

Effects of local factors on plant species richness and composition of Alpine meadows

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Abstract

The determinants of plant species richness and composition of meadows are often mutually related, showing joint effects on plant diversity. Thus, the specific objective of this paper was to evaluate the relative importance of soil, topography, and field management explanatory variables on plant species richness and composition of mown meadows in an area of the Southern Alps. The data consisted of 159 *taxa* sampled during the summer of 2003 in 56 10 × 10 m² sampling plots. For each plot, 25 explanatory variables were recorded. The variation in species richness and composition was divided into the three sets of explanatory variables using a variation partitioning method. Species richness was mostly controlled both by the short-term effect of nitrogen fertilisation, and, as stressed by studies in other landscape contexts in Europe, by the long-term effect of soil phosphorus accumulation. The decrease of plant species number on the most fertile meadows was the consequence of the dominance of few competitors or ruderals, which prevented the establishment of small stress-tolerant species. In contrast to species richness, plant species composition presented an important pure effect of topography (altitude and slope). Species composition depended on several topography, soil, and field management factors. Thus, for both conservation and restoration of species-rich hay meadows, it is necessary to maintain a low level of soil P content, and to prevent the abandonment of parcels on steep slopes and in marginal areas, because these hosted the highest level of plant diversity.

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1. Introduction

In EU, agri-environment schemes have been established to support the non-production function of grasslands. However, these schemes are mainly not well targeted. They do not adequately consider the different management systems and the diversity of the local flora, and tend to increase the homogeneity of the agricultural environment. They have been demonstrated to not effectively enhance plant diversity (Kleijn and Sutherland, 2003). In order to

improve the efficiency of management measures in future agri-environment schemes, it is necessary to understand the relative importance of the main determinants affecting plant diversity in grasslands.

Species richness and composition of vascular plants in grasslands are predominantly controlled by local factors, and only secondarily by factors operating at the landscape-scale (Wright et al., 2003). Grasslands are strongly affected by field management: it has frequently been shown that the application of high doses of fertilisers and intensive sward utilization have negative effects on plant species diversity (e.g. Garcia, 1992; Myklestad and Sætersdal, 2004). Chemical and physical soil properties are related to natural

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soil characteristics, but also to fertilisation inputs, and influence both species richness and species composition of vascular plants (Myklesstad, 2004). In particular, it is well established that the phosphorus (P) soil content is an important determinant for the reconstruction or conservation of species-rich meadows (Janssens et al., 1998; Tracy and Sanderson, 2000; Critchley et al., 2002a). Other studies have shown that abiotic environmental factors, such as topographic or climatic parameters can be important sources of variation of plant diversity, because the occurrence of many grassland species is governed by microclimatological characteristics (Sebastiá, 2004; Bennie et al., 2006).

The determinants of plant species richness and composition of meadows are often mutually related, showing joint effects on plant diversity. As there is a general lack of information about the relative importance of these factors in grasslands, the specific objective of this paper is to explore the relative effect of soil, topography, and field management explanatory variables on species richness and composition of mown meadows in an area of the Southern Alps. We hypothesised that (1) species richness was mostly controlled both by the short-term effect of nitrogen (N) fertilisation (Jacquemyn et al., 2003), and, as stressed by studies in other landscape contexts in Europe (Janssens et al., 1998; Critchley et al., 2002a), by the long-term effect of soil P accumulation; (2) species composition depended strongly not only on soil fertility and field management, but also on topography due to the highly variable Alpine environment, and (3) the decrease of the number of plant species on the most fertile meadows was the consequence of the dominance of few species (Schwab et al., 2002), which prevented the establishment of small stress-tolerant plants. To test these hypotheses, we used a variation partitioning method, which is a statistical approach to evaluate the relative effect of different sets of explanatory variables on diversity patterns.

2. Materials and methods

The study area was located in Primiero and Vanoi (46°04′–46°13′N; 11°34′–11°52′E), the south-eastern district of the

Trento province, NE Italy (Fig. 1). The geology was heterogeneous with calcareous, siliceous bedrocks and mixed sediments. The climate was humid with a mean rainfall of 1200 mm y^{-1} . The mean temperature at the minimum considered altitude (610 m a.s.l.) was 9–10 °C, while it was 4.5–5.5 °C at the maximum altitude (1440 m a.s.l.).

