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At which spatial scale are plant species composition and diversity affected in beech forests?

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Abstract

· ***Context*** Landscape structure is crucial for forest conservation in regions where the natural forest is fragmented. Practical conservation is currently shifting from local stands to a landscape perspective, although few studies have tested the relative effects of different spatial scales on plant species composition and diversity in forests.

· ***Methods*** We studied vascular plants and 17 predictor variables related to landscape (i.e. patch size or the surrounding landscape matrix) and stand conditions (i.e. soil pH and stand structure) in 50 semi-natural beech (*Fagus sylvatica* L.) forests in the northern Iberian Peninsula.

· ***Aims*** We analysed the effect of landscape heterogeneity and stand-associated environmental conditions on plant species composition and diversity. Moreover, we studied the influence of these scales on the diversity of different life forms.

· ***Results*** Plant species composition and diversity responded primarily to suitable habitat proportions in the surrounding landscape and secondarily to soil pH. The response to these factors differed among life forms. Species diversity, especially tree and shrub diversity, increased with increases in the proportion of ecologically similar habitat in the surrounding landscape (forests dominated by *Quercus* spp.). Species diversity (primarily herb diversity) also increased with increasing soil pH.

· ***Conclusion*** Future landscape management should seek to produce a heterogeneous matrix comprising patches of natural, unmanaged and managed deciduous forest and including other traditional uses and forest plantations.

Keywords Life forms · Management · pH · Richness · Shannon diversity · Surrounding landscape

1 Introduction

One of the most important contemporary environmental problems is the loss of biodiversity owing to land-use changes. These changes have caused drastic fragmentation of the landscape, thereby affecting ecosystem functions and biodiversity. Therefore, an improved understanding of the drivers of local diversity is of practical interest and is needed for the conservation and maintenance of natural and anthropogenic ecosystems (Dufour et al. 2006). In regions where the natural forest is fragmented, the landscape structure is crucial for forest conservation (Lindenmayer and Franklin 2002). Therefore, the focus of conservation is currently shifting from local stands as the main units of conservation to a broader landscape perspective. However, few previous studies have addressed the relative effects of different spatial scales on species composition and diversity in forests.

In temperate forests, different studies have demonstrated that stand-associated environmental conditions, the intensity of disturbance, or the type of management affect local species diversity (Graae and Heskjaer 1997), but the composition of forest plant communities may vary locally due to historical heritage, dispersal limitation (Aparicio et al. 2008), biotic interactions, and landscape features (Dufour et al. 2006). However, at which scales (landscape heterogeneity or stand-associated environmental conditions) are both the plant

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species composition and diversity most affected? Moreover, life forms have different structures and functions in the ecosystem. Thus, site or landscape-level conditions might affect them in diverse ways.

Since the 1960s, European rural areas have suffered strong ecological and socioeconomic changes (Agnoletti 2007). These changes have altered the functionality of many rural landscapes. In the Basque Country (northern Iberian Peninsula), the landscape has been severely modified. Currently, forest plantations (mainly the exotic *Pinus radiata* and *Eucalyptus* spp.) and grasslands occupy most of the potential forest area (Onaindia et al. 2004). Given that 53% of the surface is covered by forest ecosystems, the replacement of natural forest by rapidly growing evergreen tree species managed with environmentally more aggressive methods is decreasing forest biodiversity (Amezaga and Onaindia 1997). However, patches of native forests, such as beech (*Fagus sylvatica* L.) forests, remain well conserved in some areas. Traditionally, these beech forests were used for timber, firewood, and charcoal extraction, but these uses have been progressively abandoned. Today, these forests are conserved, and they are surrounded by a changing matrix.

Accordingly, the aims of the current study were to: (1) analyse the patterns of plant species cover and diversity distribution in beech forests in relation to stand and landscape matrix parameters; (2) analyse the effects of these spatial scales on different life forms; and (3) suggest some criteria for sustainable management and conservation planning.

2 Materials and methods

2.1 Study site

This study was conducted in the Basque Country of the northern Iberian Peninsula (42°78′ N, 02°44′ W). Moderately warm summers and mild winters characterise the climatic conditions. The long-term annual mean precipitation and temperature are 1,100 mm and 13°C, respectively. The bedrock up to 900 m altitude consists of limestone and sandstone; however, loam soils emerge in the middle altitudes. The territory is dominated by plantations of *P. radiata* and *Eucalyptus* spp. and native forests, including oak (*Quercus robur, Quercus pyrenaica, Quercus faginea, Quercus coccifera*, and *Quercus ilex*) and beech (*F. sylvatica*) forests, with pastures and crops (Onaindia et al. 2004).

2.2 Sampling design

We randomly selected 50 beech patches according to different patch size, climatic and soil conditions (Appendix A), using the cartography of the National Forest Inventory (Gobierno Vasco 1997) and digital orthophotos (from 2001 with a resolution of 1 m). In each patch, the sampling plot was selected in areas with a cover of *F. sylvatica* approaching 90% and without perturbations (e.g. paths, tracks, and streams). Moreover, to avoid a possible edge effect, the sampling plots were selected at least 100 m from the edge. In the largest patches, four plots were established several kilometres apart to avoid possible spatial correlation. In each plot, nine sub-plots of 5×2 m were established (Brower and Zar 1979), one in the centre and the other eight separated by 5-m intervals. These sub-plots formed a cross with one arm running parallel to the slope and the other arm perpendicular to the slope.

