Species richness patterns in the understorey of Pyrenean *Pinus sylvestris* forest

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Abstract. Species richness was studied in the understorey of natural *Pinus sylvestris* forest in the eastern Pyrenees. Understorey plant species were grouped in three structural groups as woody species, herbs and mosses. The response curves of total species richness and species richness of each structural group were fitted against environmental and stand-structural parameters, using Generalized Linear Models. The results suggested that, to predict species richness, environmental parameters were more important than tree-canopy structural parameters, in particular incoming radiation and soil nutrient concentration. The species richness response curve was often humped in relation to soil nutrient concentration. Different patterns of species richness were found for each structural group.

Keywords: Diversity model; Environmental relation; Life form; Structural group.

Introduction

Pinus sylvestris forests are widely distributed in the Pyrenees and constitute the main wood resource in this area. To date, no study on the biological diversity in these forests has been published. In this paper I provide an empirical study of understorey plant species diversity in monodominant *Pinus sylvestris* forest in relation to environmental parameters. A statistical modelling procedure is used for studying these relationships.

Previous studies on Pyrenean *Pinus sylvestris* forests showed clear relationships between understorey species composition and environmental factors (Pausas & Feoli in press a, b). Forest structure, growth, biomass and production are related to environmental conditions as well (Pausas & Fons 1992; Pausas 1993). The main questions addressed in this paper are: is there any relationship between environmental factors and understorey species richness? What environmental variables, if any, determine species richness in the understorey of *Pinus sylvestris* forest and how do these environmental variables limit species richness?

Reviews of the current theory of species richness can be found in Brown (1981), Giller (1984), Begon et al. (1990). On a local scale (within a region), the most important patterns of species richness can be grouped as follows: (a) availability of resources – nutrients, water and light (e.g. Grime 1979); (b) variables that have a direct physiological impact on the plants, but are not consumed – direct environmental variables *sensu* Austin (1980) such as temperature, but also stress (toxicity) factors (e.g. Rey Benayas & Scheiner 1993); (c) heterogeneity and disturbance (cf. van der Maarel 1993); (d) biological factors – competition, successional status, dispersion, predation. On a large geographical scale, historical effects should also be included (Ricklefs 1987; Glaser 1992). I studied the influence of the environmental factors a and b on species richness patterns in the study area. Variables associated with spatio-temporal heterogeneity and dispersal (Janzen 1970; Cornell & Lawton 1992; Leigh et al. 1993) were assumed to be of secondary importance. However, some variables related to spatial heterogeneity were also fitted to test this assumption.

Peet (1978) suggested that the pattern of plant species richness is different for different structural groups. Richerson & Lum (1980), Grubb (1987), Minchin (1989), Moore & Keddy (1989), S.J. Wright (1992) and Cox & Larson (1993) provided examples supporting Peet's hypothesis. However, there are not enough studies in this context available to produce any generalization. I thus studied understorey species richness patterns for total species and for three structural groups: woody species, herbs and mosses. These three structural groups can also be grouped in two taxonomic groups as vascular plants and mosses.

Methods

Field sampling

57 circular plots (radius = 10 m, area = 314 m^2) of *Pinus sylvestris* forest were located in the eastern Pyrenees. Within the area sampled, ca. 4000 km^2, only stands of natural *Pinus sylvestris* forest were included. 22 years of observation showed that the mean annual

precipitation is 1281 mm and the mean annual temperature 5.4 °C (La Molina Meteorological Station, 1704 m a.s.l.; data from the National Meteorological Service, Spain). Plot selection used the following criteria: (a) containing monodominant *Pinus sylvestris* forest; (b) not having recently been disturbed or managed, i.e. no secondary forest and plantations; (c) showing homogeneity as to environmental characteristics such as slope, aspect and bedrock type, as well as apparent uniformity of understorey and overstorey vegetation. Since a certain amount of structural heterogeneity cannot be avoided, this was also estimated, by determining the standard deviation of tree DBH (diameter at breast height).

In each plot, vascular plants and epigeic bryophytes were recorded and a volumetric soil sample from the top 10 cm of the soil was collected at the centre of the plot. The plant species recorded in the plots were divided into woody species, herbs, mosses and others; the latter group was excluded because it is small and heterogeneous, including some epigeic lichens (*Cladonia* and *Cetraria)*, and the epiphyte *Viscum album* L. The number of species in the three structural groups and the total number of species were used as dependent variables.