With a preliminary strictly vegetation analysis, four hay meadow communities could be identified in the study area: (1) lowland moderate intensive meadows (*Pastinaco-Arrhenatheretum*); (2) lowland high intensive meadows (*Ranunculo repentis-Alopecuretum pratensis*), (3) mountain intensive meadows (*Trisetetum flavescens*), and (4) semi-natural extensive low productive meadows (*Bromion erecti*). Within each of the first three vegetation types, 15 meadows were randomly selected, while for (4) only 11 were chosen (Fig. 1). The 56 meadows considered in the study belonged to 15 different farms. The phytosociological nomenclature follows Mucina et al. (1993), while the nomenclature of the vascular plants is according to Wisskirchen and Haeupler (1998).

Hay meadows were fertilised in spring and autumn with farmyard manure or liquid manure, and grazed for only a few days in autumn. Rarely, mineral fertiliser was applied once between the cuts as N–P–K ternary fertilisers (mostly 20-10-10) or ammonium nitrate (34-0-0). The range of variation in usually applied fertilisation input was 0–350 kg N $ha^{-1} y^{-1}$. The meadows with the lowest level of fertilisation (<50 kg N $ha^{-1} y^{-1}$) produced on average 3.5 t dry matter $ha^{-1} y^{-1}$, while the sites with the highest level (>250 kg N $ha^{-1} y^{-1}$) had a yield of ca. 8.5 t dry matter $ha^{-1} y^{-1}$. These yields were calculated by harvesting the biomass on 33 parcels (average of two strips of $0.1 \times 10^4 m^2$ for each meadow). The cutting frequency varied from 1 to 3 cuts per year (rarely 4) depending on altitude and intensity of fertilisation.

In each selected meadow, a square of $10 \times 10 m^2$ was randomly established. Edge effects were avoided by excluding a 10-m buffer zone from the field boundaries. For each plot, a complete floristic survey was carried out before the first cut using the van der Maarel (1979) abundance estimation scale. Species richness was estimated

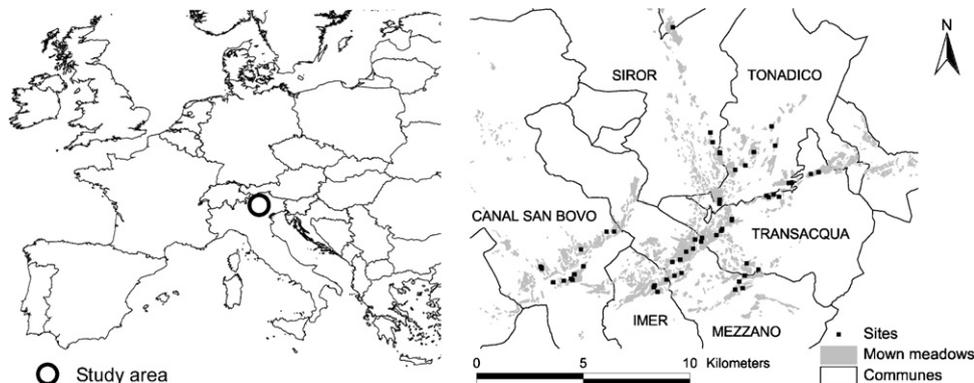


Fig. 1. Location of the 56 investigated grassland sites within the study area.

two times per site, once before the first cut and once before the second.

For all sites, 25 explanatory variables were recorded: 16 soil (*S*), 5 topography (*T*), and 4 field management variables (*M*) (Table 1). In each plot, a composite soil sample was collected during the week from 20th to 26th of August 2003. The samples were taken at a depth of 0–20 cm, after removing the organic layer, and were composed of four cores with a diameter of 12 cm taken at each of the four corners of the plot. The soil cores were bulked prior to analyses. Soil pH (measured in water), total phosphorus (aqua regia-ICPMS), total potassium (aqua regia-ICPMS), Kjeldahl total nitrogen, exchangeable magnesium (ammonium acetate extraction), Olsen phosphorus, exchangeable potassium (ammonium acetate extraction), CaO₃ (gas-volumetric determination of CO₂ with HCl), Organic Matter (Springer–Klee method), and Cation exchange capacity (method with barium chloride triethanolamine) were measured using the Italian standard soil analysis techniques (G.U., 1999). The topographic variables were calculated on the basis of a digital elevation model with a cell size of 10 × 10 m². The following quantitative explanatory variables were measured on all plots using SAGA GIS version 2.1 (available at <http://www.saga-gis.org/>): elevation, slope, mean precipitation in June (1990–