2.3 Plant species sampling

All vascular plant species were identified at the species level according to Aizpuru et al. (2000), and the percentage of soil covered by the visual projection of each species in five vertical layers (0–20 cm, 20 cm–1 m, 1–3 m, 3–7 m, and >7 m) was estimated in each sub-plot (Lindgren and Sullivan 2001). Unidentified grasses were quantified as one group (other graminoids). Species were then classified into four groups according to their life forms (trees, shrubs, herbs, and ferns) (Bhattarai and Vetaas 2003; Rodríguez-Loinaz et al. 2008) (Appendix B). For all species and for the different life forms considered in this study, the following diversity indices were calculated: the Shannon–Wiener diversity index H' ($H'=-\sum(\mathrm{pi})(\log_2 \mathrm{pi})$, where pi= percentage cover), Pielou's evenness J' ($J'=H'/H'_{\max}$; $H'_{\max}=\log_2(S)$, where S=species richness), and S (Magurran 2004). Simpson's measures of evenness and diversity were also calculated, but they were not used in further analysis because they were highly correlated with H' and J' ($P<0.001$).

2.4 Landscape and environmental data

In each plot, the following environmental factors that might influence plant distribution were surveyed: the elevation in the centre of the sample plot (as determined by GPS); the slope in the corners and in the centre of the transect running parallel with the slope (measured with a clinometer) to obtain an averaged measure and control of the variability inside the plot; and the annual mean precipitation (high-resolution interpolated raster map). In addition, in five of the sub-plots, a soil sample from the upper 15 cm was collected with a core after removal of the litter layer. Later, in the laboratory, the soil samples were sifted with 2-mm mesh, and the pH was determined in a water solution with a pH metre. Moreover, at three points of the transect running parallel with the slope (Brower and Zar 1979), living trees and shrubs with a stem diameter at breast height (DBH) greater than 5 cm were sampled (species, perimeter at breast height, and height). These trees and shrubs were selected using the point-centred quarter method. The following indices were calculated: average DBH, average height, tree density per hectare, and basal area per hectare. Light conditions were estimated using ten systematic photosynthetically active radiation measurements per plot to calculate the average relative irradiance in each plot (Augusto et al. 2003) ($\%I=(I$ under vegetation sunlight/I open sunlight$)\times 100$).

We defined the landscape matrix surrounding the sampling plot as the vegetation patches in contact with the sampling plot within a circular buffer of 1 km in diameter. These buffers were created from the plot centroid and calculated using GIS ArcInfo software (ESRI 2001). In these patches, we estimated the percentage cover of the different land uses, land-use diversity (Shannon–Wiener diversity index H' ($H'=-\sum(\text{pi})(\log\ \text{pi})$)), and land-use richness (Krauss et al. 2004). Land uses were classified into five categories: forests dominated by *Quercus* spp., beech forests, plantations, riverside or riparian forests, and non-forest ecosystems (i.e. crops or grasslands). Furthermore, we calculated patch size, shape, and the nearest neighbour distance (NND) to similar habitats for each patch using the extension vLATE in the ArcInfo software.

2.5 Statistical analysis

The data on the mean cover of each species in each plot were examined with a principal component analysis (PCA) after transformation of the data using the chi-square metric (Legendre and Gallagher 2001). Species found in fewer than four plots (frequency<8%) were removed from the PCA analysis (Singleton et al. 2001; Fontaine et al. 2007) because they exhibited a relatively low amount of mean cover compared with the other species analysed and introduced random noise into the analysis. Plant species data, coded as in Appendix B, were projected onto bi-plots of factorial axes (using untransformed data). We selected PCA because of its superiority in decreasing the number of dimensions of large data sets (Kenkel 2006; Lalanne et al. 2010). To facilitate the ecological interpretation of floristic gradients obtained in the PCA, the PCA axes were correlated with landscape (patch size, percentage cover of the different land uses, and land-use diversity) and stand (pH, slope, DBH, and relative irradiance) factors using Spearman's correlations. However, the explanatory factors that were intercorrelated (Pearson's correlation coefficient; patch shape, NND, precipitation, and elevation) were excluded from the analysis to avoid data redundancy. Patch shape and NND were correlated with patch size ($r=0.863$, $P<0.001$ and $r=-0.610$, $P<0.01$, respectively). Precipitation was correlated with soil pH ($r=-0.452$, $P\leq 0.001$), and elevation was correlated with landscape parameters (% *Quercus* around and land-use diversity ($r=-0.301$, $P<0.05$ and $r=0.351$, $P\leq 0.01$, respectively)). It is probable that the former relationship is produced by high precipitation that rapidly washes nutrients out of the topsoil and causes acidification. The correlation between elevation and landscape parameters reflects an altitudinal gradient. The optimal altitude range of *Quercus* spp. forests in the Basque Country extends to 600 m. Beech forests, plantations and pastures dominate the remaining area and increase the land-use diversity.

Diversity measures were analysed using a general linear model (GLM) to identify the ecological variables that explained total species diversity and the diversity of the different life forms. Ferns were not considered because the data could not be normalised.

The factors that explained the main trends in the distribution of species composition and diversity were determined as indicated above. A Mann–Whitney U test (for species composition) and t test (for diversity indices) were then used to compare the species cover of the different types of beech forests identified. Data that did not follow a normal distribution were transformed using an appropriate method ($\log_{10}$, arcsine α, $\sqrt{y}$, e^x). All statistical analyses were performed with SPSS (Inso Corporation 2005).

3 Results

3.1 Plant species composition: effect of landscape and stand conditions

A total of 138 species were recorded in the beech forests studied, including 18 trees, 25 shrubs (three climbing plants: *Hedera helix*, *Lonicera periclymenum,* and *Tamus communis*), 84 herbs, and 11 ferns (Appendix B). The most common and abundant species were the herbs *Viola riviniana*, *Deschampsia flexuosa*, *Euphorbia dulcis,* and other graminoids; the shrubs *Rubus* spp., *H. helix,* and *Crataegus monogyna*; the trees *Acer campestre*, *Q. robur*, and *Fraxinus excelsior* (apart from *F. sylvatica*); and the fern *Pteridium aquilinum* (Appendix B).

The PCA for plant species showed that the first component (axis 1) extracted 16.2% of the total variance and the second component (axis 2) 9.5%. Axis 1 was influenced by the landscape matrix because it was significantly and positively correlated with the percentage cover of forests dominated by *Quercus* spp. that surrounded the sample plot ($r=0.367$, $P<0.01$). In contrast, axis 2 was influenced by stand fertility because it showed a significant positive correlation with pH ($r=0.694$, $P<0.001$).

