The effect of bedrock type, temperature and moisture on species richness of Pyrenean Scots pine (*Pinus sylvestris* L.) forests

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Abstract

The relationship between environmental parameters (bedrock type, temperature and moisture index) and understorey species richness was studied from a large phytosociological data base on Pyrenean Scots pine (*Pinus sylvestris* L.) forests. Generalized linear models were used to test this relationship. Total species richness and species richness of the different life forms were considered. The results suggest different patterns for the different life forms, and that the richest forest was on the calcareous bedrock of north-facing slopes at low altitudes.

Abbreviations: GLM – Generalized Linear Modelling, MI – Moisture index

Introduction

In the south (Iberian) part of the eastern Pyrenees, forests dominated by *Pinus sylvestris* L. are widely distributed, and cover a wide range of environmental conditions. These forests are also the main wood resource of the area. Previous studies showed that growth, biomass and production of *Pinus sylvestris* (Pausas & Fons 1992; Pausas 1993) and the species composition of the understorey (Pausas & Feoli in press) were determined by environmental conditions. The hypothesis tested in this paper is that species richness is also correlated to environmental parameters. For this purpose, the relationship between species richness and environmental parameters is tested statistically using data from a phytosociological survey.

The search for patterns of species richness is one approach in addressing the conservation of biodiversity (Margules & Usher 1981). To date, no study of biological diversity in Pyrenean *Pinus sylvestris* forest has been published. Such studies are required to ensure appropriate land use and biological conservation (Probst & Crow 1991). In the light of environmental change, patterns of vegetation in relation to

environmental parameters can help to predict the vegetation response to this change.

Peet (1978) pointed out that failure to find general diversity patterns was due to a reluctance of investigators to formulate multidimensional patterns. He suggested that variations relative to all major environmental gradients should be examined simultaneously. Austin *et al.* (1990) and Austin & Gaywood (1994) have also shown the importance of searching vegetation patterns along multiple environmental gradients in order to make progress in vegetation theory.

Patterns of species richness have been reviewed elsewhere (e.g., Brown 1981; Giller 1984; Begon *et al.* 1990). We assume that in our study area environmental factors are more important predictors of plant species richness (e.g., Richerson & Lum 1980; Margules *et al.* 1987; Stevens 1992) than spatio-temporal and dispersion factors (e.g., Janzen 1970; Cornell & Lawton 1992; Leigh *et al.* 1993). Peet (1978) and Grubb (1987) suggested that patterns of plant species richness are different for different life forms. Some studies provide examples supporting this hypothesis (e.g., Richerson & Lum 1980; Minchin 1989). Minchin (1989) suggested that any adequate model of community variation along ecological gradients will need to

allow for the differences in response patterns between groups of species. Today, with the current problems of rapid environmental change and biological conservation, interest in patterns of different functional types is increasing (Chapin *et al.* 1992; Keddy 1992; see also papers in Solomon & Shugart 1993). In this context, we studied the relation of some environmental characteristics on total species richness and on the richness of different life forms (phanerophytes, hemicryptophytes, chamaephytes, geophytes and therophytes).

A characteristic of vegetation data analysis is that non classical statistical methods can be applied without violation of some important assumptions, such as a linear response or the normality of error distribution (Orlóci 1990). Therefore, different alternative numerical methods have been developed for vegetation analysis, such as methods based on fuzzy set theory (Feoli & Zuccarello 1986, 1988; Marsili-Libelli 1989), non-metric ordination (Kenkel & Orlóci 1986), entropy and information criteria (Feoli *et al.* 1984; Orlóci 1976, 1990), etc. Recent advances in statistics also offer the possibility of generating statistical models, assuming non-linear responses and different error distributions. In this context, generalized linear modelling (GLM, McCullagh & Nelder 1989), as applied in vegetation analysis by Austin *et al.*, (1984, 1990), is a suitable technique. This paper provides an example of the application of GLM in testing vegetation patterns using a phytosociological data base.

Methods

Study area

In this study, all the montane zones covered by natural *Pinus sylvestris* forests in the eastern half of the Iberian Pyrenees (between the rivers Ter and Isabena) were considered. At the eastern end of the Pyrenees, between the river Ter and the Mediterranean sea, *Pinus sylvestris* forests do not occur because of the maritime influence. Only mature stands of Scots pine were studied, and recently managed or highly disturbed forests were excluded.

