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Scale-dependent effects of land use on plant species richness of mountain grassland in the European Alps

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Traditionally managed mountain grasslands in the Alps are species-rich ecosystems that developed during centuries of livestock grazing. However, changes in land use including fertilisation of well accessible pastures and gradual abandonment of remote sites are increasingly threatening this diversity. In five regions of the Swiss and French Alps we assessed the relationship between land use, soil resource availability, cover of the unpalatable species *Veratrum album,* species richness and vegetation composition of mountain grasslands across four spatial scales ranging from 1 to 1000 m^2.

Mean species richness and the increase in the number of species with increasing area were lower in intensively grazed, fertilised pastures than in traditional pastures or in abandoned pastures. Species composition of abandoned pastures differed from that of the other management types. Plant species richness was influenced by different factors at different spatial scales. At the 1 m^2 scale, plant species richness was negatively related to soil nitrate and influenced by the cover of *V. album,* depending on land use: species richness and cover of *V. album* were negatively correlated in abandoned pastures, but positively correlated in fertilised grasslands. At the 1000 m^2 scale, a negative effect of fertilization on richness was evident. These results indicate that at small scales species richness in mountain grasslands is determined by competition for light, which should be more important if nutrient availability is high, and by positive and negative interactions with unpalatable plants. In contrast, species richness at the large scale appears to be mainly influenced by land use. This result emphasizes the importance of studying such inter-relationships at multiple scales. Our study further suggests that the maintenance of the traditional land use scheme is crucial for the conservation of plant species richness of mountain pastures as both intensification and abandonment changed species composition and reduced plant species diversity.

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In recent years changes in land use and other human activities have resulted in a decrease in species richness world-wide (Hooper et al. 2005 and references therein). Species richness is seen as an insurance against a decline in ecosystem services, such as the prevention of soil erosion and maintenance of hydrological cycles, or in ecosystem goods, such as tourism and recreation (Hooper et al. 2005). In Europe, the diversity of grasslands has dramatically decreased in lowland areas, whereas many traditionally managed mountain

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grasslands are still species-rich (MacDonald et al. 2000). However, changes in land use are threatening these habitats as well. At present we see increasing intensification of the use of well accessible sites paralleled by abandonment of less accessible sites in the European Alps (Tasser and Tappeiner 2002). When traditionally managed mountain grasslands below the tree line are abandoned, their floristic composition changes and their agricultural quality decreases, leading in the long term to reforestation and a significant reduction in biodiversity (Fischer and Wipf 2002). This development is difficult to reverse (Stampfli and Zeiter 1999), because of limited seed dispersal, recruitment and micro-site availability (Tilman 1997, Zobel et al. 2000). Intensification, in particular the application of fertiliser, has also been shown to decrease the species richness of mountain grasslands (Theodose and Bowman 1997, Nagy et al. 2003).

Most studies of the effects of land use change on plant species richness and vegetation composition in mountain grasslands were carried out at very small scales (Stampfli and Zeiter 1999, Fischer and Wipf 2002, Tasser and Tappeiner 2002, Dullinger et al. 2003, Müller et al. 2003, Kleijn and Müller-Schärer in press). However, patterns in plant species richness and the underlying mechanisms can vary considerably among different spatial scales (Huston 1999 and references therein). At the scale of an individual pasture, the traditionally managed mountain grasslands are characterized by a large number of different microsites (Austrheim and Eriksson 2001, Erschbamer et al. 2003). This diversity of microsites can be explained by small-scale variation in topography and by the effects of grazing that increases the number of microhabitats through spatially heterogeneous defoliation, trampling, wallowing and faecal deposition (WallisDeVries et al. 1998). Heterogeneous sites consisting of a large number of different microsites are considered to support a large variety of plant species (Olff and Ritchie 1998). Both the fertilisation of grasslands, because it homogenises soil nutrients, and their abandonment, because the sites are no longer grazed, are likely to reduce the spatial heterogeneity. Hence, we hypothesize that species richness will decline in both cases. This process, however, may be scale-dependent since the degree of heterogeneity changes with spatial scales.