The projection of plant species in the plane of the first two components of the PCA showed three groups of species (Fig. 1). On the right of axis 1, as mentioned above, were clustered the species whose distribution was relatively more influenced by a higher percentage cover of forests dominated by *Quercus* spp. that surrounded the sample plot. These species had a higher cover in these beech forests and primarily included trees and shrubs, including *A. campestre*, *Q. robur*, *Quercus faginea*, *Cornus sanguinea*, *Crataegus laevigata*, *C. monogyna*, *Prunus spinosa*, *Ruscus aculeatus*, *Rosa* spp. or *Rubus* spp. Some herbs, such as *E. dulcis*, *Lathyrus linifolius*, *Potentilla erecta*, *Potentilla sterilis* and *Stachys officinalis,* and the fern *P. aquilinum* also appeared. The forest that contained these species presented a high structural diversity, with several layers formed by species such as *Q. robur*, *Q. faginea, C. monogyna,* and *P. spinosa.* These beech forests were designated as "multi-layered beech forests". However, the species whose distribution was affected less by the landscape matrix and more by stand scale, i.e. by soil pH, were clustered on the left of this axis (axis 1). They were primarily herb species such as *Helleborus viridis*, *Symphytum tuberosum*, *Mercurialis perennis*, and *Hepatica nobilis* (Fig. 1). These beech forests presented an overstory dominated by *F. sylvatica*; thus, they were designated as "single-layered beech forests". Moreover, they were generally surrounded by types of land uses, such as exotic coniferous plantations, bushes, meadows, or crops, different from those that surrounded the forests dominated by *Quercus* spp.

Although these two types of beech forest shared a high number of species (Table 1), they showed significant differences in species cover. Some typical beech forest species, such as *Euphorbia amygdaloides*, *Veronica officinalis*, *M. perennis*, or *Athyrium filix-femina,* were not present in the multi-layered beech forests. Moreover, a higher species cover was found primarily for trees (43% of the tree species analysed), shrubs (64% of the shrub species

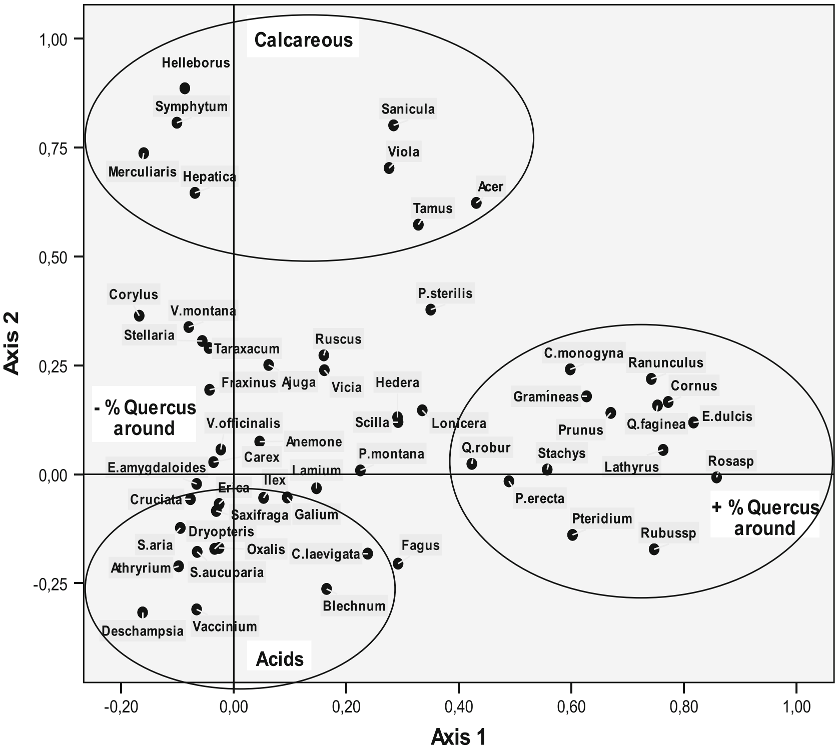

Fig. 1 Principal component analysis results for plant species distribution. *Axes 1–2*, bi-plot of plant species and three principal groups of species created on the basis of the two main factors determining species distribution (*axis 1*, proportion of *Quercus* spp. forest surrounding beech forest plots (% *Quercus* around); *axis 2*, soil pH). The abbreviations correspond to the species: *Acer A. campestre*, *Fagus F. sylvatica*, *Fraxinus F. excelsior*, *Q.faginea Q. faginea*, *Q.robur Q. robur*, *S.aria S. aria*, *S.aucuparia S. aucuparia*, *Cornus C. sanguinea*, *Corylus C. avellana*, *C.laevigata C. laevigata*, *C.monogyna C. monogyna*, *Erica E. vagans*, *Hedera H. helix*, *Ilex I. aquifolium*, *Lonicera L. periclymenum*; *Prunus P. spinosa*; *Rosasp Rosa* spp., *Rubussp Rubus* spp., *Ruscus R. aculeatus*, *Tamus T. communis*, *Vaccinium V. myrtillus*, *Ajuga A. reptans*, *Anemone A. nemorosa*, *Carex C. sylvatica*, *Cruciata C. glabra*, *Deschampsia D. flexuosa*, *E.amygdaloides E. amygdaloides*, *E.dulcis E. dulcis*, *Galium G. odoratum*, *Helleborus H. viridis*, *Hepatica H. nobilis*, *Lamium L. galeobdolon*, *Lathyrus L. linifolius*, *Merculiaris M. perennis*, *Oxalis O. acetosella*, *P.erecta P. erecta*, *P.montana P. montana*, *P.sterilis P. sterilis*, *Ranunculus R. tuberosus*, *Sanicula S. europaea*, *Saxifraga S. hirsuta*, *Scilla S. lilio-hyacinthus*, *Stachys S. officinalis*, *Stellaria S. holostea*, *Symphytum S. tuberosum*, *Taraxacum T. officinale*, *V.montana V. montana*, *V.officinalis V. officinalis*, *Vicia V. sepium*, *Viola V. riviniana*, *Gramíneas Gramineae*, *Athryrium A. filix-femina*, *Blechnum B. spicant*, *Dryopteris D. affinis*, *Pteridium P. aquilinum*