Diameter at breast height (DBH) was measured for all trees. The basal area of trees was calculated from their DBH, and the standard deviation of the DBHs was used as a measure of heterogeneity of the forest structure.

Site description and soil analysis

First, the site variables altitude, slope, aspect, topographic position and bedrock type were recorded. Soil depth was estimated by driving in a 1-m rod at 10 points systematically located within the plot. Topographic position was always mid-slope – at other positions in the study area other tree species dominated.

The soil samples were sieved and the fine fraction (< 2 mm) was analysed. Soil pH was measured in 1:2.5 water suspension with a combined electrode (Anon. 1973). Soil texture was estimated according to Klinka et al. (1984). Total carbonate content was determined with a Bernard calcimeter, C and N-concentrations with a Carlo Erba elemental analyser. Total P was extracted by wet digestion (Jackson 1964) and its concentration determined by a Induction Coupled Plasma device. Calcium was extracted with 1 M ammonium chloride (Thomas 1982) and the extract analysed with Atomic Absorption Spectrometry.

Soil moisture index

Water availability to plants depends on the capacity of the soil for water storage and the water supply (rainfall). Rainfall data of sufficient precision were not available for the studied area, so only soil water storage capacity was used to estimate water availability. Thus, a potential soil moisture index (potential hygrotope of Klinka et al. 1984) was estimated on the basis of those soil properties related to water retention. The calculated moisture index (MI) indicates the capacity of the soil for water storage. The variables used to calculate this index were: soil, depth, stoniness, soil texture, slope and topographic position. The similarity between the plots was calculated on the basis of these variables. The position along the first component (rescaled from 0 to 10) of a Principal Coordinate Analysis of the similarity values was used as a moisture index. Low values for this index (low potential soil moisture) indicate low capacity of the soil for water storage, and are associated with south-facing plots, high levels of stoniness, low soil depth or loamy to sandy soil texture.

Radiation and temperature

Annual solar radiation was estimated on the basis of slope, aspect, latitude, longitude, percentage of visible sky and the mean monthly cloud cover of the region. The percentage of visible sky was estimated by measuring the angle between the horizontal and the skyline at eight cardinal points. A program written by C. Gracia (unpubl.) was used to compute the annual radiation on the basis of these variables, both direct and diffuse radiation.

No temperature data were available, but we consider that the main sources of temperature variation in the study area are altitude and aspect. Thus, altitude and incoming radiation were used as surrogate variables.

Modelling procedure

Generalized linear modelling (GLM, McCullagh & Nelder 1989; Yee & Mitchell 1991) as implemented in GLIM (Payne 1986) was used to fit the number of species present in the plots (species richness) as a function of the environmental variables. Separate models were fitted for total understorey species richness and for species richness of three structural groups: woody plants, herbs and mosses. Because the dependent variables are counts (discrete data), a Poisson distribution of errors was assumed and a logarithmic link function was used in all fitted models (McCullagh & Nelder 1989). The predictor variables tested were soil concentration of N, P, C and Ca, soil pH, moisture index, incoming radiation, altitude, tree density, tree basal area and standard deviation of tree DBH. A forward stepwise procedure was used to enter the variables in the model, and only variables that accounted for a significant change in deviance ($p < 0.05$) were entered. Simple polynomial functions up to the order of three and interaction terms
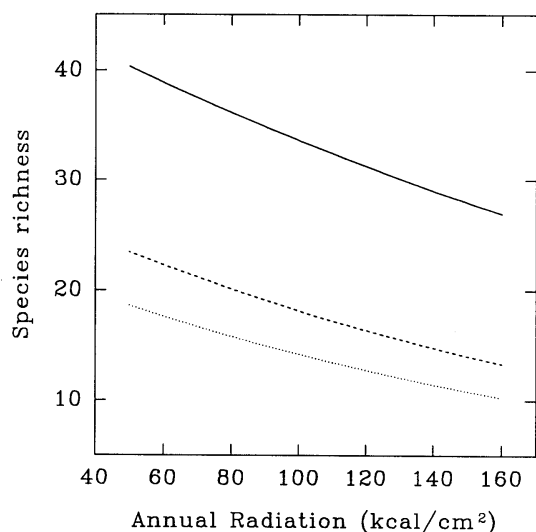
were tested. The goodness-of-fit was measured by the deviance statistic. Because overdispersion was observed, the change in deviance after including each parameter into the model was tested by an F-ratio test (McCullagh & Nelder 1989; Aitkin et al. 1989). For all figures in the Results section, the number of species is referred to the plot size, $314\,m^2$, and only significant models ($p < 0.05$) are shown. A conceptually similar statistical modelling procedure has been used to study tree species richness (Margules et al. 1987) as well as species response curves (Austin et al. 1990).