2003), sum of solar radiation in May, and topographical wetness index (Beven and Kirkby, 1979). The radiation was calculated using a constant for atmospheric transmittance of 60% and a solar constant of 1367. The mean precipitation was retrieved from Sboarina and Cescatti (2004). Field management variables (applied fertilisers and cutting frequency) were obtained from interviews using a standardized questionnaire. The total amount of N fertilisers was calculated by summing up organic and mineral N. The concentration of N for the different organic fertilisers was retrieved from Walther et al. (1994).

Prior to analyses, some explanatory variables (P_{Olsen} and N_{FERT}) were log-transformed to improve the linearity of the relations. All the other variables showed linear relations with species richness. A possible weak point of variation partitioning is caused by the potential collinearity between explanatory variables within each group of variables (Heikkinen et al., 2005). This problem can produce misleading inferences when the analysis has an explanatory approach for developing new insights (MacNally, 2000). Therefore, each of the three sets of explanatory variables was reduced to a smaller number of partially independent factors using their Pearson correlation coefficients. In case of highly correlated variables (Pearson correlation coefficient >0.6),

Table 1

Descriptive statistics of the 25 explanatory variables used in the variation partitioning procedure for plant species richness and composition of 56 mown meadows in the Italian Alps

Variables ^a	Description and unit ^b	Mean	S.D.	Min	Max
Soil (<i>S</i>)					
[SAND_2.0]	0.5 < sand fraction < 2.0 mm (g kg ⁻¹)	187.4	73.3	39.0	374.0
[SAND_0.5]	0.25 < sand fraction < 0.5 mm (g kg ⁻¹)	89.8	31.4	43.0	176.0
SAND_0.25	0.05 < sand fraction < 0.25 mm (g kg ⁻¹)	211.7	84.7	6.0	460.0
[SILT]	0.002 < silt fraction < 0.05 mm (g kg ⁻¹)	448.8	116.0	179.0	679.0
CLAY	Clay fraction < 0.002 mm (g kg ⁻¹)	61.0	30.9	10.0	180.0
pH	pH measured in water	6.0	0.7	4.9	7.3
[CaCO ₃]	Content of CaCO ₃ (g kg ⁻¹)	35.6	69.7	1.0	375.0
O.M.	Organic Matter (g kg ⁻¹)	95.6	31.6	45.0	191.0
P _{tot}	Total phosphorus (g kg ⁻¹)	1.0	0.4	0.5	2.7
K _{tot}	Total potassium (g kg ⁻¹)	3.9	1.3	1.4	7.2
[N]	Kjeldahl total nitrogen (g kg ⁻¹)	5.8	1.9	1.0	12.3
P _{Olsen}	Olsen P ₂ O ₅ (mg kg ⁻¹)	46.9	31.7	13.0	155.0
K _{ex}	Exchangeable potassium (mg kg ⁻¹)	173.7	105.3	48.0	504.0
Mg _{ex}	Exchangeable magnesium (mg kg ⁻¹)	988.7	525.4	317.0	2838.0
[CEC]	Cation Exchange Capacity (mEq kg ⁻¹)	3.1	1.0	1.5	6.7
SOIL_D	Soil depth (cm)	34.3	17.1	8.0	70.0
Topography (<i>T</i>)					
ALTIT	Altitude (m a.s.l.)	946.3	248.4	610.9	1442.5
SLOPE	Slope (%)	13.8	11.3	0.0	44.5
PREC	Mean precipitation of June (mm)	136.0	5.6	127.4	154.6
RAD	Sum solar radiation of May (kWh m ⁻²)	234.0	6.0	215.9	243.8
TWI	Topographical Wetness Index	8.7	2.2	5.5	17.4
Field management (<i>M</i>)					
CUTS	Number of cuts y ⁻¹	2.3	0.6	1.0	4.0
N _{FERT}	Total nitrogen fertilisers (kg N ha ⁻¹ y ⁻¹)	99.1	65.7	0.0	350.0
N _{FERT_M}	Mineral nitrogen fertilisers (kg N ha ⁻¹ y ⁻¹)	1.3	5.94	0.0	37.5
[N _{FERT_O}]	Organic nitrogen fertilisers (kg N ha ⁻¹ y ⁻¹)	97.8	66.1	0.0	350.0

^a Intercorrelated variables excluded after the analysis of the Pearson correlation matrix are presented in square parentheses.