Table 1 Comparison of mean species cover in single-layered and multi-layered beech forests

Species	Single-layered (mean±SE)	Multi-layered (mean±SE)	*P*
Tree species			
Acer campestre	2.86±1.09	10.95±4.07	0.001***
Quercus faginea	0.20±0.12	5.95±3.04	0.007**
Quercus robur	1.31±0.74	6.65±2.18	0.003**
Sorbus aria	0.52±0.29	0.00±0.00	0.227 ns
Sorbus aucuparia	0.19±0.14	0.00±0.00	0.334 ns
Shrub species			
Cornus sanguinea	0.08±0.06	2.24±1.38	0.000***
Crataegus monogyna	4.55±1.08	20.12±6.4	0.002**
Erica vagans	0.36±0.24	0.00±0.00	0.334 ns
Hedera helix	7.26±2.18	26.63±9.60	0.004**
Lonicera periclymenum	0.35±0.17	2.88±1.22	0.000***
Prunus spinosa	0.49±0.35	4.33±2.91	0.009**
Rosa spp.	0.87±0.30	16.93±5.19	0.000***
Rubus spp.	2.05±0.65	19.73±4.41	0.000***
Ruscus aculeatus	0.41±0.30	7.93±5.47	0.007***
Tamus communis	0.08±0.06	0.74±0.44	0.047*
Herb species			
Cruciata glabra	0.30±0.18	0.00±0.00	0.334 ns
Euphorbia amygdaloides	0.71±0.34	0.00±0.00	0.127 ns
Euphorbia dulcis	0.63±0.18	5.33±1.56	0.000***
Lathyrus linifolius	0.37±0.13	2.31±0.69	0.000***
Mercurialis perennis	0.21±0.13	0.00±0.00	0.334 ns
Potentilla erecta	0.00±0.00	0.38±0.21	0.002**
Potentilla sterilis	0.63±0.28	1.86±0.75	0.015*
Saxifraga hirsuta	0.11±0.08	0.00±0.00	0.334 ns
Stachys officinalis	0.03±0.02	1.24±0.64	0.000***
Veronica officinalis	0.46±0.19	0.00±0.00	0.104 ns
Gramineae	9.53±2.24	30.01±5.02	0.000***
Fern species			
Athyrium filix-femina	0.20±0.10	0.00±0.00	0.275 ns
Pteridium aquilinum	2.35±0.62	9.60±3.17	0.009**

Cover (%; mean±SE) of the plant species present in the single-layered and multi-layered beech forests and *P* values of the Mann–Whitney *U* tests are shown. Only representative data are shown

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$, and ns=$P > 0.05$

analysed), and graminoids in the multi-layered beech forests (Table 1). However, only 20% of the herbs had a higher species cover in these forests.

Axis 2 discriminated the species according to the soil pH (Fig. 1). The species that occurred primarily in calcareous soils clustered towards the top of this axis, whereas the species found on acid soils clustered towards the bottom of the axis. The comparison of the cover of the species present in acid-soil and calcareous-soil beech forests showed that the cover of 23 species (over half of which were herbs) was favoured by higher pH. These species included *A. campestre*, *F. excelsior*, *H. viridis*, *H. nobilis*, *P. sterilis*, *Ranunculus tuberosus*, and *V. riviniana.* However, only three species were favoured by lower pH (*Sorbus aucuparia*, *Blechnum spicant*, and *Vaccinium myrtillus*) (Table 2). Moreover, *Ajuga reptans*, *Cruciata glabra*, *M. perennis*, *Potentilla montana*, *Sanicula europaea*, *S. tuberosum*, *Veronica montana*, and *Vicia sepium* were not found in acid soils, whereas *S. aucuparia* was found only in acid soils.

3.2 Plant species diversity: effect of landscape and site conditions

The mean number of species per patch (*S*) was 19.08±1.32. The mean species diversity (*H*′) and evenness (*J*′) were 0.45±0.23 and 1.50±0.78, respectively. The highest mean values of these indices were found for herbaceous life forms, and the lowest were found for ferns. However, trees were the least uniformly distributed (Table 3).

As indicated by the PCA for species distribution, the GLM showed that the surrounding landscape matrix and soil pH determined the variation in plant species diversity

Table 2 Comparison of mean species cover in acid and calcareous beech forests

Species	Acid (mean±SE)	Calcareous (mean±SE)	*P*
Tree species			
Acer campestre	0.08±0.04	7.93±2.01	0.000***
Fraxinus excelsior	0.40±0.24	3.79±1.31	0.026*
Quercus faginea	0.00±0.00	2.29±1.11	0.005**
Sorbus aucuparia	0.34±0.25	0.00±0.00	0.025*
Shrub species			
Crataegus monogyna	2.54±1.40	11.46±2.58	0.001***
Hedera helix	3.95±1.37	16.53±4.51	0.037*
Prunus spinosa	0.04±0.03	2.16±1.11	0.008**
Rosa sp.	2.61±1.91	4.74±1.72	0.001**
Herb species			
Ajuga reptans	0.00±0.00	0.60±0.39	0.010**
Cruciata glabra	0.00±0.00	0.46±0.27	0.057 ns
Helleborus viridis	0.02±0.02	3.58±1.02	0.000***
Hepatica nobilis	0.06±0.04	2.63±0.72	0.000***
Lamium galeobdolon	0.77±0.77	1.47±0.64	0.053 ns
Mercurialis perennis	0.00±0.00	0.32±0.19	0.057 ns
Potentilla montana	0.00±0.00	0.49±0.21	0.017*
Potentilla sterilis	0.15±0.14	1.45±0.46	0.003**
Ranunculus tuberosus	0.13±0.08	1.00±0.36	0.003**
Sanicula europaea	0.00±0.00	0.23±0.10	0.017*
Scilla lilio-hyacinthus	0.02±0.02	2.24±1.26	0.061 ns
Symphytum tuberosum	0.00±0.00	0.61±0.32	0.033*
Taraxacum officinale	0.03±0.03	0.52±0.23	0.012*
Vaccinium myrtillus	6.36±2.34	0.60±0.60	0.001***
Veronica montana	0.00±0.00	0.50±0.17	0.001***
Vicia sepium	0.00±0.00	1.04±0.31	0.000***
Viola riviniana	0.79±0.26	4.32±0.96	0.001***
Fern species			
Blechnum spicant	1.08±0.61	0.29±0.25	0.018*

