

Patterns of plant species richness in Alpine hay meadows: Local vs. landscape controls

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Abstract

Habitat type and quality are recognised as important local determinants of species richness, but other processes operating at the landscape scale can also affect diversity patterns. The evidence regarding the relative importance of landscape context on vascular plants is diverse, and little is known about the effects of this complex factor in Alpine environments. Hence, the primary purpose of the study was to elucidate the relative effects of the determinants of plant species richness by decomposing the variation into local and landscape components. We sampled 99 hay meadows in the Italian Alps, and recorded 14 explanatory variables ascribed to three sets: two sets of local variables, meadow management and abiotic environment, and a set of landscape variables. Plant diversity was affected primarily by local determinants. Species richness tended to increase in less fertilised meadows, confirming the detrimental effect of intensive meadow management on plant diversity. Site conditions such as steep slopes also enhanced plant species richness, showing a most pronounced positive effect in meadows that were cut less frequently. As to the landscape determinants, a high proportion of urban elements affected species richness negatively probably due to further eutrophication. In contrast, an increased length of meadow edges had a positive effect, particularly in meadows located on shallow soils. Partitioning analyses revealed that the three sets of variables showed relatively large shared effects with each other (over half of the total variation explained). In conclusion, the composition of the surrounding landscape had a lower impact on vascular plant species richness than did meadow management and local abiotic environment.

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Zusammenfassung

Habitattyp und -qualität werden für wichtige lokale Determinanten des Artenreichtums gehalten, aber auch andere Prozesse, die auf der Landschaftsskala wirken, können Diversitätsmuster beeinflussen. Die Hinweise auf die relative Wichtigkeit dieses Landschaftszusammenhangs sind divers, und bisher ist wenig über die Effekte dieses komplexen Faktors in alpinen Umwelten bekannt. Daher war der primäre Grund dieser Untersuchung, die relativen Effekte der Determinanten des Pflanzenartenreichtums zu untersuchen, indem die Variation in lokale und Landschaftselemente zerlegt wurde. Wir beprobten neunundneunzig Heuwiesen in den italienischen Alpen und erfassten vierzehn erklärende

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Variablen, die drei Gruppen zugeordnet wurden: zwei Gruppen lokaler Variablen und einer Gruppe von Landschaftsvariablen. Die Pflanzendiversität wurde vor allem durch die lokalen Determinanten beeinflusst. Der Artenreichtum tendierte zu einer Zunahme in weniger gedüngten Wiesen und bestätigte den negativen Effekt einer intensiven Bewirtschaftung auf die Pflanzendiversität. Flächenbedingungen, wie steile Steigungen, verbesserten den Pflanzenreichtum, und zeigten einen besonders großen positiven Effekt in Wiesen, die weniger häufig gemäht wurden. In Bezug auf die Landschaftsdeterminanten beeinflusste ein hoher Anteil urbaner Elemente den Artenreichtum vermutlich aufgrund der zusätzlichen Eutrophierung negativ. Im Gegensatz dazu hatte eine zunehmende Länge der Wiesenränder einen positiven Effekt, besonders bei Wiesen auf flachgründigem Boden. Die „Partitioning“-Analyse ließ erkennen, dass die drei Gruppen von Variablen relativ große gemeinsame Effekte miteinander zeigten (mehr als die Hälfte der erklärten Variation). Es ließ sich schlussfolgern, dass die Zusammensetzung der umgebenden Landschaft einen geringeren Einfluss auf den Artenreichtum von Gefäßpflanzen hat als die Wiesenbewirtschaftung und die lokale abiotische Umwelt.

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Introduction

Habitat type and quality are recognised as important local determinants of species richness (Rosenzweig, 1995), but other processes operating at landscape level can affect diversity patterns (Whittaker, Willis, & Field, 2001). At the local scale, the current agricultural exploitation in many European countries affects biodiversity negatively, mostly due to intensification and abandonment of low-productive and traditionally managed habitats (Strijker, 2005). At the landscape scale, this change in land use has led to a homogenisation of the landscape matrix and to a fragmentation of seminatural habitats (Tschardtke, Klein, Kruss, Steffan-Dewenter, & Thies, 2005). Nowadays, two trends of meadow management can be observed in the Alps. The number of traditional farms has decreased, and many marginal sites far from the farms have been abandoned, mostly for economic reasons (Tasser & Tappeiner, 2002). The remnant farms, characterised by high stocking rates, are mostly concentrated on productive valley soils, and farm enlargement along with land consolidation has led to lower landscape heterogeneity. Moreover, as the Alps are of high tourist interest, the accompanied urbanisation continues to occupy new areas in the valleys. The consequences are the development of new plant communities related to high input management and the disappearance of rare vegetation types depending on low-to-moderate management intensity (Scotton, Marini, Pecile, Franchi, & Fezzi, 2005). Due to this change in land use, in the last decades of the 20th century, a drastic local loss of plant species related to traditionally managed grasslands has been observed (Prosser, 2001).