^b All the soil contents are referred to kg of dry soil.

only one of them was used in the model. The excluded variables are presented in Table 1 in square parentheses. The response vector for species richness consisted of the cumulative number of species encountered in each plot with the two visits. In the species composition model, the response matrix included the abundance of the species quantified before the first cut. Species with a frequency smaller than 3% in the 56 plots were excluded prior to the analyses.

As a first step, within each set of explanatory variables, we used a separate stepwise forward procedure to select the significant variables (at $P < 0.05$) that maximally accounted for variation in each response matrix. Next, the total variation explained by the two models was divided into the three groups of explanatory variables: soil (S), topography (T), and field management (M), using a series of Partial Redundancy Analyses (partial RDAs), as implemented in CANOCO version 4.5 (ter Braak and Šmilauer, 2002). RDA is an extension of Principal Component Analysis, in which the canonical vectors are linear combinations both of the response and explanatory variables (Legendre and Legendre, 1998). All analyses were tested with a Monte Carlo Permutation Test with 999 permutations. The method of variation partitioning followed Liu and Bråkenhielm (1995). The method splits the total variation explained into seven fractions: three pure effects of the singular set (S , T and M), three shared effects of each pair of sets ($S \cap T$, $S \cap M$, and $T \cap M$), and the shared effect of the three sets ($S \cap T \cap M$). The shared fractions express the joint effect of different groups of variables that can not be attributed to one group only. Since the shared effects were obtained by subtraction, they could not be tested for significance (Legendre and Legendre, 1998). As explanatory variables were not mutually independent, variation partitioning can help determine the amount of variation related to independent and shared effects, and clarify the relative influence of the sets of variables considered (Heikkinen et al., 2005).

Furthermore, the species were classified using the C (competitor), S (stress-tolerant), and R (ruderal) plant

functional types (Grime, 2001) according to Hodgson et al. (1999). For each survey, a functional signature was derived using the Excel spreadsheet-based tool proposed by Hunt et al. (2004). This C-S-R signature is a three-part index that indicates the proportion of the three strategies in a community. The sum of the three values is set to 1. We computed simple linear regressions between species richness and the single C-, S-, and R-components.

3. Results

Plant species richness and composition were affected in a different manner by soil, topography and management factors (Table 2). The number of significant variables entering the multiple regression models after the separate stepwise forward selections was four and seven for species richness and composition, respectively. In the model of species richness, P_{Olsen} was the only significant soil variable with a negative effect on the response variable. The relation we found between P and species richness was curvilinear as demonstrated in several studies in other landscape contexts in Europe (Janssens et al., 1998; Tracy and Sanderson, 2000; Critchley et al., 2002a). Among the topographic variables, only SLOPE was significantly positively related to species richness. The field management model indicated that CUTS and N_FERT affected species richness negatively. As P_{Olsen} , N_FERT presented a curvilinear relation with the number of vascular plant species. In the regression model of species composition, the significant soil variables were: P_{Olsen} , pH, and CLAY. Significant topographic variables were ALTIT and SLOPE, indicating that elevation affected species composition but not the number of species. The field management variables were the same as for species richness. The variation explained separately by each single set was composed of a pure effect, and shared effects with the other groups (Liu and Bråkenhielm, 1995).

Table 2

Results of the stepwise forward selection of the explanatory variables in the multiple regression models of plant species richness and composition for soil (S), topography (T) and field management (M) components

	Soil model (S)			Topography model (T)			Management model (M)		
	Variable	P	R^2	Variable	P	R^2	Variable	P	R^2
Plant species richness									
	P_{Olsen} (–)	0.001		SLOPE (+)	0.001		N_FERT (–)	0.025	
	Model		45.0	Model		31.9	CUTS (–)	0.001	
							Model		47.0
Plant species composition									
	P_{Olsen}	0.001		ALTIT	0.001		CUTS	0.001	
	pH	0.044		SLOPE	0.002		N_FERT	0.021	
	CLAY	0.004		Model		16.6	Model		14.6
	Model		17.1						

The data were obtained from 56 mown meadows in the Italian Alps. For each model, the total variation explained (R^2 , equivalent to the sum of all the canonical eigenvalues) is given. Directions of associations (– or +) and the P -values (Monte Carlo Permutation test, $n = 999$) for significant variables ($P < 0.05$) are presented. See Table 1 for abbreviations of variables names.