Cover (%; mean±SE) of the plant species present in the acid beech forests (acid, pH=3–5) and calcareous beech forests (calcareous, pH=5.1–8) and *P* values of the Mann–Whitney U tests are shown. Only representative data are shown

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$, and ns=$P > 0.05$

(richness, Shannon diversity, and evenness) in the beech forests. Although both factors positively affected the three indices if the overall vegetation was considered, the results were not as uniform if specific life forms were analysed. Thus, both factors significantly affected tree diversity. However, only the surrounding landscape matrix affected shrub diversity. Furthermore, only the soil pH affected herb diversity (Table 4).

Table 3 Mean diversity measures (richness (*S*), Shannon diversity (*H*′), and evenness indices (*J*′) values (mean±SE)) for the different life forms in the beech forests studied

Indices	Trees	Shrubs	Herbs	Ferns
S	2.76±0.25	4.98±0.45	10.08±0.88	1.26±0.19
H′	0.10±0.02	0.41±0.04	0.63±0.04	0.09±0.03
J′	0.16±0.02	0.53±0.05	0.65±0.03	0.20±0.05

In general, multi-layered beech forests and those on calcareous soils were more diverse than single-layered beech forests or those on acid soils. In the multi-layered beech forests, this pattern was primarily attributable to the higher diversity of trees and shrubs. In contrast, this pattern resulted primarily from the higher diversity of herbs in the forests on calcareous soils (Table 5).

4 Discussion

In the beech forests studied, the plant species composition and the diversity distribution depended on factors working at different spatial scales. The trends affecting the variation were determined primarily by the surrounding habitat and secondarily by soil pH. However, these two factors affected life-form diversity differently. Shrubs were more influenced by the surrounding landscape, whereas herbaceous species

Table 4 Results of general linear model for diversity measures in relation to the significant landscape and stand factors

	Surrounding landscape matrix				pH			
	β	r^2	F	P	β	r^2	F	P
S total	+	0.202	11.625	0.001***	+	0.311	20.757	0.000***
H' total	+	0.312	20.817	0.000***	+	0.264	16.514	0.000***
J' total	+	0.266	16.695	0.000***	+	0.178	9.975	0.003**
S tree	+	0.181	10.160	0.003**	+	0.100	5.108	0.029*
H' tree	+	0.216	12.698	0.001***	+	0.167	9.205	0.004**
J' tree	+	0.207	12.013	0.001***	+	0.158	8.651	0.005**
S shrub	+	0.276	17.517	0.000***	+	0.025	1.177	ns
H' shrub	+	0.204	11.809	0.001***	+	0.014	0.646	ns
S herb	+	0.075	3.718	ns	+	0.421	33.398	0.000***
H' herb	+	0.044	2.137	ns	+	0.397	30.297	0.000***
J' herb	+	0.003	0.153	ns	+	0.168	9.256	0.004**

Richness (S), Shannon diversity (H'), and evenness indices (J') for both total species and different life forms (tree, shrub, and herb) are shown

β standardised coefficient or beta coefficient, r^2 regression coefficient, P significance level

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$, and ns=$P > 0.05$

were more influenced by soil conditions. Both factors influenced the diversity of tree species, although the effect at the landscape level was stronger than at the stand level.

4.1 Effect of the surrounding landscape matrix on plant species composition and diversity

The results of this study showed the importance of the surrounding habitats, i.e. the surrounding landscape matrix, on the plant species composition and diversity of the beech forests, as also found for grazed old fields (Cousins and Aggemyr 2008). The presence of *Quercus* spp. forests in the surroundings favoured the presence of multi-layered beech forests, in which tree and shrub diversity were higher than in single-layered beech forests. This relationship reflects the ecological similarities between *Quercus* spp. forests and beech forests and the resulting colonisation of the multi-layered beech forests by some species from the *Quercus* spp. forests. However, single-layered beech forests were surrounded by land uses that were ecologically different from beech forests. Therefore, fewer species tended to colonise the single-layered beech forests. Species colonisation is greater in a matrix where the neighbouring patches are ecologically similar than in a matrix consisting of ecologically different patches (Collinge 1996). The findings of the current study suggest that the species in the surrounding landscape matrix were more prone to colonise and become better established in multi-layered beech forests, thereby creating a more diverse structure. Of the species analysed in this study, 35% presented a higher cover in the multi-layered beech forests.

