due to the positive correlation between pH and Ca^{2+} usually found in soil.

4.3. Soil enzyme activities and physicochemical parameters

Soil physicochemical properties, such as pH, OM content, total N, texture, etc. have been reported to affect soil enzyme activities (Acosta-Martínez and Tabatabai, 2000). In our study, soil pH, OM content, total N, C/N ratio, and P, Ca^{2+} and Mg^{2+} content have shown strong significant correlations with some enzyme activities and, most importantly, with the soil functional diversity calculated from those enzyme activities.

pH is indeed a very important soil property that affects, among other parameters, the diversity and composition of the soil microbial community (Bardgett, 2005). In turn, soil pH has been reported to affect the activity of soil enzymes through different mechanisms. Ionization or protonation of the acidic or basic groups in the enzyme active centre is thought to account for most of the decrease in enzyme activity observed when pH deviates from optimum (Wang et al., 2006). Similarly, soil pH can alter the concentration

of inhibitors, activators, and substrates (Wang et al., 2006). In agricultural soils, Acosta-Martínez and Tabatabai (2000) found the same correlations between soil pH and acid phosphatase and arylsulphatase here observed. Nonetheless, these authors also found a positive correlation between soil pH and β-glucosidase and alkaline phosphatase. Dick et al. (2000) and Wang et al. (2006) also found a negative correlation between pH and acid phosphatase. On the other hand, others authors reported a positive correlation between acid phosphatase and soil pH (Hinojosa et al., 2004; Klose et al., 2004). Many authors have also described a positive correlation between arylsulphatase and soil pH (Hinojosa et al., 2004; Klose et al., 2004; Wang et al., 2006).

In addition, we found positive correlations between OM content and β-glucosidase, acid and alkaline phosphatase, and urease. Many studies have formerly described positive correlations between β-glucosidase, arylsulphatase, phosphatase, amidase, urease, etc. with organic C (Frankenberger and Tabatabai, 1981; Dick et al., 1988; Eivazi and Tabatabai, 1990; Deng and Tabatabai, 1997; Šantrůčková et al., 2004). Turner et al. (2002) determined β-glucosidase activity over a range of soils with different C contents and found a positive correlation between this activity and total C content. OM content and C content are correlated and then the results of Turner et al. (2002) also agree with our data. In agreement with our results, Dick et al. (1988) also found a positive correlation between β-glucosidase and total N content. The strong positive correlation found in our study between β-glucosidase and both OM content and total N is not surprising, as soil organic C and N content in soils have been reported to be correlated themselves (Acosta-Martínez and Tabatabai, 2001).

On the contrary, the negative strong correlations here reported between amidase and both OM content and total N are somewhat unusual. Sowerby et al. (2005) found a remarkable inverse exponential relationship between soil OM and β-glucosidase, sulphatase, phosphatase, and leucine amino peptidase. These authors suggested that this inverse relationship could be due to the inhibition of phenol oxidase in anoxic conditions (part of their study was carried out in Wales where soils receive heavy rainfall and commonly experience water-logged anoxic conditions). Indeed, phenolic compounds are thought to inhibit soil enzyme activities and, in general terms, are found in greater quantities in soils with higher levels of OM (Sowerby et al., 2005). But, in our case, only one enzyme (amidase) showed a negative correlation with soil OM (besides, four different enzymes showed a strong positive correlation with OM content). Therefore, further work is needed to explain the nature of this negative relationships between amidase and OM content and total N.

The positive correlations here found between phosphatases and P content are unexpected since increased available (soluble) inorganic phosphate is known to decrease soil phosphatase activity (Tabatabai, 1982). In this respect, Naseby et al. (1998) found the activities of enzymes from the P cycle (acid phosphatase, alkaline phosphatase, and phosphodiesterase) to be negatively correlated with the amount of readily available P.