Unpalatable weeds are among the factors possibly influencing plant diversity and are strongly related to land use and land-use change in mountain grassland. One of the most prominent representatives of unpalatable weeds in the European Alps is *Veratrum album* (Liliaceae), a large, highly toxic monocot native to Europe and Asia. It has attained pest status in France, Switzerland, Italy, Austria and Slovenia (FAO unpubl.). Because of its tall growth, it may negatively affect species richness at small scales simply due to competition for space (Crawley and Harral 2001). However, when grazing is intense, unpalatable plants may act as facilitator species that enhance plant species richness (Bertness and Callaway 1994, Callaway et al. 2005). This suggests that the effect of unpalatable plants on species richness may depend on management. Furthermore, the interrelationship between species richness and weed abundance may also vary across spatial scales within a single management type. For example, while competition may lead to a negative relationship between weed abundance and species richness at small scales, extrinsic factors such as disturbance or propagule supply may affect species richness and weed abundance in a similar way at larger scales and thereby mask factors operating at neighbourhood scales (Levine et al. 2002). In a study in mountain grasslands of the Rocky Mountains, Stohlgren et al. (1999) found that native species richness and number of exotic weeds were negatively correlated at small scales (1 m^2), but positively correlated at large scales (1000 m^2).

The aim of this study was to investigate the effects of land use, soil properties, and the abundance of *V. album* on the species richness of mountain grasslands at four spatial scales. We addressed the following questions: 1) is there an effect of land use on plant species richness and is this effect scale-dependent? 2) How well do management, soil chemistry and the abundance of *V. album* explain plant species richness at small and at large spatial scales? 3) Does the effect of *V. album* on plant species richness depend on land use and spatial scale?

Methods

Study sites

Fifteen sites below the tree line with a high presence of the unpalatable plant *Veratrum album* (Liliaceae) were selected in five different regions of the Alps (Beaufortin, Bauges, Chablais in France, and Chablais and Lac de Dix in Switzerland, cf. Appendix 1). *Veratrum album* is an important weed of many mountain grasslands. It is typically found in natural grasslands above the tree line and in open woodlands, but has invaded semi-natural grasslands below the tree line. Large herbivores do not browse on *V. album* due to the high alkaloid concentration in all plant parts (Binns et al. 1972; for more details see Kleijn and Steinger 2002).

Within each region three sites were selected: a traditionally used unfertilised pasture (hereafter called "traditional pasture"), a grazed and fertilised pasture ("fertilised pasture"), and a grassland that had been abandoned for at least 5 yr ("abandoned pasture"). In the following we refer to these three categories as "land use" and to grazing or fertilisation as "management". Fertilised grasslands had received either inorganic fertiliser or liquid manure for several years. Because abandoned pastures were rarest, they were chosen first. Then, the other two pasture types were selected within 5 km of this site, as similar as possible with regard to altitude, exposition and inclination. Information about time since abandonment, fertiliser application and duration of application were obtained from the farmers.

Vegetation and soil

At each site one modified Whittaker plot (MWP, Stohlgren et al. 1999) of 50 × 20 m was established in an homogeneously managed area (cf. Fig. 1). The minimum distance to adjacent areas with different land use was at least 15 m for abandoned sites and 50 m for sites with other management. The MWP was placed with its long side along the main slope. Nested in the MWP was one 100 m^2 subplot (5 × 20 m) in the centre and two 10 m^2 subplots (5 × 2 m) in opposite corners of the plot. Ten 1 m^2 subplots (each 0.5 × 2 m) were regularly spaced within the MWP, six of them along the inner border of the 1000 m^2 plot and four along the outer border of the central 100 m^2 subplot. For each MWP, elevation and main exposition in degrees from north were recorded with a GPS and the inclination of the slope was calculated using the elevation of the upper and lower corner of the MWP recorded by the GPS. All sites were sampled in summer 2003 or 2004.

In the 1 m^2 subplots of the MWP, the foliar cover of all plant species and the area covered by bare ground and rocks were estimated to the nearest percent. Species with a cover of <1% were assigned a cover value of 0.5%. Species richness (total number of species in a sample area) was recorded separately at each scale and each plot.

Twelve soil samples were taken in each 1 m^2 plot (ø 2.5 cm, depth 10 cm) to analyse soil chemical properties and moisture content. Soil samples were pooled per 1 m^2 plot, transferred to a deep-freezer (−18°C) within a few hours after sampling and kept frozen until further processing. NH_4 and NO_3-concentrations were measured with a colorimeter (Flow analyser, Skalar San Plus, The Netherlands) after solving 50 g soil in 250 ml of 1 m KCl, and ortho-phosphate with the Olsen method (Olsen et al. 1954). Soil pH was measured after shaking 1 ml soil in 5 ml distilled water (all analyses were carried out by SADEF, Aspach, France).