Table 5 Comparison of diversity measures in the different types of beech forests investigated in this study

	Single-layered	Multi-layered	P	Acid	Calcareous	P
S total	17.46±1.42	26.44±2.32	0.008**	14.43±1.59	23.04±1.72	0.001***
H' total	1.72±0.14	2.91±0.20	0.000***	1.49±0.18	2.31±0.16	0.002**
J' total	0.42±0.02	0.62±0.03	0.001***	0.38±0.04	0.51±0.03	0.006**
S tree	2.44±0.25	4.22±0.55	0.004**	2.26±0.33	3.19±0.34	ns
H' tree	0.24±0.06	0.68±0.15	0.002**	0.17±0.07	0.45±0.08	0.010*
J' tree	0.12±0.02	0.31±0.06	0.003**	0.09±0.03	0.22±0.03	0.016*
S shrub	4.22±0.46	8.44±0.53	0.000***	4.57±0.63	5.33±0.64	ns
H' shrub	1.16±0.14	2.26±0.15	0.000***	1.24±0.19	1.46±0.19	ns
J' shrub	0.49±0.05	0.74±0.03	0.002**	0.52±0.07	0.55±0.06	ns
S herb	9.51±0.99	12.67±1.69	ns	6.30±0.75	13.3±1.19	0.000***
H' herb	2.02±0.16	2.40±0.24	ns	1.51±0.17	2.58±0.17	0.000***
J' herb	0.64±0.04	0.67±0.04	ns	0.58±0.05	0.71±0.03	0.041*
S fern	1.29±0.23	1.11±0.20	ns	1.30±0.27	1.22±0.28	ns
H' fern	0.35±0.10	0.13±0.11	ns	0.41±0.14	0.23±0.11	ns
J' fern	0.21±0.06	0.13±0.11	ns	0.28±0.09	0.12±0.06	ns

Richness (S), Shannon diversity (H'), and evenness indices (J'; mean±SE) values for both total species and different life forms (tree, shrub, herb, and fern), and P values of t tests are shown

***$P \leq 0.001$; **$P \leq 0.01$; *$P \leq 0.05$, and ns=$P > 0.05$

Nevertheless, this effect was detected only for the composition and diversity of trees and shrubs, not for herb diversity. Different studies have shown that the natural regeneration of woodland communities, particularly the ground layer, is possible only in sites immediately adjacent to sources of woodland-species diaspores because the dispersal distances of herbaceous plant species are very small (Brunet and von Oheimb 1998; Honnay et al. 1999). Thus, the existence of ecologically similar ecosystems in the vicinity of the beech forests does not appear to be sufficient for colonisation by some herbs because not only the dispersal but also the establishment of herb species is more complex than for woody species (Dzwonko 2001). In the multi-layered beech forests, we observed that more generalised understory species (*E. dulcis*, *L. linifolius*, *P. erecta*, *P. sterilis*, *S. officinalis*, and *P. aquilinum*) were more likely to become established. These species were primarily favoured by the high structural complexity of these forests, which tends to produce greater habitat and environmental heterogeneity (Crow et al. 2002; Atauri et al. 2005) compared with single-layered beech forests. A higher tree and shrub diversity in the overstory influence the herb layer by changing resource availability and environmental conditions in this layer (Barbier et al. 2008). This effect of the overstory facilitates colonisation by understory species without necessarily affecting diversity, a result in contrast to the findings of Gilliam (2007).

4.2 Effect of soil pH on plant species composition and diversity

Although pH represents a complex gradient because it is correlated with many edaphic and climatic factors (Tyler 2003), it can be considered a direct environmental factor because it has a direct physiological effect on plant growth and on resource availability. Thus, plant species richness and diversity increased if soil acidity decreased, as previously observed in other studies (Ewald 2003; Pärtel et al. 2004). Moreover, the pH effect was primarily observed for herbaceous species. This finding agrees with previous studies in which pH often represented the primary driver of diversity and cover in the herb layer (Kooijman 2010; Vockenhuber et al. 2011). Forest herb-layer species are well-known indicators of site conditions (Mölder et al. 2008) because they root in the topsoil horizon. Hence, they are more sensitive to the environment and respond faster than woody plants (Knoop and Walker 1985; Rodríguez-Loinaz et al. 2008).

4.3 Management and conservation implications

The beech forests in the Basque Country are in an advanced stage of maturity, as shown by the presence of several ancient-forest indicator species (i.e. *Lamium galeobdolon*, *M. perennis*, *A. campestre*, and *A. filix-femina*) (Honnay et al. 1999) and a very low number of pioneer species, such as *Betula alba*, *Castanea sativa*, *Glechoma hederacea*, and *Moehringia trinervia* (Hermy et al. 1999). These forests are highly important to conservation because regeneration can take centuries even if the plot in question is adjacent to ancient woodland (Brunet and von Oheimb 1998). Therefore, management practices should mimic natural structural complexity to protect the biodiversity related to these native beech forests and to maintain mature communities with ancient woodland species. Thus, controlled clear-cutting and grazing is required to conserve the diversity and the cover of those species characteristic of natural ancient woodlands. Moreover, species are not affected by the same factors in the same way. Accordingly, the evaluation of beech forests for conservation and management should be based not only on species diversity but also on plant species quality (Honnay et al. 1999) because all species do not have the same conservation value.

Furthermore, the significant influence of the surrounding landscape matrix on species diversity and species distribution patterns in beech forests enhances the importance of the landscape level in future management planning. We therefore recommend increasing native forests in the vicinity of beech forests because the native forests help to maintain the pool of typical forest species in the beech forests.

5 Conclusions

In the Basque Country, the species composition and diversity of trees and shrubs in beech forests responded primarily to suitable habitat proportions in the surrounding landscape, whereas the species composition and diversity of herbs responded to soil pH. Integrated management of beech forests with the surrounding landscape matrix is therefore needed to conserve the biodiversity of this forest. Future landscape management should seek to produce a heterogeneous matrix comprising patches of natural, unmanaged and managed deciduous forest and including other traditional uses and forest plantations.