Table 3

Variation partitioning of plant species richness and composition into soil (*S*), topography (*T*) and field management (*M*) components (R^2 in %)

	Pure effects			Shared effects				TVE ^a
	<i>S</i>	<i>T</i>	<i>M</i>	<i>S</i> ∩ <i>T</i>	<i>S</i> ∩ <i>M</i>	<i>T</i> ∩ <i>M</i>	<i>S</i> ∩ <i>T</i> ∩ <i>M</i>	
Plant species richness	9.0 (0.003)	2.4 (0.099)	7.4 (0.011)	2.3	12.4	5.9	21.3	60.7 (0.001)
Plant species composition	10.5 (0.001)	7.6 (0.001)	4.4 (0.001)	−0.1	1.1	3.5	5.6	32.6 (0.001)

The data were obtained from 56 mown meadows in the Italian Alps. The *P*-values of the pure effects and of the total model with all variables are given in brackets (Monte Carlo Permutation test, $n = 999$).

^a TVE: total variation explained.

In the variation partitioning of species richness, the total variation explained was 60.7%, indicating that the chosen variables explained a large amount of the total variation (Table 3). The pure effects of soil and of field management components were relatively large, while the pure effect of topography was not significant. The joint effects of topography, management and soil (*S*∩*T*∩*M*), and of soil and field management (*S*∩*M*) were the most important components. The model of species composition with all significant variables of the three groups together accounted for 32.6% of the total variation (Table 3). Of the pure components, the soil was again the most important component, but the pure topography component gained in importance in explaining species composition, contrasting to species richness. The two shared fractions of topography and management were also relatively important.

The response of the 28 species with a fit-range above 20% to the seven significant variables is presented as an RDA biplot (Fig. 2). The first axis accounted for 15.0% of the total variation and separated most species based on a gradient of management intensity and topography. Intensive lowland hay meadows with a high level of nitrogen fertilisation and cutting frequency were dominated by tall-growing grasses, as *Alopecurus pratensis* or *Poa trivialis*, and by competitive forbs, as *Anthriscus sylvestris* and *Rumex* sp.pl. In less intensive meadows on steeper slopes, mostly stress-tolerant grasses and forbs with a low growth-rate were found: e.g. *Festuca rupicola* and *Trifolium montanum*. On the plots at higher altitudes, there was a well-defined group of species typical of the mountain level: e.g. *Rumex arifolius* and *Trollius europaeus* differentiated these meadows from those at lower altitudes. The second axis was less important, capturing only 5.6% of the total variation, and dividing the species mainly according to the clay fraction, and further according to altitude and slope.

The simple regression models between species richness and C-, S-, and R-components of the functional signature showed significant results. The highest species richness was found in plots with high values of the S-component and with low values of the C- and R-components (Fig. 3). The S-component regression model indicated a strong positive relation between high species richness and the presence of small stress-tolerant species, while the presence of ruderals

and competitors had a negative effect. The C- and R-components were not significantly correlated.

4. Discussion

The results suggest that plant species richness and species composition responded in a different manner to the considered determinants. In line with our first hypothesis,