Local grassland characteristics have been demonstrated to be important drivers of species richness due to different management (Gough, Osenberg, Gross, &

Collins, 2000; Jacquemyn, Brys, & Hermy, 2003), abiotic environment (Bennie, Hill, Baxter, & Huntley, 2006; Sebastià, 2004), and soil characteristics (Critchley et al., 2002). A recent study on the effects of local factors on plant diversity in Alpine meadows (Marini, Scotton, Klimek, Isselstein, & Pecile, 2007) revealed that the long- and short-term effects of fertiliser applications are the main determinants of plant species richness and composition. However, additional processes operating simultaneously at a larger scale can cause variation on local species richness (Whittaker et al., 2001). It is also well established that landscape processes have an important effect on species richness of various animal taxa (e.g. Kleijn & van Langevelde, 2006; Söderström, Svensson, Vessby, & Glimskär, 2001). The relevant scales at which landscape processes potentially affect animal diversity depend on size, mobility, and functional traits of the different taxa (Tschardtke et al., 2005). Less is known about the influence of the surrounding landscape on sessile organisms such as vascular plants, and the evidence regarding the relative importance of this complex factor is varied. For instance, Söderström et al. (2001) and Roschewitz, Gabriel, Tschardtke, and Thies (2005) demonstrated that plant species richness was generally lower in sites surrounded by a large proportion of arable land, while Weibull, Östman, and Granqvist (2003) reported that the number of plants was affected positively by small-scale landscape heterogeneity. Other studies stressed a non-significant relation with the surrounding landscape (Dauber et al., 2003; Krauss, Klein, Steffan-Dewenter, & Tschardtke, 2004). The potential importance of landscape factors on vascular plants of grassland in Alpine environments has still received limited attention. Thus, the analysis of the ecological interactions between local and landscape processes is an important task in determining which factors influence changes in local

communities, with important implications for conservation planning (Kleijn & van Langevelde, 2006; Mazerolle & Villard, 1999).

The primary aim of this study was to evaluate the relative effects of meadow management, abiotic environment, and landscape context, and their potential interactions on local species richness of vascular plants in Alpine hay meadows. Our hypotheses were: (1) plant species richness is primarily controlled by local determinants due to the strong effect of grassland management (Jacquemyn et al., 2003), and the abiotic environment (Bennie et al., 2006; Sebastià, 2004), and (2) the surrounding landscape has a significant effect on species richness depending on the level of disturbance due to urbanisation (Thompson & Jones, 1999) and by influencing the pool of species surrounding the sites (Freestone & Harrison, 2006; Shmida & Wilson, 1985). To test these hypotheses, we used variation partitioning and hierarchical partitioning in a complementary manner to evaluate the contribution of local and landscape determinants in explaining plant species richness.

Materials and methods

Study site

The surveys were carried out between 2002 and 2003 in five administrative districts of the Trento Province (NE Italy): Low Valsugana and Tesino, High Valsugana, Primiero, Fiemme Valley, and Fassa Valley. Mean annual rainfall in the area was ca. 1050 mm; mean annual temperature at the minimum elevation considered (319 m a.s.l.) was ca. 12 °C, and it was ca. 3.5 °C at the maximum elevation (1910 m a.s.l.). The mown meadows in the study area were located mainly in two different landscape contexts due to topography and land use: (1) relatively highly urbanised flat valleys, where the agricultural and dairy farming activities were concentrated; here, the agricultural landscape was characterised by hay meadows, forage cultures, and, in the external valleys, by apple plantations; (2) little urbanised steeper mountain slopes mainly covered by forests, and secondarily by mown meadows.