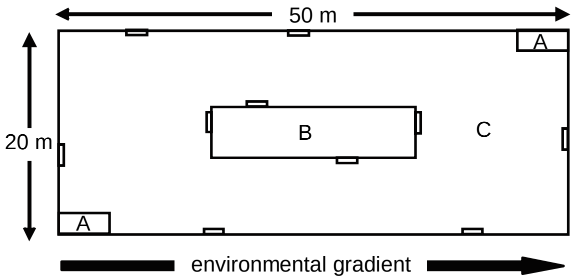

Fig. 1. Layout of the modified Whittaker plot (MWP) to study plant species diversity. The 1000 m^2 whole plot (C) contains one 100 m^2 subplot (B, 5 × 20 m), two 10 m^2 subplots (A, 5 × 2 m) and ten 1 m^2 subplots (0.5 × 2 m).

Statistical analysis

Cover data were used to calculate the mean Ellenberg light indicator value (mL, Ellenberg et al. 1991) for each 1 m^2 plot as $mL = \Sigma L_i \times p_i$, where L_i is the light indicator value of species i and pi its relative abundance. Mean Ellenberg nitrogen (mN), humidity (mH) and reaction indicator values (mR) were computed analogously. To elucidate differences among land use types with regard to site and soil characteristics, vegetation diversity indices, mean Ellenberg indicator values, and *V. album* and grass cover, ANOVAs were carried out using region (n = 5) and land use type (n = 3) as fixed factors. If an ANOVA revealed significant effects, Tukey's HSD test was used to identify significant differences between types of land use at the $p < 0.05$ level. The effect of management type (grazing, fertilisation) on species richness across multiple scales (1–1000 m^2) was assessed using a hierarchical general linear model with region, grazing, fertilisation and log(area) as fixed factors and site as a random factor. In this model, the sums of squares for each factor were adjusted for all factors that preceded it in the model.

To examine whether plant species richness was affected by different factors at different spatial scales, we calculated two separate hierarchical general linear models using the data from the smallest and the largest sampling scale (1 and 1000 m^2). At the 1 m^2 scale, the model included region, grazing and fertilisation as fixed factors, site as a random factor, and nitrate, ammonium, total phosphate, pH, and cover *of V. album* as covariates. Soil variables were not or only moderately correlated with each other (all $r < 0.4$). We subsequently removed non-significant variables, but because we were specifically interested in the effect of *V. album* on plant species richness, we kept the cover of *V. album* and its interactions with grazing and fertilisation in the reduced models. Because the full model that included all soil variables at the 1 m^2 scale was not significantly different from the reduced model with nitrate as only soil variable (ANOVA, $p > 0.6$), the simpler model was preferred. Similarly, at the 1000 m^2 scale, the model contained region, grazing and fertilisation as fixed factors, and nitrate and cover of *V. album* as covariates.

To assess whether vegetation composition differed among land use types, the log-transformed cover values of the species in the 1 m^2 plots were analysed by the ordination technique non-metric multidimensional scaling (NMDS, Shepard 1962, Kruskal 1964), with the

Bray-Curtis coefficient as distance measure. NMDS is commonly seen as the most robust unconstrained ordination method in community ecology (Minchin 1987). To find indicator species for the different land use types, indicator species analyses (Dufrene and Legendre 1997) followed by a randomisation test were carried out with the log-transformed cover data.

All statistical analyses were carried out using the R statistical language (<http://cran.r-project.org/>), except for the indicator species analyses which were carried out with PC-ORD (McCune and Mefford 1999).

Results

Site characteristics

Elevation, inclination of the slope, exposition of the MWPs, and all soil variables measured did not differ among the land use types (ANOVA, all $p > 0.15$), but elevation ($F_{4,8} = 7.4$) and exposition ($F_{4,8} = 7.1$, both $p < 0.01$) differed significantly among regions.

Plant species richness

Plant species richness was significantly lower in fertilised pastures than in traditional pastures pooled over all scales (Table 1, Fig. 2). The slope of the species-area relationship was lower in the fertilised than in the traditionally used, unfertilised pastures (see significant interaction between the effects of fertilisation and spatial scale in Table 1, Fig. 2). As a consequence, species richness at 1000 m^2 was much higher in traditionally used grasslands (73.6 ± 2.01 species) than in fertilised grasslands (54.8 ± 1.48), while species richness at abandoned sites (62.8 ± 2.10) was intermediate (ANOVA, $F_{2,8} = 4.26$, $p = 0.055$; followed by Tukey's HSD test).