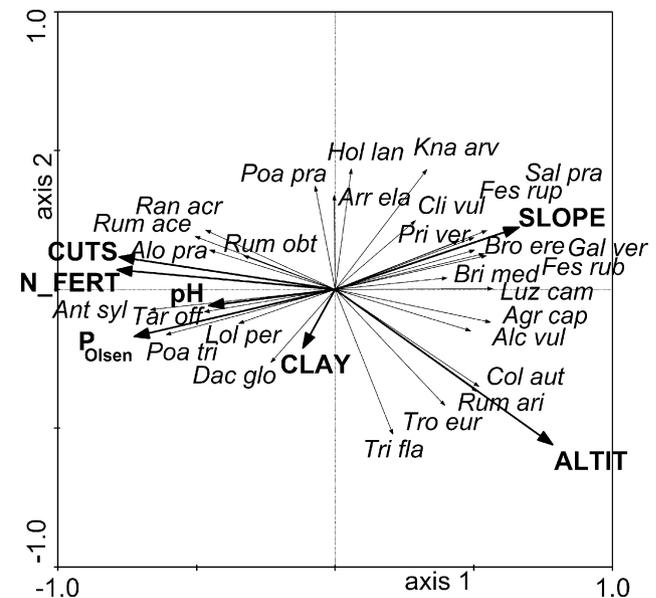


Fig. 2. Ordination plot of vascular plant species and explanatory variables along the first two axes of RDA constrained with the seven significant variables of the variation partitioning model. Only those 28 species with a fit-range above 20% are shown. The axes are scaled in standard deviation units. The data were obtained from 56 mown meadows in the Italian Alps. See Table 1 for abbreviations of variables names. Abbreviations of species' names: Agr cap: *Agrostis capillaris*; Alc vul: *Alchemilla vulgaris* agg.; Alo pra: *Alopecurus pratensis*; Ant syl: *Anthriscus sylvestris*; Arr ela: *Arrhenatherum elatius*; Bri med: *Briza media*; Bro ere: *Bromus erectus*; Cli vul: *Clinopodium vulgare*; Col aut: *Colchicum autumnale*; Dac glo: *Dactylis glomerata*; Fes rub: *Festuca rubra* agg.; Fes rup: *Festuca rupicola*; Gal ver: *Galium verum*; Hol lan: *Holcus lanatus*; Kna arv: *Knaulia arvensis*; Lol per: *Lolium perenne*; Luz cam: *Luzula campestris*; Poa pra: *Poa pratensis*; Poa tri: *Poa trivialis*; Pri ver: *Primula veris*; Ran acr: *Ranunculus acris*; Rum ace: *Rumex acetosa*; Rum ari: *Rumex arifolius*; Rum obt: *Rumex obtusifolius*; Sal pra: *Salvia pratensis*; Tar off: *Taraxacum officinale* Sect. *Ruderalia*; Tri fla: *Trisetum flavescens*; Tro eur: *Trollius europaeus*.

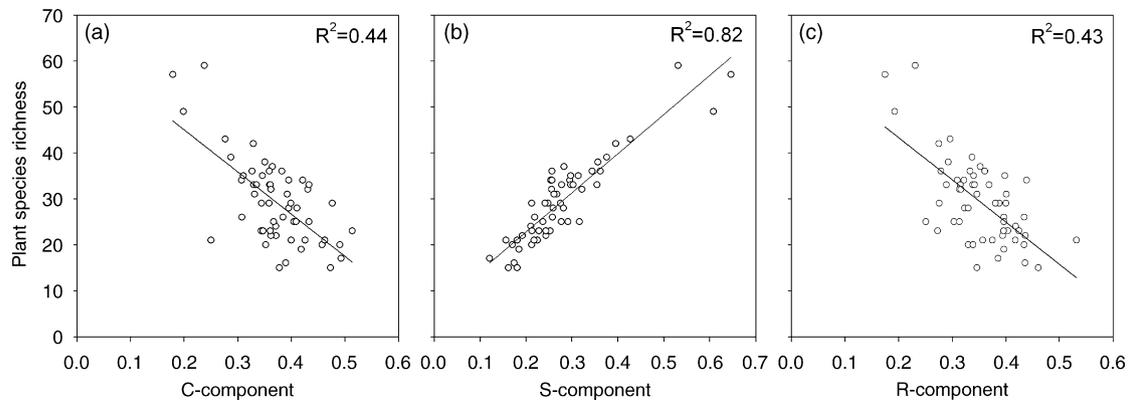


Fig. 3. Simple linear regressions of plant species richness vs. (a) C-component, (b) S-component, and (c) R-component of the functional signature according to Hunt et al. (2004). The data were obtained from 56 mown meadows in the Italian Alps. All regressions were significant at $P < 0.01$ (F -test).