The relief of the study area consists of long, straight valleys, perpendicular to the main Pyrenean axis. There is also a secondary range (Cadí-Puigmal-Canigó) that is a barrier to the moist mediterranean winds. This relief and the distance to the sea determine the main climatic conditions in the study area.

The data

292 relevés of forest dominated by *Pinus sylvestris* were extracted from the Data Base at the *Departament de Biologia Vegetal* of the *Universitat de Barcelona*. This Data Base contains phytosociological relevés (following Braun-Blanquet's method) and their physical parameters (i.e., altitude, aspect, bedrock type, relevé size, slope, topographic position). Topographic position was always mid-slope, because in lower-slopes and gullies deciduous forests occur. Of the 292 relevés, 81 were unpublished, and the rest of the relevés came from the literature (Carreras 1993; Carreras *et al.* 1993; Carrillo & Ninot 1993; Gruber 1978; Molero & Vigo 1981; Pausas & Feoli in press; Rivas Martínez 1968; Soriano 1991; Vigo 1974, 1979). 93.2% of the total relevés used (i.e., unpublished and most of the published relevés) were collected by our research group during summer field trips. The sizes of the relevés ranged from 80 to 300 m^2 with a mean of 165 m^2, but most of them (70%) were between 100 and 200 m^2.

The species were grouped into Raunkiaer life forms (phanerophytes, hemicryptophytes, chamaephytes, geophytes and therophytes). Phanerophyte species were subdivided into deciduous and evergreen (broad-leaved and needle-leaved) species, and hemicryptophytes were subdivided into graminoids (grasses) and non-graminoids (forbs) species. For each relevé, the total number of vascular plant species and the number of species of each life form was calculated. To assign the species to a life form we mainly followed Bolòs & Vigo (1984-in press). Bryophytes and lichens species were not considered since these groups are not always recorded in phytosociological surveys.

A moisture index (MI) was assigned to each relevé, on the basis of its aspect. The maximum gradient was considered from SSW as the driest aspect ($MI = 1$) to NNE as the moistest aspect ($MI = 9$). Bedrock types were grouped into 5 classes. Three were rocks without carbonates (siliceous bedrock): (a) schists; (b) acid sandstone and acid conglomerates; and (c) granites, gneiss and eruptive acid rocks. The other two rock types were rich in calcium carbonate (limestones): (d) calcoschists and (e) hard calcareous rocks. Two additional rock types were added for the relevés for which bedrock type information was not clear: (f) calcareous bedrock *sensu lato*; and g) siliceous bedrock *sensu lato*. For each relevé, mean annual temperature was estimated on the basis of data from 18 meteorological stations, the altitudinal thermal gradient calculated in the study area (0.55 °C/100 m, Xercavins

1981, see also Woodward 1987), and the aspect. The effect of aspect on temperature was previously studied with an experimental work in the study area (Pausas unpubl.), and the difference in the mean annual temperature between north-facing and south-facing forest was estimated as 2.2 °C.

Numerical analysis

Multiple polynomial regression models, based on generalized linear models, were used to test the relationship between the environment and the species richness of the understorey in Pyrenean *Pinus sylvestris* forests. The environmental variables used to fit species richness were slope, bedrock type, relevé size, moisture index and mean annual temperature. Because of the nature of the dependent variable (count), Poisson error distribution was assumed and a logarithmic link function was used. The forward stepwise procedure was used to choose the variables to enter in the model and the order of entry. The goodness-of-fit was tested by the deviance statistic. The change in deviance after including a terme was evaluated by the F-statistic, and only terms significant at $p<0.05$ were entered. Linear, quadratic and cubic terms were tested for each continuous variable. Interaction and covariates were also tested. A conceptually similar statistical method to fit species richness was used by Vicent & Haworth (1983) and Margules *et al.* (1987). The models were fitted for total vascular species richness and for the richness of the different life forms considered. Only models significant at $p<0.05$ are shown.

Results

The total number of vascular plants found in the understorey of Scots pine forests was 422. The richest understorey observed had 48 species and the poorest had 5 species. The mean number of species in the 292 relevés was 25.2. Table 1 summarizes these results for the different life forms, and Table 2 shows the first step of the stepwise procedure for total vascular plants (see below).

The order of variables included in the model depends on the life form considered (Table 3). In no case did the quadratic or cubic form of the continuous variable show a significant effect. Neither slope nor plot size showed a significant effect on the pattern of species richness in the forests studied.