Before accepting any model, the dependent variable, fitted values and residuals were plotted against environmental variables to reveal in a graphical way possible outliers, high potential influence values and the sensitivity of the model to single plots (Pregibon 1981). One plot at 750 m a.s.l. was removed from the analysis because all other sample plots were located between 1000 m and 1800 m, and the influence of this plot on the model was relatively high. Thus, the number of plots used to fit the final models was 56.

Results

The observed minimum, maximum and mean number of species for the structural groups and the total assemblage are shown in Table 1; Table 2 lists the explanatory variables tested and the range observed in the present study. The range of the environmental variables is relatively wide. For example, soil pH ranges from strongly acid (pH < 4.5) to basic (pH ≈ 8); some nutrient concentrations had a wide range as well (Table 2). Table 3 shows the correlation between all explanatory variables.

Table 1. Minimum, maximum and mean number of species for different structural groups and all groups together in 56 plots of $314\,m^2$ in *Pinus sylvestris* forest.

	Minimum	Maximum	Mean
Total	17	56	33.91
Woody species	3	19	8.88
Herbs	5	34	18.46
Mosses	1	13	6.16
Others	0	3	0.40

Table 2. Minimum, maximum and mean values of the explanatory variables tested.

Variable[1]	Minimum	Maximum	Mean	Units
Altitude	1050	1750	1448	m a.s.l.
Tree density	477.7	4108.0	1248.0	trees/ha
Tree basal area	14.31	65.51	40.59	m^2/m^2
SD-DBH	4.20	19.70	9.38	cm
Radiation	52.26	151.50	98.32	$kcal \cdot cm^{-2} \cdot yr^{-1}$
Nitrogen	0.084	0.686	0.285	%
Carbon	1.220	11.120	4.453	%
Phosphorus	0.154	0.828	0.404	g/kg
Calcium	0.242	26.72	9.096	cmol(+)/kg
Soil pH	4.43	8.06	6.28	units
Moisture Index	0.05	8.39	5.11	units

[1] = Nitrogen, Carbon, Phosphorus and Calcium refer to the concentration of the top 10 cm of the soil; SD-DBH: standard deviation of the tree diameter at breast height.

The results of the GLM model fits for the four species groups are shown in Table 4.

Table 3. Correlation between the explanatory variables. See Table 2 for details of the variables. ($*** = p < 0.001$; $** = p < 0.01$; $* = p < 0.05$).

	1	2	3	4	5	6	7	8	9	10	11
1. Tree density	1.0	− 0.229	− 0.316 *	− 0.101	0.204	− 0.331 *	0.243	0.226	0.090	− 0.046	0.095
2. Tree basal area		1.0	0.137	0.368 **	− 0.394 **	0.473 ***	0.072	0.132	0.068	0.141	0.079
3. SD-DBH			1.0	0.537 ***	− 0.059	0.238	0.066	0.090	0.103	0.052	0.149
4. Altitude				1.0	− 0.372 **	0.497 ***	0.219	0.242	− 0.068	0.141	− 0.022
5. Moisture Index					1.0	− 0.724 ***	− 0.083	− 0.007	0.352 **	− 0.208	0.342 **
6. Radiation						1.0	0.014	0.007	− 0.253	0.101	− 0.261
7. Carbon							1.0	0.724 ***	0.664 ***	0.212	0.409 **
8. Nitrogen								1.0	0.550 ***	0.167	0.357 **
9. Calcium									1.0	0.207	0.841 ***
10. Phosphorus										1.0	0.376 **
11. Soil pH											1.0

Fig. 1. Response of species richness to annual radiation (kcal/cm^2): Total (solid line), Herbs (broken line) and Non-graminoid- herbs (dotted line). Changes in deviance are 16.06*, 16.71** and 14.74** respectively (* = $p < 0.05$; ** = $p < 0.01$). For woody species and mosses, no significant model was obtained.
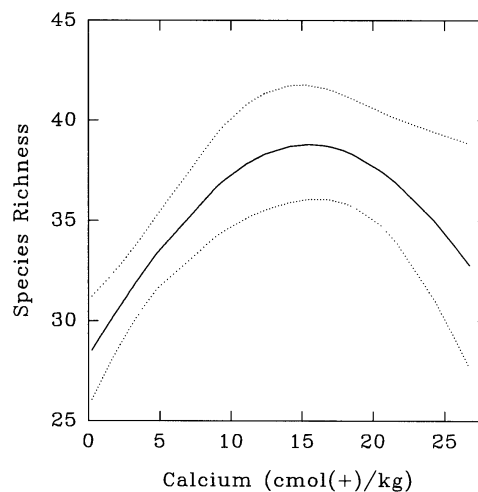