Sampling

We selected 99 management units from the five districts in close collaboration with the farmers using as selection criterion the characteristics of meadow management in order to sample a large gradient of management intensity. Then, we carried out the floristic, environmental, and landscape surveys. The minimum distance between the studied meadows was 1 km. The

management unit area ranged from 0.08 to 3.50 ha. In each selected meadow, a square of 10 × 10 m was randomly established. Edge effects were reduced by excluding a 10 m buffer zone from the management unit boundaries. All the vascular plants in the square were identified to species and recorded by visiting the sites once before the first and once before the second cut. In all the analyses, species richness was the cumulative number of species per 100 m² found during the two visits. The sampled meadows covered a wide range of Alpine herbaceous mown vegetation from extensively to intensively managed hay meadows.

Explanatory variables

For each meadow, we determined 14 explanatory variables belonging to three different groups: two sets of local variables, meadow management (*M*) and abiotic environment (*E*), and a set of landscape variables (*L*) (Table 1).

Four meadow management variables were obtained by interviews with the farmers using a standardised questionnaire. The meadows were cut one to four times per year, and sometimes young cattle grazed the aftermath for a few days in autumn. The fertilisation was mostly organic and was applied in spring and autumn, while mineral fertilisers were very rarely used once between the cuts as NPK fertilisers (mostly 20-10-10) or ammonium nitrate (34-0-0). The contents of nitrogen (N) in organic fertilisers were taken from Walther et al. (1994). As N, phosphorus (P), and potassium (K) in fertilisers were highly correlated ($r > 0.9$), only the N content was included in further analyses. Both fertiliser N and cutting frequency were considered as measures of management intensity in this study.

Except for soil depth, the abiotic environmental variables were calculated in SAGA GIS Version 1.2 (available at <http://www.saga-gis.org/>) using a digital elevation model with a cell size of 10 × 10 m. The precipitation data were retrieved from continuous raster-based maps provided from Sboarina and Cescatti (2004). For each meadow, soil depth was determined as the mean depth of four holes dug at the corners of the vegetation square.

The landscape variables were derived from a detailed vector-based land use map (Territory Informative Systems of the Trento Province). We defined six classes of land use: (1) urban elements (houses, streets, and other urban land uses), (2) grassland and forage cultures, (3) woody cultures (mostly apple), (4) forests, (5) water bodies, and (6) other land uses. For each meadow, around the geographic centre of the sampling plot, we calculated a circular buffer with a 500 m radius to quantify the surrounding landscape. This spatial scale

Table 1. Descriptive statistics of the 14 explanatory variables considered for each of the 99 hay meadows in the Italian Alps

Set	Name	Description and unit	MEAN	SE	MIN	MAX
Meadow management (<i>M</i>)	CUT	Number of cuts per year	2.18	0.1	1	4
	NTot	Total amount of fertiliser nitrogen (kg N ha ⁻¹ yr ⁻¹)	107.44	0.877	0	439
	NOrg ^a	Amount of organic fertiliser nitrogen (kg N ha ⁻¹ yr ⁻¹)	96.42	0.826	0	350
	NMin	Amount of mineral fertiliser nitrogen (kg N ha ⁻¹ yr ⁻¹)	10.92	0.285	0	300
Abiotic environment (<i>E</i>)	SLO	Mean slope of the management unit (deg)	7.17	0.062	0	28.85
	ALT	Altitude of the management unit (m a.s.l.)	979.71	3.564	319	1910
	RAD	Cumulative radiation of May (kWh m ⁻²)	176.81	0.109	140.77	199.97
	PRE	Cumulative precipitation of May, June, July, August and September (mm)	545.42	0.693	434.3	673.2
	SOIL	Mean soil depth (cm)	34.10	0.158	8	76
Landscape context (<i>L</i>)	URB	Proportion of urban elements within 500 m radius (%)	11.85	0.116	0	45.87
	GRA	Proportion of grassland area within 500 m radius (%)	38.56	1.533	10.08	86.22
	FOR ^a	Proportion of forest area within 500 m radius (%)	40.09	23.821	3.66	84.61
	EDGE	Length of edges between meadows and the other land-use classes within 500 m radius (m)	8268.35	40.385	160	21060
	AREA	Area of the management unit (m ²)	4833.44	619.224	801	34998

^aNOrg and FOR were excluded because strongly correlated with NTot and GRA, respectively.

was chosen in view of the fact that vascular plants are sessile and that for plants landscape processes could operate at this spatial scale (Söderström et al., 2001; Tschardt et al., 2005). Prior to further analyses, we checked the accuracy of land-use classes within the buffers using aerial photographs to avoid classification errors. Then, we processed the buffers with FRAGSTATS 3.3 (available at www.umass.edu/landeco/research/fragstats/fragstats.html) to calculate the landscape metrics related to our hypotheses (Table 1). We selected the proportion of urban elements surrounding each meadow as a surrogate of human disturbance, the length of meadow edges as potential neighbouring sources of propagules, the proportion of grassland as a simple measure of structural connectivity (Moilanen & Nieminen, 2002), and the management unit area.