Regarding the correlations found between physicochemical parameters and soil functional diversity (i.e., strong positive for pH, strong negative for OM content, negative for total N, positive for Ca^{2+}), firstly, it is important to emphasize that, as above mentioned, although Shannon's diversity values (H') usually account for both species richness and evenness, in this work, our H' values for soil functional diversity reflect only "evenness". Soil is a very biodiverse, complex environment that (i) shows an inherent degree of fluctuation, (ii) has several trophic levels, (iii) an overwhelming number of different species, and (iv) also exhibits a high level of functional redundancy. As a consequence, it is always difficult to interpret correlations such as those here described.

4.4. Interactions between aboveground vegetation and belowground enzymes and functional diversity

Aboveground and belowground components of terrestrial ecosystems are implicitly dependent on each other (Porazinska et al., 2003). For instance, the loss of plant species in a certain ecosystem can lead to changes in the community of soil decomposers which, in turn, affects the mineralization of OM with consequences for other ecosystem processes (Spehn et al., 2000). Lately, an increasing number of reports are appearing in the literature on the relationship between vegetation structure and the activity and diversity of soil biota (Johnson et al., 2003; Porazinska et al., 2003; De Deyn et al., 2004; Salamon et al., 2004). Although, occasionally, positive and negative correlations have been found between aboveground and belowground components of terrestrial ecosystems, these correlations do not necessarily imply mechanistic linkages, but they are a first, fundamental step in assessing whether such linkages exist (Hooper et al., 2000).

The positive correlation here found between dehydrogenase and diversity indexes for ferns (strong) and herbaceous plants (not strong) could be due to the possibility that a higher plant diversity might have led to higher values of plant productivity, resulting in higher amounts of organic C entering the soil system. Although the relationship between plant species diversity and plant productivity is still controversial, there are many works in the literature reporting a higher productivity in species-rich than in species-poor plant communities (Tilman and Downing, 1994; Naeem et al., 1996; Tilman et al., 1996, 1997).

Ferns showed a strong negative correlation between acid phosphatase and S and H'. This negative correlation could be explained by the fact that, under favourable conditions (such as P sufficiency), plant communities regulated by competition are thought to have a lower biodiversity owing to competitive exclusion.

Most importantly, we have found a strong positive relationship between soil functional diversity and the diversity of ferns and herbaceous plants. The lack of correlations for the other three growth forms (climbing plants, trees, and shrubs) is again most likely due to our sampling procedure (see above). Although, in our study, the H' values for soil functional diversity reflect only evenness, interestingly enough, we have not found any correlations between plant evenness and soil functional diversity.

Stephan et al. (2000) found a positive correlation between plant diversity and soil microbial functional diversity in grasslands. These authors concluded that the increase in the amount and diversity of resources that entered the soil was responsible for the higher values of soil microbial functional diversity. Similarly, Benizri and Amiaud (2005) found a positive correlation between plant diversity and soil microbial functional diversity, inferring that it was probably due to differences in the composition of the rhizosphere between plant species and also between different phenological stages within the same species.

Much further research is still needed to unravel the linkages that might exist between aboveground vegetation structure and belowground soil functional diversity. The understanding of the linkages between biodiversity aboveground and belowground may provide crucial information for the conservation of the soil ecosystem and the functions and services it freely bestows to humanity. After all, those linkages might be essential for the sustainable functioning of terrestrial ecosystem processes.

We conclude that there are strong positive and negative correlations between (i) soil physicochemical parameters and vegetation diversity, (ii) soil physicochemical properties and soil enzyme activities, (iii) soil physicochemical properties and soil functional diversity, (iv) vegetation diversity and soil enzyme activities, and, most importantly, (v) vegetation diversity and soil functional diversity. Although these correlations between vegetation diversity and soil functional diversity might possibly be due to the fact that higher values of plant richness and diversity result in a greater habitat heterogeneity in the soil, current knowledge on the topic is mixed and very incomplete and, then, one must be extremely cautious when interpreting such correlations. Certainly, much further research is still needed to understand the linkages that exist between aboveground vegetation and belowground soil communities.

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