Fig. 2. Response of Total species richness to Soil Ca-concentration (cmol(+)/kg). Dotted lines indicate 95 % confidence limits.

Table 4. GLM models for total species richness and for the three structural groups. The levels of significance refer to the change in deviance associated with the addition of the terms. *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$.

Model[1]	Deviance	df	Change in deviance	F	p
Total species richness					
No terms added	181.45	55			
Radiation	165.39	54	16.06	5.24	*
Ca + Ca^2	161.22	53	20.23	3.33	*
Woody species richness					
No terms added	111.34	55			
N + N^2	94.33	53	17.01	4.78	**
+ Altitude	77.51	52	16.82	11.28	***
+ Ca	69.20	51	8.31	6.12	**
+ SD-DBH	62.80	50	6.40	5.10	*
Herb species richness					
No terms added	151.63	55			
Radiation	134.92	54	16.71	6.69	*
Moss species richness					
No terms added	61.74	55			
MI + MI^2	50.79	53	10.95	5.71	**
+ pH	46.43	52	4.36	4.88	*

[1] Ca = Soil Ca-concentration; MI= Soil moisture index; N = Soil N-concentration; pH = Soil pH; Radiation = Total annual radiation; SD-DBH = Standard deviation of DBH measurements. Ca^2, N^2 and MI^2 are quadratic terms.

Total species richness

Radiation and soil Ca-concentration are the only variables which are significantly related to the total species richness in the understorey vegetation. When one of these variables was added to the model, neither environmental variables, nor forest heterogeneity accounted for a significant change in deviance. Hence, two models with one explanatory variable are shown in Table 4. Species richness decreased with amount of radiation (Fig. 1). For Ca-concentration a humped quadratic response was found (Fig. 2). The maximum number of species occurs at intermediate levels of Ca-concentration or at low incoming solar radiation (north-facing slopes).

Woody species richness

Soil N-concentration and altitude, followed by Ca-concentration and forest heterogeneity, were the best predictors of woody species richness in the forest understorey. N-concentration showed a humped quadratic response with a maximum at intermediate levels of N (Fig. 3a). Altitude (and by implication, temperature) showed a negative relationship while Ca-concentration showed a positive relationship. Structural overstorey heterogeneity also showed a positive relationship with woody understorey species richness (Fig. 4). The maximum number of woody species found in the understorey of *Pinus sylvestris* forests would be expected to occur in low altitude forest with an intermediate N-concentration and a high Ca-concentration in the soil, and with a relatively heterogeneous overstorey.
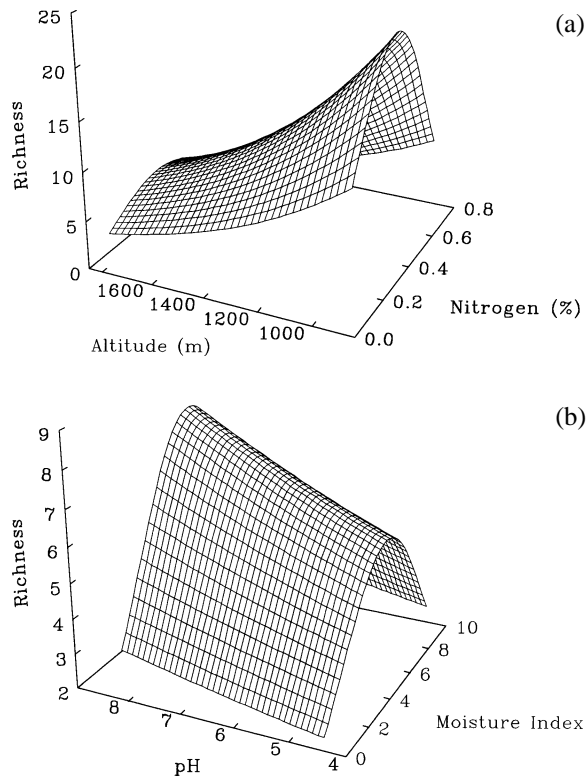
Fig. 3. Two-dimensional gradient models of woody species richness (a) and moss species richness (b) as predicted by the models in Table 4. Woody species richness is fitted for intermediate levels of both Ca-concentration and stand heterogeneity.
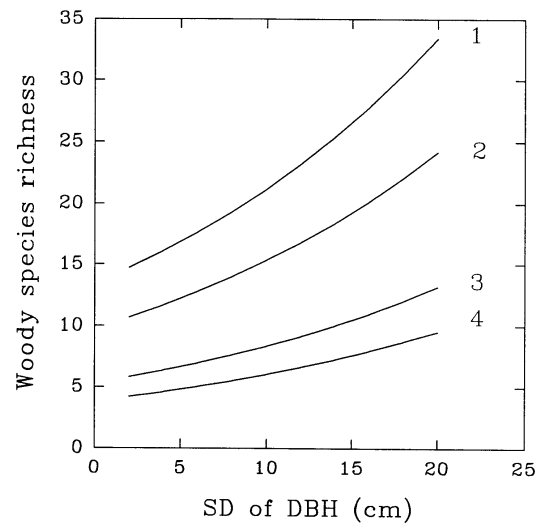