Plant species richness was influenced by different variables at different spatial scales (Table 2). At the 1 m^2 level, species richness was negatively related to nitrate and cover of *V. album.* Nitrate concentration and cover of *V. album* were not correlated with each other ($p > 0.4$). At the 1000 m^2 level, species richness was negatively affected by fertilisation, and only marginally negatively correlated with nitrate.

Table 1. General linear model of the effects of region, grazing, fertilisation and survey area on the number of plant species in mountain pastures of the Alps. The effects of region, grazing and fertiliser were tested against the residual variation among sites, all other effects against the residual. Significant p-values ($p < 0.05$) are in bold-face.

Source	DF	F	p
Region	4	1.23	0.371
Grazing	1	0.32	0.586
Fertiliser (within grazing)	1	5.63	**0.045**
Site	8	11.04	**<0.001**
Log (area)	1	578.58	**<0.001**
Region × Log (area)	4	7.80	**<0.001**
Grazing × Log (area)	1	0.07	0.796
Fertiliser × Log (area)	1	11.02	**0.002**
Residual	38		
Total	60		

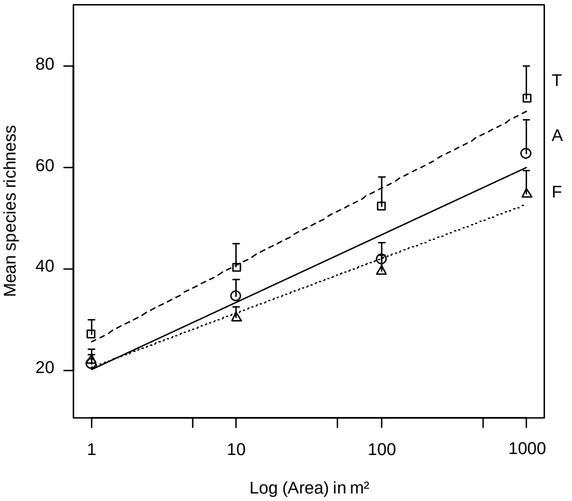

Fig. 2. Species–area relationship in mountain pastures of the Alps that had been subjected to different types of land use. Error bars indicate one standard error for each combination of land use type and area. Triangles: fertilised pastures (F); squares: traditional pastures (T); circles: abandoned pastures (A).

Vegetation composition

Plant species composition did not differ between regions (ANOVA of NMDS scores along axis 1, $p > 0.05$), but was influenced by land use ($F_{2,8} = 4.61$, $p = 0.047$), probably due to change in grass cover. The cover of grasses was highest in fertilised pastures (49.9 ± 1.3), lower in traditional pastures (40.8 ± 1.4) and lowest in abandoned pastures (30.3 ± 2.8) (ANOVA, $F_{2,8} = 4.91$, $p = 0.040$, followed by Tukey's HSD). Abandoned sites had significantly lower scores along the first NMDS axis than the two other types of land use (Tukey's HSD; Fig. 3). The scores along the first NMDS axis were negatively correlated with the Ellenberg indicator value for soil reaction ($r = 0.91$) and soil nitrogen ($r = 0.81$), suggesting that plants that typically grow at higher pH values and higher nutrient availability were more abundant in abandoned pastures. The mean light indicator value was positively related to the first NMDS axis ($r = 0.74$), suggesting that abandoned pastures contain more shade-tolerant plants than sites subjected to the two other types of land use (for all linear regressions: DF = 13, $p < 0.001$).

Mean Ellenberg indicator values for soil reaction ($F_{2,8} = 4.39$, $p = 0.051$) and light ($F_{2,8} = 3.34$, $p = 0.088$) were marginally different between land use types.

Table 2. General linear model of the effects of region, grazing, fertiliser, cover of *V. album,* and soil nitrate concentration on plant species richness in mountain pastures of the Alps at two spatial scales. The effects of region, grazing and fertiliser were tested against the residual variation among sites, all other effects against the residual. Marginally significant p-values ($0.1 > p > 0.05$) are in italics, significant p-values ($p < 0.05$) are in bold-face.