Table 1. Number of relevés in which the different life forms occur, number of species for each life form in the data set (total), maximum number of species found together for each life form, and mean number of species of each life form in the 292 relevés.

| | N. of relevés | N. of species | | |
		Total	Maximum	Mean
Vascular plants	292	422	48	25.13
Phanerophytes	290	78	18	6.17
Deciduous	271	56	14	3.84
Evergreen	280	22	6	2.33
Hemicryptophytes	291	243	33	15.14
Graminoids	291	42	11	3.23
Non-graminoids	291	201	27	11.92
Chamaephytes	262	52	9	2.37
Geophytes	188	35	5	1.22
Therophytes	62	14	3	0.23

Table 2. Analysis of deviance of the 3 environmental variables for total vascular species richness.

Model	Deviance	df	F	p
null	922.60	291		
Bedrock	865.12	290	19.27	<0.0001
MI	904.73	290	5.73	0.017
Temperature	914.37	290	2.61	0.107

No significant species richness pattern was found for chamaephytes, therophytes or geophytes. This may be because of the low number of species found together for these life forms (Table 1). Thus, only the major life forms were considered (phanerophytes and hemicryptophytes).

The number of species was more dissimilar between calcareous and siliceous bedrock than within each of these two rock types (usually not significant). The bedrock was therefore classified either as siliceous (rock types without carbonates such as schists, granites, gneiss, etc.) or calcareous (carbonated rocks such as calcoschists and hard calcareous rocks).

Total vascular plant richness

The main variable explaining total species richness in the understorey vegetation was rock type (Table 2). Total species richness was higher on calcareous bedrock than on siliceous bedrock (Fig. 1). Within the

Table 3. Variables entered in the GLM model of understorey species richness for each life form and the F-statistic test (*** $p<0.001$; ** $p<0.01$; * $p<0.05$).

	Model	Deviance	df	F	p
a)	Total vascular richness				
	null	922.60	291		
	+ Bedrock	865.12	290	19.27	***
b)	Phanerophyte richness				
	null	485.03	291		
	+ Temperature	416.98	290	47.33	***
	+ Moisture	384.14	289	24.71	***
	+ Bedrock	373.48	288	8.22	**
c)	Deciduous phanerophytes richness				
	null	580.68	291		
	+ Temperature	524.49	290	31.07	***
	+ Moisture	482.29	289	25.29	***
	+ Bedrock	472.27	288	6.11	**
	+ Bedrock * Moisture	460.39	287	7.41	**
d)	Evergreen phanerophytes richness				
	null	177.71	291		
	+ Temperature	163.39	290	25.42	***
e)	Hemicryptophyte richness				
	null	775.74	291		
	+ Bedrock	747.96	290	10.77	***
f)	Non-graminoid richness				
	null	757.60	291		
	+ Bedrock	719.77	290	15.25	***
	+ Temperature	708.48	289	4.61	*

Table 4. Mean values of the main characteristics of the top 10 cm of soil on calcareous bedrock (Ca) and on siliceous bedrock (Si) in 59 plots of *Pinus sylvestris* forests. C and N is expressed as percentage, and cations as cmol(+)/kg. Significance for the t-test: ***, $p<0.001$; **, $p<0.01$; *, $p<0.05$; ns, no significative. Data from Pausas (1994).

	Bedrock type		
	Ca	Si	t-test
n	27	32	
pH	7.329	5.334	***
C	5.614	3.455	***
N	0.351	0.223	***
Ca	16.588	2.721	***
Mg	0.740	0.377	*
Na	0.054	0.048	ns
K	0.298	0.208	**
Al	0.051	0.326	***
CEC	17.731	3.680	***

later, schist was the rock type with significantly fewer species. Moisture index also showed a significant and positive relationship. However, when bedrock type was in the model, neither MI nor temperature explained a significant proportion of the deviance. So, following the forward stepwise procedure, only bedrock type was considered in the final model (Table 3a).