Besides local and landscape factors, regional variation is very likely to affect local patterns of species richness (Borcard, Legendre, & Drapeau, 1992). In order to account for such large-scale gradients, we took the spatial structure into account, using a trend surface analysis based on the longitude (*X*) and latitude (*Y*) of each management unit. The spatial variables were calculated by including all terms for a cubic trend surface regression (*X*, *Y*, *X*², *Y*², *XY*, *X*²*Y*, *XY*², *X*³, *Y*³). Before the analysis, the coordinates were centred on their respective means to reduce multicollinearity among the terms (Legendre & Legendre, 1998).

Data analysis

To determine the relative influence of the three sets of variables on the response variable, we applied ordinary least square (OLS) linear regression with variation partitioning (Borcard et al., 1992) and hierarchical partitioning (Chevan & Sutherland, 1991). Since a clear statistical rationale needs to be developed before partitioning analyses can be safely generalised to non-OLS situations (Araújo & Guisan, 2006), we did not apply a Poisson error distribution, although species richness data were counts. The explanatory variables were standardised to mean zero and unit standard deviation to make the coefficient estimates comparable in terms of importance.

Given that multicollinearity among explanatory variables can hamper the identification of the most causal variables (MacNally, 2000), we calculated the Pearson correlation matrix of the variables and out of every highly correlated pair ($r > 0.60$) only one variable was retained for further analyses (Table 1).

First, we performed a forward stepwise regression of the 12 explanatory variables ($P < 0.05$) to select significant predictors, which most accounted for the variation in species richness. To allow for curvilinear effects of the explanatory variables, we incorporated their linear and quadratic terms. Then, the significant variables were further analysed by means of a variation

partitioning approach to determine the relative influence of meadow management, abiotic environment, and landscape on species richness (Borcard et al., 1992). The variation in species richness was decomposed using a series of (partial) regression analyses with redundancy analysis (RDA), implemented in the program CANOCO version 4.5 (ter Braak & Šmilauer, 2002). All the RDAs were tested for significance with a Monte Carlo Permutation test (No = 1000). The total variation in species richness was decomposed into eight components (Heikkinen, Luoto, Virkkala, & Raino, 2004): the pure effect of meadow management (M), the pure effect of abiotic environment (E), the pure effect of landscape (L), the joint effect of abiotic environment and landscape ($E \cap L$), the joint effect of meadow management and environment ($M \cap E$), the joint effect of meadow management and landscape ($M \cap L$), the joint effect of the three sets ($M \cap E \cap L$), and the variation unexplained by the variables included in the analysis (Un).

Besides variation partitioning, we applied hierarchical partitioning to determine the relative effect of the individual variables on species richness by splitting the variation explained into independent and joint effects (Chevan & Sutherland, 1991). The hierarchical partitioning procedure was performed using the ‘Hier. part.’ package version 0.5–1.0 (MacNally & Walsh, 2004), which runs in conjunction with R version 2.4.1 (available at <http://www.R-project.org>). Since hierarchical partitioning depends on monotonic relationships between the response variable and predictors, fertiliser N and urban elements were log-transformed to improve linearity. The statistical significance of the independent effects was tested by a randomisation procedure as described by MacNally (2002).

In addition, to reveal more complex relations between the investigated explanatory variables and plant species richness, we tested the first-order interactions by applying a forward selection procedure ($P < 0.05$) of these terms in the variation partitioning model. However, the significant interactions in multiple regressions could not be considered in partitioning analyses, because their contributions cannot be attributed to any of the predictors involved in the interaction (Araújo & Guisan, 2006).

Lastly, we performed a backward stepwise regression by including the nine spatial terms of the trend surface equation into the final model consisting of the significant main effects and interactions (Legendre & Legendre, 1998).