Fig. 4. Number of woody species per plot depending on forest heterogeneity (SD-DBH, DBH in cm) in four situations: 1. Low altitude and high Ca-concentration; 2. Low altitude and low Ca-concentration; 3. High altitude and high Ca-concentration; 4. High altitude and low Ca-concentration. Predictions by the model in Table 4 for intermediate-low N-concentration.

Discussion

In no case were forest structural variables, such as tree basal area or tree density, significant. This means that within the studied range of tree densities and tree basal areas, these variables are not important in the diversity of understorey species. Only within-stand forest heterogeneity accounts for a significant deviance in woody species richness (Table 4). However, this variable was entered in the model after the environmental variables. We may conclude that the main determinants of species richness in the forests sampled are the environmental variables, with solar radiation, soil N-concentration, altitude and soil moisture as the most important ones, for explaining patterns in understorey species richness.

Resources

Experimental studies have shown that soil nitrogen is a major nutrient limiting plant growth and determining the composition and diversity of herbaceous vegetation (e.g. Tilman 1988; Goldberg & Miller 1990). We found a significant relationship with soil N-concentration only for woody species, i.e. a humped curve with a maximum at intermediate levels of the variable. This observation is consistent with the main vegetation models (Grime 1979; Huston 1979; Tilman 1982, 1988;

Herb species richness

The most important variable to explain herb species richness is radiation (Table 4). A negative relationship for radiation (similar to total species richness) was found (Fig. 1). When this variable was entered into the model, neither environmental variables nor heterogeneity indicators accounted for significant change in deviance. The maximum number of herbs in the understorey was expected on shallow north-facing slopes.

Moss species richness

The variables entered in the moss species richness model were soil pH and soil moisture index (Table 4). A humped curve was found with maximum species richness at intermediate moisture levels (Fig. 3b). Also, a positive relationship for pH was found. No additional variables account for a significant change in deviance. The maximum number of moss species was expected at intermediate values of the moisture index in alkaline soils.

Keddy 1990). The number of moss species is more limited by soil moisture than by soil nutrients and a humped curve with a maximum at intermediate levels of soil moisture was found (Fig. 3b).

Calcium is the most important exchangeable cation and is related to nutrient availability (on average, 81 % of the cation exchange capacity, CEC, is due to Ca, and the CEC-Ca correlation coefficient is 0.998, $p < 0.0001$; Pausas unpubl.). Pausas & Feoli (in press a, b) found that pH was the most important parameter tested to discriminate a vegetation classification in Pyrenean *Pinus sylvestris* forests (correlation pH-Ca = 0.84, $p < 0.0001$; Table 3). We found a humped response curve for total and woody species richness in relation to Ca-concentration (Fig. 2). For woody species, this response showed a significant negatively skewed curve, but when part of the deviance was explained by altitude and nitrogen, Ca-concentration entered into the model in the linear and positive form (Table 4). These results are consistent with those of Peet & Christensen (1988), albeit they studied a narrower range of soil Ca-concentration. They found a positive relationship between species richness and soil cation concentration in North Carolina forests, and they suggested that understorey species richness tends to have a negatively skewed response to nutrient gradients.