Phanerophyte richness

The order of variables entered in the model were as follows: temperature, moisture index and rock type (Table 3b). The same order of importance was found for deciduous species (Table 3c) as for the total phanerophyte species. Otherwise, evergreen species only showed a significant relationship to temperature (Table 3d). The number of phanerophytes increases with temperature (Fig. 2 and 3), and this increase is greater in deciduous species than in evergreen species
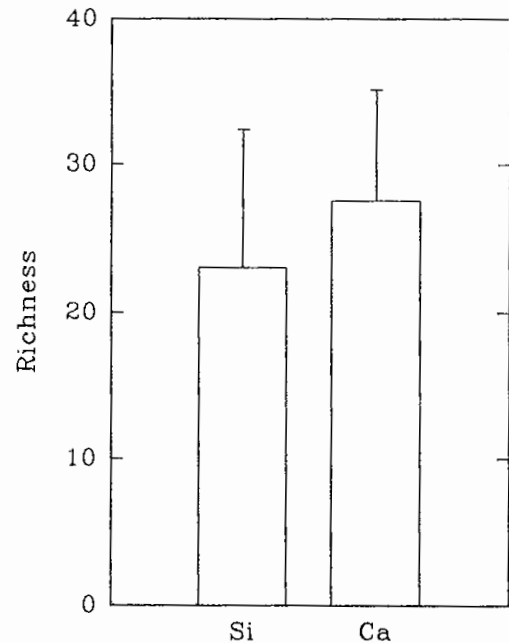

Fig. 1. Mean number of vascular plants species in the two bedrock types (Si = siliceous; Ca = calcareous). The vertical lines indicate the standard deviation. The means are significatively different at $p<0.0001$.
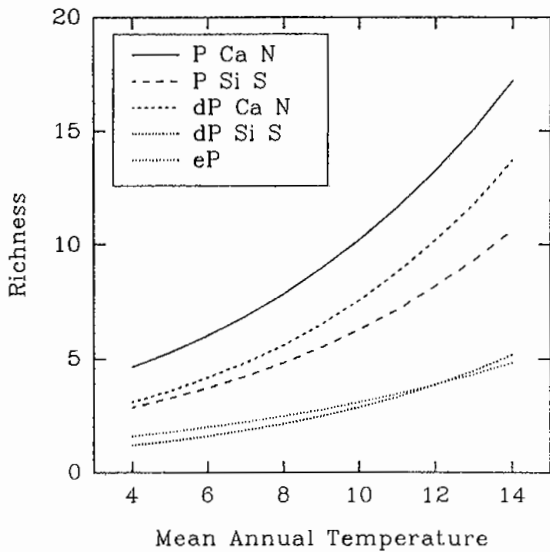
Fig. 2. Phanerophyte understorey species richness along a temperature gradient in different aspects and bedrock types. Ca = calcareous bedrock; Si = siliceous bedrock; N = north-facing slopes; S = south-facing slopes; P = total number of phanerophytes; dP = number of deciduous phanerophytes; eP = number of evergreen phanerophytes. See Table 3c for significance of the fit.
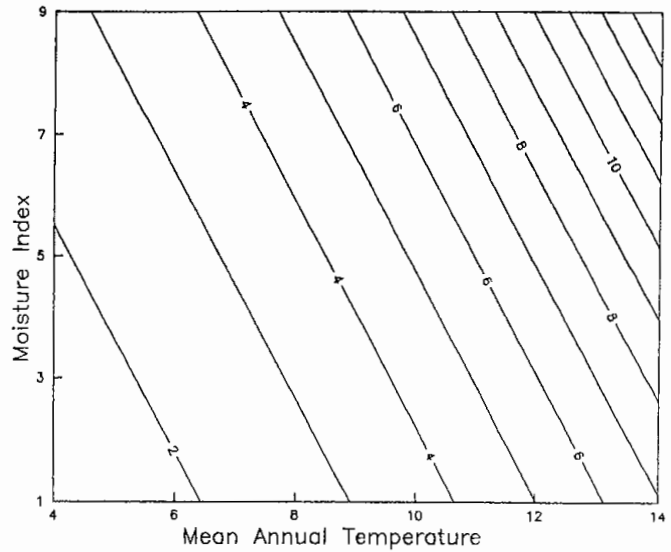

Fig. 3. Two-dimensional gradient model of deciduous phanerophyte richness in understorey of *Pinus sylvestris* forests. The model was fitted before taking account the bedrock type.

Fig. 4. Total, non-graminoid (forbs), and graminoid (grasses) hemicryptophyte species richness on calcareous rock types (Ca) and on siliceous rock types (Si). Significant differences ($p < 0.001$) between the two rock types are indicated by $***$; ns = no significant differences ($p > 0.05$). Vertical bars refers to standard deviation.

(Fig. 2). Figure 3 shows the variation of deciduous phanerophyte richness in the temperature and moisture space (without taking account the bedrock type). The effect of aspect and rock type on phanerophyte richness is similar to that for total species richness. Thus, the maximum phanerophyte richness in the understorey of *Pinus sylvestris* forest was found on calcareous bedrock, in north-facing slopes and at high temperature. In the area studied, high annual temperature is mainly related to low altitude.