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Appendix A

Table 6 Location and environmental and landscape factors determined for all 50 research sites

Beech forests	UTM X	UYM Y	Size (Ha)	Precipitation (mm.)	Elevation (m)	pH	Slope (%)	DBH (m)
AltA	508815	4762157	1,824	750	449	5.13	7	0.29
AltB	510899	4759890	1,824	750	567	4.45	9	0.49
AltC	511337	4759200	1,824	650	682	3.59	20	0.32
AltD	511056	4760192	1,824	750	596	3.78	6	0.37
Vit2	533233	4737319	4,518	350	774	4.89	26	0.33
Vit6	531524	4736672	4,518	350	752	5.02	30	0.32
Acido	536636	4739167	4,518	350	695	6.88	17	0.24
Ac6	538605	4739284	4,518	350	677	6.89	17	0.31
CalMA	555828	4740657	7,256	550	1,057	6.37	6	0.36
CalMB	557616	4738892	7,256	550	1,023	6.50	0	0.52
CalMC	556046	4741496	7,256	550	1,021	5.81	0	0.30
CalMD	558188	4741171	7,256	550	985	5.75	13	0.33
Cal1A	506501	4760918	601.61	650	508	5.01	7	0.21
Cal1B	508187	4761382	601.61	650	360	4.73	11	0.37
Cal1C	505405	4761040	601.61	550	683	6.01	33	0.40
Cal1D	507554	4761143	601.61	650	402	5.02	4	0.09
Cal23b	516169	4768029	575.24	1,450	1,106	5.59	17	0.20
Cal19b	542011	4759738	58.50	750	910	4.92	22	0.25
Cal22	541589	4757622	152.83	750	1,084	4.48	22	0.18
cal25b	500488	4756953	156.29	450	458	4.74	9	0.26
Cal24	520418	4762475	146.66	950	780	6.47	39	0.23
Cal45	542611	4730651	163.19	450	889	5.43	30	0.52
Cal30	506032	4754853	513.42	450	729	4.60	24	0.24
Cal28b	481931	4748426	210.51	250	944	7.65	33	0.44
Ñ	542688	4757734	177.75	750	1,117	3.68	11	0.29
R	422679	4780298	138.47	750	570	4.21	26	0.79
N	559418	4753909	206.47	750	790	4.83	24	0.13
A	509395	4757148	480.61	550	592	4.82	33	0.13
M	507213	4756244	76.87	450	637	5.01	17	0.05
I	539418	4729867	104.00	550	931	4.76	35	0.33
Z	562101	4753680	177.89	850	640	6.10	13	0.09
H	533577	4757734	122.83	650	677	4.23	33	0.19
P12	511471	4781785	8.34	750	424	3.69	20	0.47
P81	532114	4786862	3.28	950	874	4.20	39	0.35
P10	523727	4769949	2.64	1,150	540	4.17	11	0.60
P11	524267	4770538	1.97	1,150	663	3.92	52	0.33
P27	550672	4754375	4.17	750	843	3.77	20	0.38
P8	516381	4752261	7.90	450	754	7.03	33	0.16
P1	548681	4729977	13.08	450	780	6.03	22	0.29
P90	546217	4755990	3.99	750	998	4.52	28	0.22
P73	528519	4770328	11.97	950	667	4.05	30	0.13
C6	502221	4763231	1.61	550	451	6.02	19	0.30
C26	541192	4760375	5.99	750	1,037	4.58	9	0.46
C4b	493315	4764965	4.83	450	468	5.49	22	0.22
C11	495931	4768324	21.77	450	476	5.57	30	0.28
C30	503878	4750450	11.06	450	815	5.82	22	0.23
C8	500933	4750960	9.18	450	848	6.71	0	0.35
C3	549852	4739232	4.84	450	1,006	6.92	2	0.20
C23	511468	4751376	9.82	450	777	5.20	33	0.08
C12	481962	4750295	3.62	250	803	7.48	15	0.18