	Species richness at 1 m^2			Species richness at 1000 m^2		
Source	DF	F	p	DF	F	p
Region	4	0.29	0.878	4	7.06	**0.042**
Grazing	1	1.08	0.330	1	0.14	0.725
Fertiliser	1	1.76	0.222	1	19.30	**0.012**
Site	8	23.09	**<0.001**	–	–	–
Nitrate	1	9.81	**0.002**	1	4.65	*0.097*
Cover of *V. album*	1	4.51	**0.035**	1	1.20	0.336
V. album × grazing	1	0.01	0.923	1	3.36	0.141
V. album × fertiliser	1	2.89	*0.092*	1	5.06	*0.088*
Residual	130			4		
Total	149			15		

Abandoned pastures had the lowest indicator values for light (6.7±0.05) and the highest for soil reaction (6.4±0.05) and those were significantly different from those for the other two types of land use (fertilised pastures: mL 7.3±0.03, mR 5.5±0.15; traditional pastures: mL 7.1±0.06; mR 5.6±0.11).

Veratrum album and land use

The cover of *V. album* did not differ among land use types at any spatial scale (all $p > 0.75$), but the marginally significant interaction between the effects of fertilisation and cover of *V. album* at both scales on species richness (Table 2) suggested management-dependent effects of *V. album* on species richness. Linear regressions of species richness at the 1 m^2 scale on the abundance of *V. album* revealed different effects, depending on land use (Fig. 4). In abandoned pastures, species richness was negatively related to the cover of *V. album,* whereas the opposite was true for fertilised grasslands; in traditional pastures species richness was not related to the abundance of *V. album.* At the large scale (1000 m^2) there was no relationship between species richness and *V. album* ($p > 0.3$), but statistical power was low ($n = 5$ for each land use type).

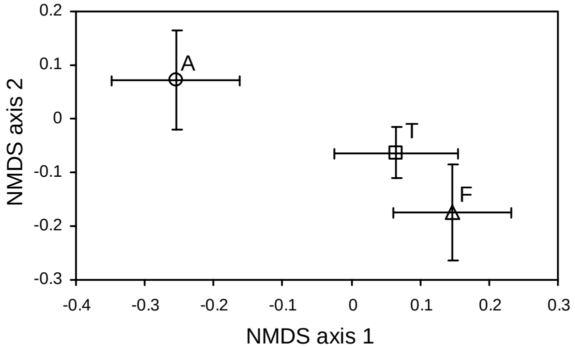

Fig. 3. Ordination diagram of a non-metric multi-dimensional scaling of the vegetational composition of mountain pastures in the Alps with different land use. Fertilised pastures (F); traditional pastures (T); abandoned pastures (A). The first NMDS axis was negatively correlated with the mean Ellenberg indicator value for soil reaction and soil nitrogen, and positively with the mean light indicator value.

Discussion

Land use, spatial scale and vegetation

Our results suggest that the effect of land use on plant species richness in mountain grasslands is scale-dependent. Fertilised pastures had an overall lower species richness, and the increase in species richness with area was smaller in fertilised pastures than in traditional pastures (cf. Fig. 2, Table 1). The different increase in species richness with area may be explained by the varying degree of heterogeneity at a given spatial scale. At the smallest scale, the ecological interactions between individual plants appear to differ among land use types, as indicated by the different vegetation composition, but they result in a similar plant species richness. At the scale of pastures, factors such as geology, topography, hydrology and management are considered to be main determinants of plant species richness by creating a matrix of habitats with variable plant species composition (Crawley and Harral 2001). This is in agreement with our findings, indicating that at the scale of 1000 m^2 traditional pastures harbour a more diverse matrix of habitats than fertilized pastures. We hypothesize that fertiliser application has lead to the homogenisation of some of the heterogeneity initially present at the largest scale. As a consequence, fertilised plant communities were dominated by a few plant species (mainly grasses) well adapted to the increased availability of nutrients and to intense grazing pressure, whereas the traditional pastures contained a high number of subdominant species with different micro-habitat requirements (Appendix 2).