Results

In the 99 investigated hay meadows, we found 237 vascular plant species, 43 were monocotyledons and 194 dicotyledons. The mean species richness was 31 per

100 m², with a minimum of 15 and a maximum of 59 per 100 m². Plant species richness tended to be greater in meadows with low management input and meadows located on steep slope. The proportion of urban elements had a negative influence on the number of species, while the length of meadow edges had a positive effect (Table 2). The amount of variation captured by all the significant explanatory variables was 51.2%.

The variation partitioning indicated that all three sets had a significant pure effect on the response variable (Table 3), confirming that species richness was controlled by both local and landscape determinants. Overall, plant species richness in managed grasslands was best explained by the explanatory variables reflecting meadow management (12.3%), while the environmental site conditions (4.6%) and landscape (6.2%) presented smaller pure effects. The analysis showed also large fractions of shared variation, i.e. variation which

Table 2. Summary of the explanatory variables’ influences on plant species richness in the multiple linear regression model resulting from the stepwise selection of the linear and quadratic terms ($P < 0.05$)

Variables ^a	Standard coefficient	Standard error	<i>t</i>	<i>P</i>
Intercept	31.0707	0.5924	52.45	<0.001
SLO	2.0281	0.6834	2.97	0.004
NTot	−7.6978	1.8418	−4.18	<0.001
NTot ²	5.3863	1.7633	3.05	0.003
EDGE	1.5971	0.6416	2.49	0.015
URB	−1.5273	0.6603	−2.31	0.023

^aVariable names are according to Table 1.

Table 3. Partitioning of the plant species richness variation explained in the multiple regression model resulting from the stepwise selection of the linear and quadratic terms of the explanatory variables ($P < 0.05$)

	Variable set ^a	<i>R</i> ² (%) ^b	<i>P</i> ^c
Pure effects	<i>M</i>	12.3	0.001
	<i>E</i>	4.6	0.001
	<i>L</i>	6.2	0.001
Shared effects	$M \cap E$	8.5	—
	$M \cap L$	6.7	—
	$E \cap L$	3.9	—
	$M \cap E \cap L$	9.0	—
TVE		51.2	0.001
Unexplained		48.8	—

^a*M*: meadow management, *E*: abiotic environment, *L*: landscape context. TVE: total variation explained.

^b*R*² corresponds to the amount of explained variation (sum of all canonical eigenvalues in pRDAs).

^c*P*-value of Monte Carlo permutation test (No = 1000). The shared effects were obtained by subtraction and could not be tested for significance.

cannot be attributed to any group exclusively. Among these shared effects, the largest part was accounted for by the joint effect of the three sets and by the joint effect of meadow management with abiotic environment.

The results of the hierarchical partitioning confirmed that a relatively large part of the explained variation was related to joint effects of the explanatory variables. Nevertheless, many predictors had a significant independent contribution ($P < 0.01$). N fertiliser had the greatest independent contribution (7.7%), followed by slope (3.9%), number of cuts (3.4%), and proportion of urban elements (3.1%). Radiation, soil depth, and the length of meadow edges had only limited pure effects (Fig. 1). The independent effects resulting from hierarchical partitioning were generally comparable to those obtained through variation partitioning.

The additional analysis of the first-order interactions revealed two significant terms, the interaction between cutting frequency and slope (standardised coefficient = -4.122 ; SE = 1.738; $t = -2.371$; $P = 0.020$) and the interaction between edge length and soil depth (standardised coefficient = -3.254 ; SE = 1.604; $t = -2.029$; $P = 0.045$). The former indicated a more pronounced positive relation between species richness and slope in meadows that were cut less frequently, while the latter indicated a more pronounced positive relation between species richness and the edge length in meadows that were located on more shallow soils. In the model with interactions, the main effects of cutting frequency and

soil depth were not significant, while all the other variables remained significant. The model with the two interaction terms explained 59.2% of the total variation in species richness.

The backward procedure testing the nine spatial terms did not find any significant term ($P < 0.05$), indicating the absence of spatial structuring in the model residuals.

Discussion

Both local and landscape determinants significantly influenced plant species richness in the 99 Alpine hay meadows studied. The partitioning analyses demonstrated that vascular plants were primarily controlled by local variables, such as meadow management and environmental site characteristics, and secondarily by factors operating at the landscape scale (Fig. 1 and Table 3). A relatively large part of the variation captured was related to shared effects of the predictors. In particular, we found important joint effects of meadow management with abiotic environment and landscape context.