As to light, another major resource for plants, it has been suggested that the capacity of the environment to support species is mainly determined by the availability of energy (Brown 1981; D.H. Wright 1983; Currie 1991; Rohde 1992). However, our results show a negative relationship between solar radiation and species richness (Fig. 3). This may be explained by taking the constraints and trade-offs between light and water availability into account, as suggested by Smith & Huston's model (1989). Pausas & Fons (1992) showed that water availability was a limiting factor for plant growth and production in Pyrenean pine forest. In the study area, high solar radiation implies high evapotranspiration (AET), which leads to reduced water availability to plants. And, we find fewer species in drier conditions than in wetter ones.

Other environmental variables

Altitude and latitude are indirect environmental variables indicative of average temperature. Altitudinally and latitudinally determined gradients in species richness are widespread and well-known (see reviews by Rohde 1992; Stevens 1989, 1992). Our results showed a negative relationship between altitude and woody species richness. At high altitudes, no or few deciduous species can occur due to low temperatures, while the low-altitudinal forests are often rich in deciduous shrubs.

The short growth period in cold climates (as at high altitudes) prevents deciduous species from completing their annual cycle. No significant relationships were found for the other structural groups studied. Similar richness patterns in woody species in relation to altitudinal gradients have been often reported (e.g. in Alaska, Tennessee and Costa Rica as reviewed by Stevens 1992).

Soil pH is related to nutrient availability and toxicity to plants (Barber 1984). Table 3 shows that pH is correlated with nutrient concentration. The use of nutrient availability (e.g. nitrogen) was shown to be a better predictor of species richness than pH, at least for woody species. However, no significant relationship was found between nutrients and number of moss species, although pH showed a positive relationship to moss species richness. This could be explained because most of the nutrients obtained by forest bryophytes come from the throughfall and leachate of trees and other forest plants (Rieley et al. 1979) and thus, mosses are more independent of the mineral soil than herbs or woody plants. But mosses are not independent of the litter and humus layers. The soil pH is related to the humus pH ($r = 0.493$, $p < 0.001$), however, soil nutrient contents are not related to humus nutrient contents (e.g. for N: $r = 0.206$, $p > 0.1$; for C: $r = 0.176$, $p > 0.1$; Pausas unpubl.).

Heterogeneity

The sample plots were selected to avoid the effect of disturbance and heterogeneity in searching for environmental limitations of species richness. However, some heterogeneity is inevitable. Only woody species richness showed a significant relationship with forest heterogeneity, and this relationship was positive (Fig. 4). The effect of this structural heterogeneity is more important in low altitude forests (Fig. 4). This variable entered into the model after the environmental variables, which means that in our study, woody species richness is more limited by the environment than by spatial heterogeneity. Richerson & Lum (1980) also showed a positive relationship of species richness in California with spatial (topographic) heterogeneity, and in that study, environmental variables were also more important than heterogeneity variables. For a wider range of stand-structural characteristics (in temperate montane forests of North America), Peet & Christensen (1988) showed a relationship between species richness and forest successional stages.

Species groups

After fitting the models, total species richness remains with a high residual deviance (deviance/df ≈ 3, Table 4, Fig. 2). The residual deviance decreased when

species were subdivided into different structural groups. So, the environmental predictiveness increases when each structural group is taken separately. This is certain mainly for woody species and mosses. The herb species model still remains with a high residual deviance (deviance/df ≈ 2.5). A subdivision of herbaceous species into functional groups could improve the prediction of the species richness models.

The three main structural groups growing in the understorey of *Pinus sylvestris* forest showed different species richness patterns. Similar results were found by Minchin (1989) for trees, shrubs, herbs and graminoids in Tasmanian forests. Recently, S.J. Wright (1992) reviewed some examples of different species richness patterns between trees, understorey shrubs, and herbs in tropical forests, and he suggested the importance of rooting depths in understanding those different patterns.

All these facts support Peet's (1978) hypothesis of different species richness patterns for different structural groups.

Conclusion

In this paper evidence is provided that environmental factors determine understorey vegetation patterns in mature monodominant *Pinus sylvestris* forest. Soil nutrient concentrations and moisture-related parameters are the main factors in predicting species richness in the understorey of this forest type. A humped response curve of species richness in relation to soil nutrient concentration and soil moisture was often found. However, different patterns of species richness were found for different structural groups. The biggest difference in species richness pattern was found for the two contrasting taxonomic levels, vascular plants and mosses.

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