Hemicryptophyte richness

The total hemicryptophyte richness showed a significant relationship with rock type only (Table 3e, Fig. 4). The number of total hemicryptophyte species, as well as the non-graminoid hemicryptophyte species was higher on calcareous bedrock than on siliceous bedrock (Fig. 4 and 5). A significant decrease of non-graminoid species richness was found along a temperature gradient (Fig. 5). No significant trends were found for graminoid species richness.
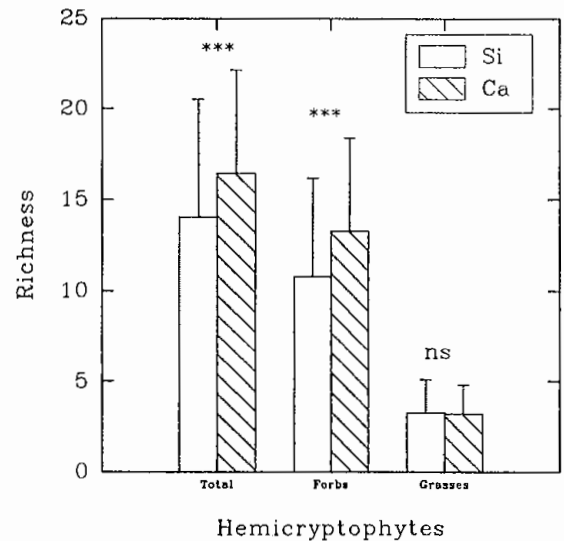
Discussion

Life form groups

Total species richness showed a significant relationship with rock type only, and the model obtained has a large residual variation (deviance/df $\approx$ 3, Table 3a).
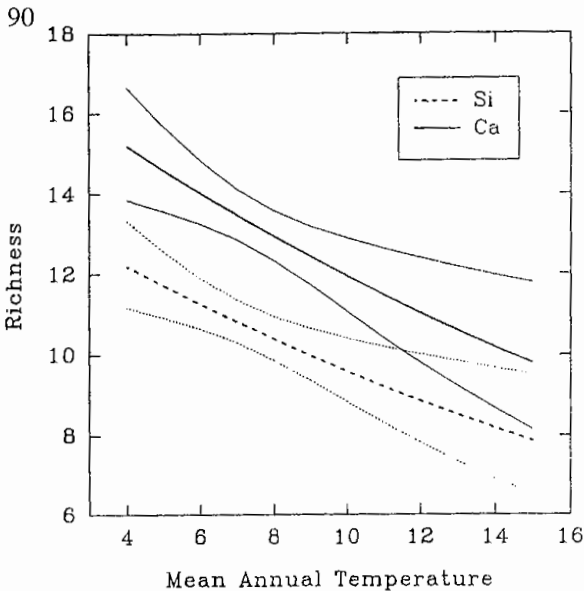
Fig. 5. Non-graminoid hemicryptophyte species richness along a temperature gradient in the two considered bedrock types (Si = siliceous; Ca = calcareous). Fitted lines and 95% confidence intervals are shown. Fitted lines are significant at $p<0.05$ level. Differences between the two bedrock types are significant at $p<0.01$ (see Table 3f).

When the species were subdivided by different life forms, moisture and temperature also became important for explaining species richness. The residual variation was also reduced after the subdivision ($0.5<$deviance/df<2.5). These features support Peet's (1978) and Grubb's (1987) suggestion that patterns of diversity in plant communities are clarified if species are divided into growth-forms. This may be due to the more direct competition within each life form. Richerson & Lum (1980) and Minchin (1989) provide additional examples of species richness patterns in different growth-forms.

Moisture

In all life form groups in which moisture index was significant, species richness showed a positive relationship to the moisture gradient. North-facing slopes are more species-rich than south-facing ones (Fig. 2 and 3), mainly due to deciduous shrubs. Water is a resource for plants and a humped curve of species richness along a moisture gradient should be expected (Grime 1979; Tilman 1982). We did not find such a pattern. This could be due to a relatively short moisture gradient sampled (in the study area, Scots pine forests occur in mid-slope only). Moreover, soil characteristics (e.g., stoniness, depth, texture) should be

included in the moisture index for a better estimation of the water availability to plants.