In line with our first hypothesis, the results of the partitioning methods suggested that species richness was mainly affected by meadow management. The analyses showed that species richness tended to increase in less fertilised meadows. These findings conform to several studies, which found pronounced decreases in species diversity after nutrient enrichment (e.g. Gough et al., 2000; Marini et al., 2007). According to the total competition hypothesis (Rajaniemi, 2002), the combination of above-ground and below-ground competition in the highly fertilised meadows reduces species richness due to interspecific competitive exclusion. Intensive management tends to create a vegetation dominated by tall grasses and competitive forbs, which reduce light availability for the smaller plants (Jacquemyn et al., 2003). In contrast, extensively fertilised meadows, where resources such as nutrients or soil moisture are generally limiting, promote diversity by enabling coexistence due to niche overlaps. Site conditions such as steep slope also contributed to high plant species richness. Both the relatively large pure positive effect of slope and its significant interaction with cutting frequency indicated that grassland swards on steep slopes were probably more resistant to invasion by high-growing competitive species than on flatter sites. Steeper slopes with poor soils are characterised by more extreme microclimatological conditions (Pykälä, Luoto, Heikkinen, & Kontula, 2005), which may increase species diversity by enabling less competitive plant species to co-exist.

Regarding our second hypothesis, the partitioning results confirmed that the landscape context influenced species richness significantly. First, the negative relation

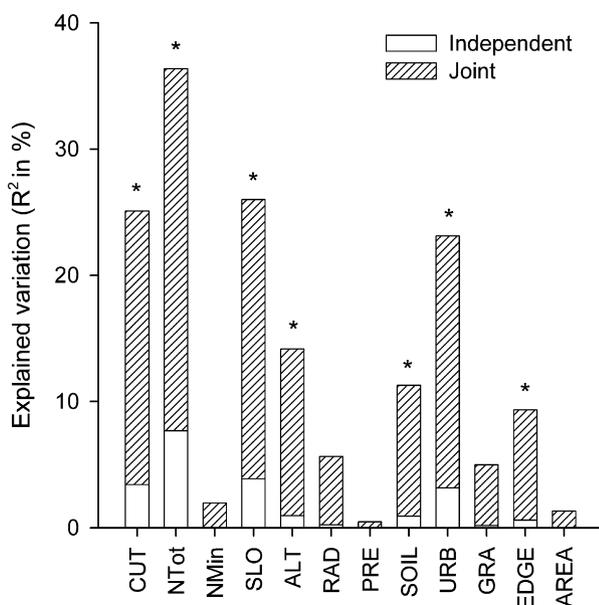


Fig. 1. Independent and joint contributions (R^2 in %) of the considered explanatory variables for plant species richness as estimated by hierarchical partitioning for 99 meadows in the Italian Alps. Variable names are according to Table 1. NTot and URB were log-transformed. Variables showing significant independent effects ($P < 0.01$) resulting from the z -randomisation procedure (No = 200) are indicated (*).

between the proportion of urban elements in the surrounding landscape and species richness was possibly due to additional nutrient inputs into the meadows located in urbanised and intensively managed agricultural areas (Stevens, Dise, Mountford, & Gowing, 2004). These areas act as important sources of nutrients, which derive from cowshed emissions and leaks, vehicular traffic, and from the relatively extensive use of fossil fuels (Thompson & Jones, 1999). This explanation is supported by the fact that, in the study area, most of the cowsheds were located in urbanised areas. This variable did not interact with any of the local ecological gradients, indicating that the level of urbanisation may affect species richness independent of local constraints on the plant community.

