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

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Received 25 August 2006; accepted 18 June 2007

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 beprobierten neunundneunzig Heuwiesen in den italienischen Alpen und erfassten vierzehn erklärende...
Introduction

Habitat type and quality are recognised as important local determinants of species richness (Rosenzweig, 1995), but other processes operating at landscape scale 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 semi-natural habitats (Tscharntke, Klein, Krues, 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, Olsen, Gross, & Collins, 2000; Jacquemyn, Brys, & Hermy, 2003), abiotic environment (Bennie, Hill, Baxter, & Huntley, 2006; Sebastiä, 2004), and soil characteristics (Crichtley et al., 2000). 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 (Tscharntke 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, Tscharntke, 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, & Tscharntke, 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...
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; Tscharntke 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, X², Y², XY, X²Y, XY², X³, Y³). 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...

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

<table>
<thead>
<tr>
<th>Set</th>
<th>Name</th>
<th>Description and unit</th>
<th>MEAN</th>
<th>SE</th>
<th>MIN</th>
<th>MAX</th>
</tr>
</thead>
<tbody>
<tr>
<td>Meadow management</td>
<td>CUT</td>
<td>Number of cuts per year</td>
<td>2.18</td>
<td>0.1</td>
<td>1</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>NTot</td>
<td>Total amount of fertiliser nitrogen (kg N ha⁻¹ yr⁻¹)</td>
<td>107.44</td>
<td>0.877</td>
<td>0</td>
<td>439</td>
</tr>
<tr>
<td></td>
<td>NOrg</td>
<td>Amount of organic fertiliser nitrogen (kg N ha⁻¹ yr⁻¹)</td>
<td>96.42</td>
<td>0.826</td>
<td>0</td>
<td>350</td>
</tr>
<tr>
<td></td>
<td>NMin</td>
<td>Amount of mineral fertiliser nitrogen (kg N ha⁻¹ yr⁻¹)</td>
<td>10.92</td>
<td>0.285</td>
<td>0</td>
<td>300</td>
</tr>
<tr>
<td>Abiotic environment</td>
<td>SLO</td>
<td>Mean slope of the management unit (deg)</td>
<td>7.17</td>
<td>0.062</td>
<td>0</td>
<td>28.85</td>
</tr>
<tr>
<td></td>
<td>ALT</td>
<td>Altitude of the management unit (m a.s.l.)</td>
<td>979.71</td>
<td>3.564</td>
<td>319</td>
<td>1910</td>
</tr>
<tr>
<td></td>
<td>RAD</td>
<td>Cumulative radiation of May (kWh m⁻²)</td>
<td>176.81</td>
<td>0.109</td>
<td>140.77</td>
<td>199.97</td>
</tr>
<tr>
<td></td>
<td>PRE</td>
<td>Cumulative precipitation of May, June, July, August and September (mm)</td>
<td>545.42</td>
<td>0.693</td>
<td>434.3</td>
<td>673.2</td>
</tr>
<tr>
<td></td>
<td>SOIL</td>
<td>Mean soil depth (cm)</td>
<td>34.10</td>
<td>0.158</td>
<td>8</td>
<td>76</td>
</tr>
<tr>
<td>Landscape context</td>
<td>URB</td>
<td>Proportion of urban elements within 500 m radius (%)</td>
<td>11.85</td>
<td>0.116</td>
<td>0</td>
<td>45.87</td>
</tr>
<tr>
<td></td>
<td>GRA</td>
<td>Proportion of grassland area within 500 m radius (%)</td>
<td>38.56</td>
<td>1.533</td>
<td>10.08</td>
<td>86.22</td>
</tr>
<tr>
<td></td>
<td>FOR</td>
<td>Proportion of forest area within 500 m radius (%)</td>
<td>40.09</td>
<td>23.821</td>
<td>3.66</td>
<td>84.61</td>
</tr>
<tr>
<td></td>
<td>EDGE</td>
<td>Length of edges between meadows and the other land-use classes within 500 m radius (m)</td>
<td>8268.35</td>
<td>40.385</td>
<td>160</td>
<td>21060</td>
</tr>
<tr>
<td></td>
<td>AREA</td>
<td>Area of the management unit (m²)</td>
<td>4833.44</td>
<td>619.224</td>
<td>801</td>
<td>34998</td>
</tr>
</tbody>
</table>

\(^{a}\)NOrg and FOR were excluded because strongly correlated with NTot and GRA, respectively.
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 ∩ L), the joint effect of meadow management and environment (M ∩ E), the joint effect of meadow management and landscape (M ∩ L), the joint effect of the three sets (M ∩ E ∩ 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)

<table>
<thead>
<tr>
<th>Variables</th>
<th>Standard coefficient</th>
<th>Standard error</th>
<th>t</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>31.0707</td>
<td>0.5924</td>
<td>52.45</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SLO</td>
<td>2.0281</td>
<td>0.6834</td>
<td>2.97</td>
<td>0.004</td>
</tr>
<tr>
<td>NTot</td>
<td>-7.6978</td>
<td>1.8418</td>
<td>-4.18</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>NTot²</td>
<td>5.3863</td>
<td>1.7633</td>
<td>3.05</td>
<td>0.003</td>
</tr>
<tr>
<td>EDGE</td>
<td>1.5971</td>
<td>0.6416</td>
<td>2.49</td>
<td>0.015</td>
</tr>
<tr>
<td>URB</td>
<td>-1.5273</td>
<td>0.6603</td>
<td>-2.31</td>
<td>0.023</td>
</tr>
</tbody>
</table>

*Variable 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)

<table>
<thead>
<tr>
<th>Variable set</th>
<th>R² (%)</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pure effects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M</td>
<td>12.3</td>
<td>0.001</td>
</tr>
<tr>
<td>E</td>
<td>4.6</td>
<td>0.001</td>
</tr>
<tr>
<td>L</td>
<td>6.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Shared effects</td>
<td></td>
<td></td>
</tr>
<tr>
<td>M ∩ E</td>
<td>8.5</td>
<td>—</td>
</tr>
<tr>
<td>M ∩ L</td>
<td>6.7</td>
<td>—</td>
</tr>
<tr>
<td>E ∩ L</td>
<td>3.9</td>
<td>—</td>
</tr>
<tr>
<td>M ∩ E ∩ L</td>
<td>9.0</td>
<td>—</td>
</tr>
<tr>
<td>TVE</td>
<td>51.2</td>
<td>0.001</td>
</tr>
<tr>
<td>Unexplained</td>
<td>48.8</td>
<td>—</td>
</tr>
</tbody>
</table>

*M: meadow management, E: abiotic environment, L: landscape context. TVE: total variation explained. R² corresponds to the amount of explained variation (sum of all canonical eigenvalues in pRDAs). 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 $\beta = -4.122$; SE = 1.738; $t = -2.371$; $P = 0.020$) and the interaction between edge length and soil depth (standardised coefficient $\beta = -3.254$; 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 microclimatico- logical 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...
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.

Acknowledgements

We would like to thank R.H. Marrs (Liverpool) and N. Wrage (Göttingen) for their constructive comments and for improving the English. We wish to thank also two anonymous referees for their useful comments and suggestions that greatly improved this paper. We are grateful to P. Rodaro for carrying out the floristic and management surveys, and to M. Anesi and M. Vettori for their support in the field work. This research has been financially supported by the Agricultural Institute of San Michele all’Adige (Trento), and by the Aldo Gini Foundation (Padova). GIS data were provided by the Agriculture Department of the Trento Province.

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