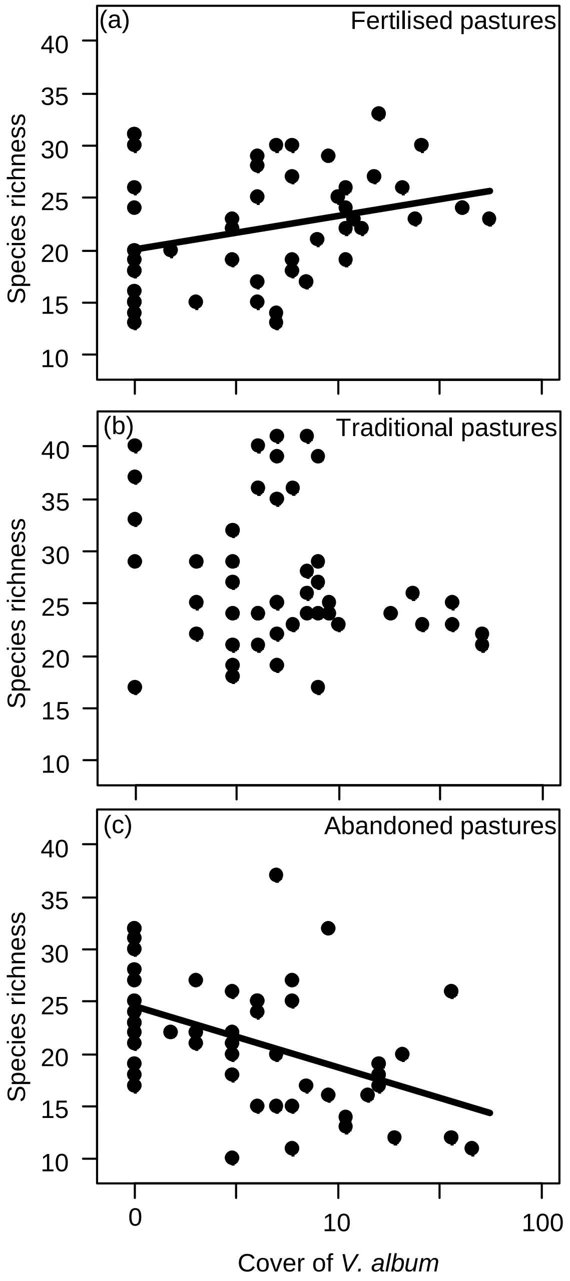

Fig. 4. The relationship between the species richness in 1 m^2 plots and the cover of the unpalatable plant *Veratrum album* at sites with different management in the Alps, (a) Fertilised ($r = 0.30$, $p < 0.05$), (b) traditionally used ($p > 0.1$), and (c) abandoned ($r = -0.46$, $p < 0.001$) mountain pastures ($n = 50$ for each type of land use).

Apart from spatial heterogeneity, species richness of grasslands may also be strongly influenced by the disturbance regime (Milchunas et al. 1988). In agreement with the intermediate disturbance hypothesis (Connell 1978, Huston 1979), we found the species richest communities in traditional pastures, where the level of disturbance is intermediate between that at fertilized and abandoned sites. Grazing pressure and thus disturbance is high in fertilised pastures, whereas at abandoned sites there is no grazing and thus little disturbance. In fertilized pastures mainly grasses were found as characteristic species (Appendix 2). In mountain grasslands, most forbs are adapted to low nutrient conditions and less tolerant to grazing than grasses (Oksanen 1990, Oksanen and Moen 1994). At fertilised sites with intense grazing pressure grasses may thus outcompete the less grazing-tolerant forbs. In the case of abandoned sites, shade-tolerant species (e.g. *Chaerophyllum hirsutum*, *Geranium sylvaticum*, *Equisetum sylvaticum*; Appendix 2) were more dominant, suggesting increased competition for light.

The plant community of abandoned grasslands differed from that of traditional and fertilised pastures, although the sites had only been abandoned for 5–40 yr. In mountain grasslands of the Alps shifts in vegetational composition can occur rapidly and may be already detectable four years after abandonment (Stampfli 1992). The absence of continuous grazing by livestock allowed some common forest species to establish and spread, but at the same time reduced the abundance of a number of uncommon or rare plant species characteristic for traditional pastures, such as *Arnica montana* and *Orchis maculata* (Appendix 2). Thus, abandonment resulted in a decrease in conservation value due to changes in species composition even though species richness did not decline significantly.

Scale-dependent responses of species richness

Our study indicates that factors influencing species richness in mountain grasslands vary with scale, probably due to different mechanisms operating at different scales. For example, at small spatial scales interactions between *V. album* and other plant species as well as soil nitrate concentration influenced species richness. At small spatial scales in grasslands, competition for space generally is very important (Tilman 1994). *Veratrum album* is one of the tallest and largest plants of its community. It is also one of the first plants that starts growing in spring and it reaches its maximal shoot biomass about two months before most other plants (Kleijn and Müller-Schärer in press). It therefore may have a competitive advantage over smaller forbs and grasses due to asymmetric competition for light (Newman 1973).