Second, local plant communities were expected to respond to landscape processes based on the assumption that both colonisation from neighbouring ‘source’ habitats and regional extinction should be important processes (Zonneveld, 1995). According to the mass effect hypothesis (Shmida & Wilson, 1985), grasslands could be affected by propagule colonisation from the surrounding landscape, particularly after the creation of small-scale disturbances such as vegetation gaps due to grazing or cutting. Large areas covered by urban elements may negatively affect the species pool surrounding the meadows. The negative relation between the proportion of an inhospitable habitat and grassland species richness conforms to the findings of Söderström et al. (2001), who found that species richness was generally lower in pastures surrounded by a large proportion of arable land. In contrast, the length of meadow edges in the surrounding landscape had a positive effect on local species richness. Meadow edges are characterised by a less intensive management (Marshall & Moonen, 2002), and are typically accompanied by a transition in the diversity and structural complexity of plant communities (Harper et al., 2005). Edges are likely to host a greater number of species (Saunders, Hobbs, & Margules, 1991), which could potentially disperse into the meadow sites. The positive effect of edge length on species richness was more pronounced in extensive meadows on shallow than on deep soils probably due to natural P limitations in the more superficial soils (Bennie et al., 2006). As demonstrated by Freestone and Harrison (2006), the propagule availability from the species pool surrounding the sites may consistently enrich local communities, even if other limiting processes such as local competition, abiotic gradients, and habitat heterogeneity operate at the local scale.

In conclusion, the composition of the surrounding landscape had a lower impact on vascular plant species richness than did meadow management and local abiotic environment. Further studies considering explicitly the surrounding pool of species may therefore be necessary

to provide a better explanation of the observed response of plant species richness to the landscape context. To preserve plant diversity in Alpine mown meadows, our results indicate that conservation policy should focus on extensive management practices. However, landscape factors should also be considered when making conservation decisions, because plant communities responded significantly to landscape processes.

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References

- Araújo, M. B., & Guisan, A. (2006). Five (or so) challenges for species distribution modelling. *Journal of Biogeography*, *33*, 1677–1688.
- Bennie, J., Hill, M. O., Baxter, R., & Huntley, B. (2006). Influence of slope and aspect on long-term vegetation change in British chalk grasslands. *Journal of Ecology*, *94*, 355–368.
- Borcard, D., Legendre, P., & Drapeau, P. (1992). Partialling out the spatial component of ecological variation. *Ecology*, *73*, 1045–1055.
- Chevan, A., & Sutherland, M. (1991). Hierarchical partitioning. *The American Statistician*, *45*, 90–96.
- Critchley, C. N. R., Chambers, B. J., Fowbert, J. A., Sanderson, R. A., Bhogal, A., & Rose, S. C. (2002). Association between lowland grassland plant communities and soil properties. *Biological Conservation*, *105*, 199–215.
- Dauber, J., Hirsch, M., Simmering, D., Waldhardt, R., Otte, A., & Wolters, V. (2003). Landscape structure as an indicator of biodiversity: Matrix effects on species richness. *Agriculture, Ecosystems & Environment*, *98*, 321–329.
- Freestone, A. L., & Harrison, S. (2006). Regional enrichment of local assemblages is robust to variation in local productivity, abiotic gradients, and heterogeneity. *Ecology Letters*, *9*, 95–192.
- Gough, L., Osenberg, C. W., Gross, K. L., & Collins, S. L. (2000). Fertilization effects on species density and primary productivity in herbaceous plant communities. *Oikos*, *89*, 428–439.
- Harper, K. A., MacDonald, S. E., Burton, P. J., Chen, J., Brosfoske, K. D., Saunders, S. C., et al. (2005). Edge