Temperature

Temperature has a direct physiological impact on plant growth. In our study, a positive relationship was found for phanerophytes and a negative relationship was found for non-graminoids. Cody (1991) also found a positive relationship between deciduous trees and mean annual temperature in arid environments of North America. Using an altitudinal gradient (that is negatively related to temperature), Stevens (1992) reviewed negative relationships of such a gradient with tree species richness in different environments (Alaska, Tennessee and Costa Rica). Woody species richness was also negatively related with altitude in a subset of the data used here (Pausas 1994). The positive relationship between woody species richness and temperature seems to be a general trend. In our study area, this pattern is mainly due to the deciduous species. At low temperature, no or only few deciduous species occur because the short vegetative growth period prevents deciduous species from completing the annual cycle. The relationship between temperature and the occurrence of tree species has been studied by Austin and colleagues (Austin *et al.* 1990, 1994) in temperate sclerophyllous forests. They show that there is a temperature below which the probability of tree occurrence declines.

The negative relationship that we found between non-graminoid species richness and temperature can be explained because in colder environments (of our sampled area) there are fewer phanerophytes (Fig. 2) and thus, more light reaches the herb layer. Light can be a limiting factor to species richness in the bottom layer of forests. However, graminoid species did not show such a trend. To improve the study of the temperature effect on species richness, extreme temperature (e.g., maximum temperature of the hottest month, minimum temperature of the coldest month) should be tested in addition to mean annual temperature. The role of climatic extremes in determining local species richness was suggested by Rapoport (Rapoport's rule, reviewed by Stevens 1989, 1992).

Bedrock

Significantly different species richness between calcareous bedrock and siliceous bedrock was found in all the species groups except for evergreen phanero-

phytes and graminoids. In all these cases, the number of species was higher in calcareous bedrock. Pausas (1994) has shown the influence of soil calcium concentration on understorey species richness for a subset of the data used here. Pausas & Feoli (in press) also report that soil pH is one of the main factors explaining understorey composition (correlation pH-carbonate content = 0.69, $p<0.0001$, n = 59) for the same subset. An analysis of the data from Pausas (1994) showed (Table 4) significantly higher concentrations of calcium, potassium, magnesium, carbon, nitrogen and also more cation exchange capacity (CEC), in the soil of forests on calcareous bedrock than in the soils on siliceous bedrock. Furthermore, the soil concentration of aluminium, which is a toxic ion for plants, was significantly higher in the soils on siliceous bedrock. These trends may explain the differences in species richness. The chemical differences between both types of soils (Table 4) are consistent with the general trends of soil developed in the two bedrock types considered.

Environmental space

Many studies have reported patterns of species richness along a single environmental gradient (e.g., Huston 1980; Wilson & Keddy 1988). Although there is evidence that species respond simultaneously to several environmental variables (Austin *et al.* 1990; Westman 1991; Leathwick & Mitchell 1992), little description of patterns of species richness in a multi-dimensional space has been done (Richerson & Lum 1980; Margules *et al.* 1987; Minchin 1989; Pausas 1994). Austin & Gaywood (1994) have suggested that to advance in vegetation theory, patterns of vegetation should be studied using multidimensional gradients. The present study provides an example of that in the Pyrenean forests (Table 3). Figure 3 displays graphically the pattern of shifting number of species (deciduous phanerophyte) in two-dimensional environmental space. Margules *et al.* (1987) and Minchin (1989) have shown species richness patterns in a similar environmental space. Temperature and moisture are two important parameters in determining forest productivity. Figure 3 can therefore be interpreted as the pattern of deciduous phanerophyte richness in the productivity space. The richest forest in phanerophyte species was found at high levels of both gradients. Because we studied a limited moisture and temperature gradient (e.g., gullies and ridges are not considered) no further considerations can be done about the interdependence of species

richness and productivity. A decrease of species richness in the most productive sites would be expected if a larger environmental gradient was sampled (Al-Mufti *et al.* 1977; Grime 1979; Tilman 1982; Wilson & Keddy 1988). But *Pinus sylvestris* forests do not occur at the extremes of the environmental gradient and we cannot test such a hypothesis.

Conclusion

Species richness of the understorey in *Pinus sylvestris* forests is related to environmental factors. The richest forests were found on calcareous bedrock on north-facing slopes at low altitudes. The importance of the different factors and the response to them, depends on the life form. For total species as well as for the hemicryptophytes, richness is mainly related to bedrock type (i.e., nutrient availability), while temperature was the main deciding factor for woody species richness. In the light of climate change, woody species may be more affected than herbs. Therefore, we can expect that the community will change not only in geographical (latitudinal and altitudinal) distribution, but also in species composition.

Acknowledgments

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