Ammonium was the predominant form of inorganic soil nitrogen in our study sites, which is typical for many mountain areas (Körner 1999). Nevertheless, species richness was not influenced by ammonium, but by nitrate levels. Nutrient enrichment experiments at arctic and alpine sites revealed that a higher availability of nitrogen increases the productivity of these sites (Nordin et al. 2004, van Wijk et al. 2004) and alters their species composition (Graglia et al. 2001, Richardson et al. 2002). McKane et al. (2002) provide evidence that plants growing in cold climatic zones differ in timing, chemical form, and depth of nitrogen uptake. It remains unclear, though, why particular forms of nitrogen should be more strongly linked to species richness than others. Probably, high nitrate availability mainly increases grass biomass, which may lead to an out-shading of less competitive forb species (Willems et al. 1993).

At the 1000 m^2 scale, the only significant factor explaining species richness was fertiliser application. It should be noted, though, that the statistical power to detect effects of the covariates at the 1000 m^2 scale was much lower than at the 1 m^2 scale (denominator DF at 1000 $m^2 = 4$; at 1 $m^2 = 130$). This may have influenced the results and explain why nitrate and the *V. album* × fertiliser interaction were only marginally significant at the 1000 m^2 scale. Nevertheless, our results indicate that management interventions such as fertiliser application, which usually are carried out at the level of whole pastures, are more important determinants of large-scale species richness than parameters describing small-scale resource availability.

The interacting effects of *Veratrum album* and land use on species richness

Our study provides evidence that, apart from the well established direct effects of land use on species richness, there is also a link between land use and species richness via "mediator species" which promote or reduce species richness depending on land use. In our study, species richness was positively related to the abundance of the toxic *V. album* in fertilised pastures, where grazing pressure was strong. Our findings are in agreement with the results of Callaway et al. (2000) and Smit et al. (2006) and suggest indirect facilitation of other species by *V. album.* However, at abandoned sites species richness decreased with increasing abundance of *V. album* suggesting competition. At such sites *V. album* may out-compete other species due to decreased light availability under *V. album* (Kleijn and Müller-Schärer in press). Similarly, Callaway et al. (2005) reported that removing *Veratrum lobelianum* from sites where cattle grazing was permitted reduced species richness, whereas inside an exclosure the removal of *Veratrum* increased community richness. *Veratrum album* is generally seen as an undesirable species for agriculture, as it reduces fodder quality, but like other unpalatable species (Ellenberg 1989, Callaway et al. 2000), it may have positive effects on plant diversity if grazing is intense (Bertness and Callaway 1994).

At large scales, we found neither a relationship between species richness and the abundance of *V. album* nor between the land use types and the abundance of *V. album,* but both might be due to the low statistical power. One could assume that pastures with a high abundance of weeds are preferentially abandoned because of their low forage quality. We did not find support for this in our study, since the cover of *V. album* was similar at sites with different land use. Nevertheless, it is likely that, once a pasture has become invaded by *V. album,* cattle stocking will be reduced due to decreased forage quality. This in turn may promote the further spread of *V. album,* because trampling by cattle limits establishment of seedlings of *V. album* (Treier pers. comm.). Moreover, the presence of *V. album* increases the survival of tree saplings (Smit et al. 2006) in grazed pastures, and may therefore accelerate the process of a gradual abandonment and of reforestation of mountain grasslands.

Conclusions

Our study across five regions of the Alps indicates that different mechanisms influence species richness at different spatial scales. Unpalatable plants play an important role as mediator species by modifying the effect of land use on plant species diversity. At small scales nutrient availability and positive and negative interactions with unpalatable species determine species richness. *Veratrum album* reduces species richness in abandoned pastures, but preserves plant diversity when grazing is intense. At larger scales, plant species richness and vegetational composition are determined by management. This finding emphasizes the importance of studying effects of land use on species diversity especially at larger scales. Maintaining the traditional land use appears to be the most promising approach to conserve the high biodiversity of mountain grasslands.

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Ecography

E4631
Spiegelberger, T., Matthies, D., Müller-Schärer, H. and Schaffner, U. 2006. Scale-dependent effects of land use on plant species richness of mountain grassland in the European Alps. – Ecography 29: 541–548.

Appendix 1. Description of study sites in France (F) and Switzerland (CH). Type of land use: F, fertilised; T, traditional; A, abandoned pasture.