Appendix B

Table 7 List of vascular plant species present in all beech forests investigated

Species	Cover (mean±SE)	Frequency
Tree species		
Acer campestre L.	4.32±1.21	40
Acer pseudoplatanus L.	0.06±0.05	4
Betula alba L.	0.17±0.17	2
Castanea sativa Miller	0.04±0.02	6
Fagus sylvatica L.	161±5.92	100
Fraxinus excelsior L.	2.23±0.75	32
Prunus avium L.	0.02±0.01	4
Quercus faginea Lam.	1.24±0.62	16
Quercus ilex L.	0.04±0.04	6
Quercus pyrenaica Willd.	0.12±0.12	4
Quercus robur L.	2.27±0.77	32
Quercus rubra L.	0.002±0.0	2
Quercus x subpyrenaica Huguet del Villar	0.24±0.24	2
Sorbus aria (L.) Crantz	0.43±0.24	12
Sorbus aucuparia L.	0.16±0.12	8
Sorbus torminalis (L.) Crantz	0.002±0.0	2
Taxus baccata L.	0.002±0.0	2
Ulmus glabra Hudson	0.002±0.0	2
Shrub species		
Arbutus unedo L.	0.03±0.03	2
Calluna vulgaris (L.) Hull	0.17±0.15	6
Cornus sanguinea L.	0.47±0.27	16
Corylus avellana L.	1.43±0.58	16
Crataegus laevigata (Poiret) DC.	2.55±1.04	16
Crataegus monogyna Jacq.	7.35±1.65	66
Daboecia cantabrica (Hudson) C. Koch	0.16±0.13	6
Daphne laureola L.	0.08±0.08	2
Erica arborea L.	0.26±0.18	4
Erica cinerea L.	0.27±0.21	4
Erica vagans L.	0.30±0.20	8
Euonymus europaeus L.	0.12±0.12	2
Frangula alnus Miller	0.01±0.01	2
Hedera helix L.	10.7±2.65	68
Ilex aquifolium L.	2.84±0.84	50
Ligustrum vulgare L.	0.06±0.06	2
Lonicera periclymenum L.	0.80±0.29	30
Malus sylvestris Miller	0.01±0.01	2
Prunus spinosa L.	1.18±0.61	30
Rosa sp.	3.76±1.28	40
Rubus sp.	5.23±1.34	70
Ruscus aculeatus L.	1.77±1.05	16
Salix atrocinerea Brot.	0.17±0.12	4
Tamus communis L.	0.20±0.10	14
Vaccinium myrtillus L.	3.25±1.19	22
Herb species		
Ajuga reptans L.	0.32±0.22	20
Allium ursinum L.	0.04±0.04	2
Anemone nemorosa L.	1.23±0.32	38
Aquilegia vulgaris L.	0.01±0.01	2
Arum maculatum L.	0.08±0.05	6
Cardamine flexuosa With.	0.05±0.04	4
Cardamine hirsuta L.	0.04±0.03	4
Carex remota L.	0.07±0.07	2
Carex sylvatica Hudson	1.88±0.62	48
Cerastium arvense L.	0.05±0.03	4
Cirsium vulgare	0.01±0.01	2
Conopodium pyrenaeum (Loisel.) Miégeville	0.05±0.04	4
Crepis lampsanoides (Gouan) Tausch.	0.02±0.02	2
Crocus nudiflorus Sm.	0.11±0.09	6
Cruciata glabra (L.) Ehrend.	0.25±0.15	8
Deschampsia flexuosa (L.) Trin.	6.85±1.73	54
Digitalis purpurea L.	0.08±0.08	2
Euphorbia amygdaloides L.	0.58±0.28	18
Euphorbia dulcis L.	1.48±0.40	52
Fragaria vesca L.	0.29±0.23	6
Galeopsis tetrahit L.	0.002±0.0	2
Galium aparine L.	0.05±0.05	2
Galium odoratum (L.) Scop.	0.17±0.07	12
Galium saxatile L.	0.06±0.06	4
Geranium molle L.	0.03±0.03	2
Geranium robertianum L.	0.33±0.32	6
Glechoma hederacea L.	0.22±0.22	2
Helleborus foetidus L.	0.07±0.07	4
Helleborus viridis L.	1.94±0.60	42
Hepatica nobilis Schreber.	1.45±0.42	42
Hieracium officinarum.	0.002±0.0	4
Hypericum pulchrum L.	0.05±0.04	6
Isopyrum thalictroides L.	0.01±0.01	2
Lamium galeobdolon (L.) L.	1.15±0.49	16
Lathraea clandestina L.	0.02±0.02	2
Lathyrus linifolius (Reichard) Bässler	0.72±0.19	36
Lilium martagon L.	0.04±0.04	2
Luzula multiflora (Retz.) Lej.	0.002±0.0	2
Luzula sylvatica (Hudson) Gaudin	0.09±0.05	6
Lysimachia nemorum L.	0.03±0.02	6
Medicago lupulina	0.002±0.0	2
Melittis melissophyllum L.	0.06±0.05	4
Mercurialis perennis L.	0.17±0.11	8
Moehringia trinervia (L.) Clairv.	0.22±0.22	2

Table 7 (continued)

Species	Cover (mean±SE)	Frequency
Mycelis muralis (L.) Dumort.	0.01±0.01	2
Oxalis acetosella L.	1.24±0.34	44
Parietaria judaica L.	0.01±0.01	2
Potentilla erecta (L.) Raeuschel	0.07±0.04	8
Potentilla montana Brot.	0.27±0.12	12
Potentilla reptans L.	0.02±0.02	2
Potentilla sterilis (L.) Garcke	0.86±0.27	34
Primula elatior	0.02±0.02	2
Prunella vulgaris L.	0.01±0.01	4
Pulmonaria longifolia (Bast.) Boreal	0.03±0.03	2
Ranunculus acris L.	0.002±0.0	2
Ranunculus ficaria L.	0.26±0.24	4
Ranunculus tuberosus Lapeyr.	0.60±0.20	42
Rubia peregrina L.	0.36±0.31	6
Sanicula europaea L.	0.12±0.06	12
Saxifraga hirsuta L.	0.09±0.07	8
Scilla lilio-hyacinthus L.	1.22±0.69	14
Scrophularia alpestris Gay ex Bentham	0.11±0.11	2
Sedum sediforme	0.12±0.12	2
Solidago virgaurea L.	0.01±0.01	2
Stachys officinalis (L.) Trevisan	0.25±0.13	14
Stellaria holostea L.	0.16±0.09	10
Stellaria media (L.) Vill.	0.05±0.04	4
Symphytum tuberosum L.	0.33±0.18	16
Taraxacum officinale Weber	0.30±0.13	20
Teucrium scorodonia L.	0.01±0.01	2
Trifolium repens	0.19±0.15	6
Tussilago farfara L.	0.02±0.02	2
Urtica dioica L.	0.10±0.07	4
Valeriana montana L.	0.02±0.02	2
Veronica chamaedrys L.	0.26±0.19	4
Veronica hederifolia L.	0.20±0.20	2
Veronica montana L.	0.27±0.10	20
Veronica officinalis L.	0.38±0.16	20
Vicia pyrenaica Pourret	0.01±0.01	2
Vicia sepium L.	0.56±0.18	24
Vincetoxicum hirudinaria Medicus	0.04±0.04	2
Viola hirta L.	0.02±0.02	4
Viola riviniana Reichenb.	2.70±0.58	64
Other graminoids	13.2±2.32	80
Ferns		
Asplenium adiantum-nigrum L.	0.02±0.02	4
Asplenium ceterah L.	0.01±0.01	2
Asplenium ruta-muraria L.	0.01±0.01	4
Asplenium trichomanes L.	0.04±0.03	4
Athryrium filix-femina (L.) Roth	0.16±0.08	10
Blechnum spicant (L.) Roth	0.65±0.31	20
Dryopteris affinis (Lowe) Fraser-Jenkins	0.25±0.11	14
Dryopteris filix-mas (L.) Schott	0.02±0.02	4
Polystichum aculeatum (L.) Roth	0.002±0.0	4
Polystichum setiferum (Forsskal) Woynar	0.04±0.03	4
Pteridium aquilinum (L.)Kuhn	3.65±0.84	60

Mean cover (%) and frequency (%) of vascular plants present in 50 Basque beech forests

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