- influence on forest structure and composition in fragmented landscapes. *Conservation Biology*, 19, 768–782.
- Heikkinen, R. K., Luoto, M., Virkkala, R., & Raino, K. (2004). Effects of habitat cover, landscape structure and spatial variables on the abundance of birds in an agricultural-forest mosaic. *Journal of Applied Ecology*, 41, 824–835.
- Jacquemyn, H., Brys, R., & Hermy, M. (2003). Short-time effects of different management regimes on the response of calcareous grassland vegetation to increased nitrogen. *Biological Conservation*, 111, 137–147.
- Kleijn, D., & van Langevelde, F. (2006). Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. *Basic and Applied Ecology*, 7, 201–214.
- Krauss, J., Klein, A. M., Steffan-Dewenter, I., & Tscharntke, T. (2004). Effects of habitat area, isolation, and landscape diversity on plant species richness of calcareous grasslands. *Biodiversity and Conservation*, 13, 1427–1439.
- Legendre, P., & Legendre, L. (1998). *Numerical ecology* (2nd ed.). Amsterdam: Elsevier Science BV.
- MacNally, R. (2000). Regression and model-building in conservation biology, biogeography and ecology: The distinction between—and reconciliation of—‘predictive’ and ‘explanatory’ models. *Biodiversity and Conservation*, 9, 655–671.
- MacNally, R. (2002). Multiple regression and inference in ecology and conservation biology: Further comments on identifying important predictor variables. *Biodiversity and Conservation*, 11, 1397–1401.
- MacNally, R., & Walsh, C. (2004). Hierarchical partitioning public-domain software. *Biodiversity and Conservation*, 13, 659–660.
- Marini, L., Scotton, M., Klimek, S., Isselstein, J., & Pecile, A. (2007). Effects of local factors on plant species richness and composition of Alpine meadows. *Agriculture, Ecosystems & Environment*, 119, 281–288.
- Marshall, E. J. P., & Moonen, A. C. (2002). Field margins in northern Europe: Their functions and interactions with agriculture. *Agriculture, Ecosystems & Environment*, 89, 5–21.
- Mazerolle, M. A., & Villard, M. (1999). Patch characteristics and landscape context as predictors of species presence and abundance: A review. *Ecoscience*, 6, 117–124.
- Moilanen, A., & Nieminen, M. (2002). Simple connectivity measures in spatial ecology. *Ecology*, 83, 1131–1145.
- Prosser, F. (2001). *Lista rossa della flora del Trentino. Pteridofite e fanerogame*. Museo Civico di Rovereto. Trento: Edizioni Osiride.
- Pykälä, J., Luoto, M., Heikkinen, R. K., & Kontula, T. (2005). Plant species richness and persistence of rare plants in abandoned semi-natural grasslands in northern Europe. *Basic and Applied Ecology*, 6, 25–33.
- Rajaniemi, T. K. (2002). Why does fertilization reduce plant species density? Testing three competition-based hypotheses. *Journal of Ecology*, 90, 316–324.
- Roschewitz, I., Gabriel, D., Tscharntke, T., & Thies, C. (2005). The effects of landscape complexity on arable weed species diversity in organic and conventional farming. *Journal of Applied Ecology*, 42, 873–882.
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Saunders, D. A., Hobbs, R. J., & Margules, C. R. (1991). Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, 5, 18–32.
- Sboarina, C., & Cescatti, A. (2004). *Il clima del Trentino. Distribuzione spaziale delle principali variabili climatiche*. Report 33. Trento: Centro di Ecologia Alpina.
- Scotton, M., Marini, L., Pecile, A., Franchi, R., & Fezzi, F. (2005). Notes on the floral evolution of the manured meadows in the Sole Valley (Trentino, NE Italy). *Grassland Science in Europe*, 10, 525–528.
- Sebastià, M. T. (2004). Role of topography and soils in grassland structuring at the landscape and community scales. *Basic and Applied Ecology*, 5, 331–346.
- Shmida, A., & Wilson, M. V. (1985). Biological determinants of species diversity. *Journal of Biogeography*, 12, 1–20.
- Söderström, B., Svensson, B., Vessby, K., & Glimskär, A. (2001). Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. *Biodiversity and Conservation*, 10, 1839–1863.
- Stevens, C. J., Dise, N. B., Mountford, J. O., & Gowing, D. J. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science*, 303, 1876–1879.
- Strijker, D. (2005). Marginal lands in Europe – causes of decline. *Basic and Applied Ecology*, 6, 99–106.
- Tasser, E., & Tappeiner, U. (2002). Impact of land use changes on mountain vegetation. *Applied Vegetation Science*, 5, 173–184.
- Ter Braak, C.J.F., & Šmilauer, P. (2002). *CANOCO Reference manual and CanoDraw for Windows User's guide: Software for Canonical Community Ordination (version 4.5)*. Ithaca: Microcomputer Power.
- Thompson, K., & Jones, A. (1999). Human population density and prediction of local plant extinction in Britain. *Conservation Biology*, 13, 185–189.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8, 857–874.
- Walther, U., Menzi, H., Ryser, J.-P., Flisch, R., Jeangros, B., Maillard, A., et al. (1994). Grundlagen für die düngung im acker- und futterbau. *Agrarforschung*, 1, 1–40.
- Weibull, A.-C., Östman, Ö., & Granqvist, Å. (2003). Species richness in agroecosystems: The effect of landscape, habitat and farm management. *Biodiversity and Conservation*, 12, 1335–1355.
- Whittaker, R. J., Willis, K. J., & Field, R. (2001). Scale and species richness: Towards a general hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453–470.
- Zonneveld, I. S. (1995). Vicinism and mass effect. *Journal of Vegetation Science*, 6, 441–444.