Country	Region	Land use	Elevation	Inclination	Exposition	Cattle density ha^{-1}	% cover *V. album*
F	Bauges	F	1628 m	18%	W	1.2	15.9
F	Bauges	T	1607 m	27%	W	0.8	3.5
F	Bauges	A	1755 m	36%	NW	–	3.2
F	Beaufortin	F	1914 m	25%	NWN	1.3	3.3
F	Beaufortin	T	1891 m	23%	NNW	0.4	3.5
F	Beaufortin	A	1838 m	29%	WNW	–	3.6
F	Chablais	F	1550 m	36%	NNW	1.4	3.3
F	Chablais	T	1470 m	36%	NNW	1.0	4.0
F	Chablais	A	1470 m	36%	NNW	–	2.0
CH	Chablais	F	1539 m	47%	W	1.8	4.3
CH	Chablais	T	1409 m	20%	W	0.9	24.6
CH	Chablais	A	1517 m	31%	WSW	–	24.3
CH	Lac de Dix	F	1255 m	36%	NW	1.4	4.3
CH	Lac de Dix	T	1646 m	32%	WSW	0.8	5.5
CH	Lac de Dix	A	1507 m	79%	SW	–	4.5

Appendix 2. Indicator species analysis (Dufrene and Legendre 1997) for plant species of mountain grasslands in the Alps. All p-values <0.01. Species are arranged according to the land use type they indicate (F = fertilised pastures; T = traditional pastures; A = abandoned pastures).

Species	Indicator species for	Cumulative presence			Mean cover		
		F	T	A	F	T	A
Festuca rubra	F	46	45	35	9.4	8.6	3.1
Cynosurus cristatus	F	35	21	19	6.0	2.6	2.2
Anthoxanthum odoratum	F	29	21	12	3.6	1.7	1.2
Taraxacum officinale	F	25	10	10	1.4	0.5	0.6
Luzula alpinopilosa	F	24	22	1	2.0	0.9	0.1
Leontodon autumnalis	F	22	8	1	1.1	0.3	0.1
Carum carvi	F	17	7	3	2.7	0.4	0.0
Phleum phleoides	F	10	0	0	3.1	0.0	0.0
Knautia dipsacifolia	F	7	0	1	0.1	0.0	0.0
Trifolium pratensis	T	36	38	15	1.7	2.6	0.8
Leucanthemum vulgare	T	5	21	12	0.1	0.5	0.3
Lotus corniculatus	T	8	18	4	0.3	0.9	0.1
Geum montanum	T	5	17	3	0.2	0.5	0.1
Crepis aurea	T	6	16	0	0.1	0.7	0.0
Homogyne alpina	T	1	15	4	0.0	0.6	0.2
Phyteuma orbiculare	T	4	14	2	0.1	0.4	0.0
Cirsium acaule	T	0	14	0	0.0	0.7	0.0
Hieracium lactucella	T	6	12	0	0.2	0.6	0.0
Polygala vulgaris	T	0	10	1	0.0	0.2	0.0
Phyteuma betonicifolium	T	0	10	0	0.0	0.2	0.0
Arnica montana	T	0	10	0	0.0	1.5	0.0
Alchemilla flabellata	T	0	10	0	0.0	0.5	0.0
Poa pratensis	T	0	9	2	0.0	2.2	0.4
Myosotis sylvatica	T	1	9	0	0.0	0.2	0.0
Galium mullogo	T	0	9	1	0.0	0.1	0.0
Holcus mollis	T	0	8	1	0.0	1.2	0.0
Centaurea pseudophrygia	T	3	8	0	0.2	0.8	0.0
Carex sempervirens	T	0	8	0	0.0	0.5	0.0
Orchis mascula	T	0	6	0	0.0	0.1	0.0
Gagea fistulosa	T	0	6	0	0.0	0.1	0.0
Deschampsia caespitosa	A	7	25	28	0.7	4.2	8.4
Chaerophyllum hirsutum	A	33	43	48	1.9	4.6	6.5
Geranium sylvaticum	A	22	34	39	1.4	2.5	5.1
Heracleum sphondylium	A	2	0	7	0.1	0.0	2.6
Phleum pratensis	A	0	10	16	0.0	0.9	1.6
Rubus sp.	A	0	0	7	0.0	0.0	1.3
Bromus erectus	A	3	0	8	0.1	0.0	1.2
Equisetum sylvaticum	A	0	0	8	0.0	0.0	0.8
Hypericum maculatum	A	9	14	21	0.1	0.2	0.7
Carex montana	A	0	0	6	0.0	0.0	0.6
Rosa canina	A	0	0	8	0.0	0.0	0.4
Myosotis decumbens	A	0	0	8	0.0	0.0	0.4
Centaurea jacea	A	6	2	15	0.1	0.0	0.4
Cardamine pratensis	A	0	0	8	0.0	0.0	0.1