species richness depended mainly on the long-term effect of field management intensity, expressed by the soil P content, as well as on the short-term effect due to N fertilisers. The pure soil component explained more variation than the pure management. However, it has to be kept in mind that the measured soil chemical variables were linked not only to the natural fertility of the site, but also to long-term management inputs. Similar relationships between species richness, soil and management were found by several authors (e.g. Schellberg et al., 1999; Myklesstad, 2004). The large P content in the more fertilised soils was probably caused by the low removal of P with harvested forage in comparison to the inputs. As demonstrated by Ekholm et al. (2005), most of the P surplus tends to accumulate in the soil in stable forms that can only relatively slowly be transported to surface waters. Our results demonstrated that P_{Olsen} has been shown to be a key factor determining the number of species. Willems and van Nieuwstadt (1996) demonstrated that the increase of species richness after the cessation of fertilisation was slower in P-rich soils than in N-rich ones, confirming the long-term effect of this element. In our study, only one plot with a P_{Olsen} content larger than 60 mg kg^{-1} contained more than 26 species per 100 m^2 . Furthermore, no plot with a content larger than 25 mg kg^{-1} had more than 40 species per 100 m^2 .

The important pure effect of field management demonstrated that soil was not solely explaining species richness. N pools are usually more dynamic in soil so that the N fertilisers can affect species richness only in the short-term after their applications (Jacquemy et al., 2003). The N fertilisers variable must be considered as an indicator of the total input of nutrients. In fact, potassium (K) and P in fertilisers were excluded from the study because they were highly correlated with N due to the prevalence of organic fertilisation.

Despite the correlation between N, P and K in fertilisers, their distribution pattern in soil is obviously different. When the P content (total and Olsen) was excluded from the analyses, total N did still not become significant. In contrast to P, the soil N content was not correlated with the

application of fertilisers, because it is quickly transformed and very dynamic in soil, and because it can be renewed from other important sources, such as atmospheric deposition, organic matter mineralization, and N fixation. Without P_{Olsen} , exchangeable K became significant but had a weaker explanatory power, indicating that moderately large K contents were compatible with high species numbers. The plots with the highest level of diversity were those with an exchangeable K content of $120\text{--}140 \text{ mg kg}^{-1}$. K has a rather high mobility in soil, but leaching losses are small compared to plant uptake, which represents the major sink in the K budget (e.g. Kayser and Isselstein, 2005). Thus, the weaker relation between exchangeable K and species richness was probably due to the removal of the herbage and to mobility of K.

The positive relation between increasing slope and species numbers was probably caused by different field management practices. This may be a consequence of the behaviour of the farmers, who managed the most accessible, less steep sites more intensively. Therefore, the relation between topography and species richness was due to a joint effect with field management and soil, and not to an independent effect. The altitude had not a significant effect on species number. In fact, species richness did not differ between the sites located on high altitude compared to the low-altitude ones.

According to our second hypothesis, species composition was affected not only by soil fertility but also by topography probably due to the high variability of the Alpine environments. As demonstrated by several authors (e.g. Snow et al., 1997; Critchley et al., 2002b; Myklesstad, 2004), P_{Olsen} is a key factor explaining the variation of species composition. Topography is also a main driver due to the strong effect of altitude and slope on temperature, and consequently on the length of the growing season, confirming that the occurrence of many grassland species is governed by microclimatological characteristics (Sebastiá, 2004; Bennie et al., 2006). Several variables had to be included in the model, most of them presenting an equivalent marginal contribution. The variation of the floristic

composition along the fertility gradient indicated the negative effect of soil P and N fertilisers on the presence of stress-tolerant species, which are normally those with the major conservationist interest (Prosser, 2001).

The regression between species richness and the C-, S-, and R-components indicated that the decrease of species richness in fertile plots was probably caused by the dominance of species with C- and R-strategies, confirming our third hypothesis that high N and P availability determined low species richness resulting from the dominance of a few competitors and ruderals. The ability of large, fast-growing perennial herbs to suppress the growth of smaller neighbours was particularly evident in the studied vegetation types. Both a reduction in species richness and an increasing dominance of few species are a common phenomenon in highly fertilised grasslands (Berendse and Elberse, 1990). P-limited meadows showed the coexistence of many individuals of different *taxa*, due to the presence of stress-tolerant species with low potential growth-rates, and small stature.

In conclusion, both field management and soil fertility were main determinants of vascular plant species richness, while for species composition topography gained in importance. Thus, for both conservation and restoration of species-rich hay meadows, it is necessary to maintain a low level of soil P content (in our study beneath a threshold of 60 mg kg⁻¹) and to prevent the abandonment of parcels on steep slopes and in marginal areas, because these hosted the highest level of plant diversity.

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