Vascular plant and Orthoptera diversity in relation to grassland management and landscape composition in the European Alps

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Summary

1. Several recent studies have considered the relative effects of local vs. landscape factors on diversity of several animal taxa in grasslands. However, very few have considered vascular plant or Orthoptera species, both of which are important biotic components of grassland ecosystems. The general aim of this study was to determine the effect of grassland management and landscape composition, and their potential interactions, on diversity patterns of vascular plants and Orthoptera in Alpine hay meadows.

2. We considered three groups of management regimes defined by different amounts of fertilizer nitrogen applied and cutting frequency: (i) extensive, (ii) low intensive and (iii) intensive meadows situated in different landscape contexts. To evaluate the relative importance of meadow management and landscape composition on diversity patterns, we applied analysis of covariance and variation partitioning analyses.

3. Diversity patterns of both taxonomic groups were affected primarily by grassland management. The extensive management regime was most suitable for conserving high species richness of both taxonomic groups. The intensive meadows were characterized by plant communities dominated by a few ruderal and competitor species, and by Orthoptera communities composed of only a few abundant Caelifera species (e.g. *Chorthippus parallelus*), while Ensifera species had very low individual densities.

4. Regarding the landscape determinants, plant diversity patterns were not significantly related to any landscape composition variables. In contrast, a high proportion of urban elements and grassland in the surrounding landscape (radius 500 m) affected Orthoptera species richness negatively.

5. *Synthesis and applications.* The implementation of well-targeted agri-environment schemes for compensation payments against intensification and abandonment of extensive hay meadows seems to be a promising tool to protect both taxonomic groups. In this context, we suggest that the existing Swiss ecological compensation area (ECA) hay meadow agri-environment scheme, which requires at least one cut every year and no fertilizer application, might also be suitable for the Italian Alps. Moreover, the significant influence of landscape composition on Orthoptera diversity suggests that the effectiveness of measures applied at a field scale may be improved by integration of protected area schemes, promoting extensive management at a farm scale.

Key-words: agri-environment schemes, Caelifera, conservation management, cutting frequency, Ensifera, fertilization, hay meadows, urbanization

Introduction

In temperate European countries, changes in land-use practices associated with agricultural intensification have led to a structural transformation of the rural landscape. In the Alps, as in other marginal mountain areas in Europe, increasing

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economic pressure to maintain farm incomes has resulted in intensification of the more accessible, productive soils and in a partial abandonment and fragmentation of semi-natural habitats characterized by soils with a low nutrient status and farms with high labour requirements (MacDonald *et al.* 2000). Along with these processes, the regional species pool of the Alps is affected by re-allocation of agricultural land for urban areas and high-density road networks (Favry &

Pfefferkorn 2005). These changes of local habitat quality and landscape structure threaten the survival of plant and animal species that depend on semi-natural habitats (Tscharntke *et al.* 2005).

At a local scale, there is an increasing consensus that high-input grassland management reduces both plant (Zechmeister *et al.* 2003) and invertebrate diversity (Vickery *et al.* 2001; Schwab *et al.* 2002). At a broader spatial scale, landscape composition and configuration are related to the abundance of several taxonomic groups (Söderström *et al.* 2001) but these relationships are scale dependent, as species respond differently to the surrounding landscape according to their size, mobility and functional traits (Tscharntke *et al.* 2005). Numerous recent studies have considered the relative effects of local vs. landscape factors on diversity patterns of several invertebrate taxa such as bugs (Di Giulio, Edwards & Meister 2001) and butterflies (Collinge, Prudic & Oliver 2003). However, few studies consider vascular plants or Orthoptera, both of which are regarded as important biotic components of grassland ecosystems. Orthoptera are important components of the energy budget of grassland ecosystems, consuming about 3·5% of the annual production in temperate grasslands (Ingrisch & Köhler 1998) and being important prey sources for many predators such as birds (Vickery *et al.* 2001) and spiders (Belovski & Slade 1993).

Plant diversity patterns are predominantly explained by local determinants such as resource competition, disturbance and biotic interactions (Grime 2001). Less is known about the relative effects of landscape structure, and several studies have reported diverse results (Söderström *et al.* 2001; Dauber *et al.* 2003; Krauss *et al.* 2004). However, there is evidence that plant community structure and its dynamics may be affected by landscape structure via effects on the regional species pool, dispersal limitations and habitat neighbourship (Poschlod, Tackenberg & Bonn 2005).

Most studies regarding the effect of local factors on Orthoptera have stressed that both species richness and abundance may benefit from extensive grassland management (Craig *et al.* 1999; Kruess & Tscharntke 2002; Gardiner 2006; Knop *et al.* 2006), for example extensive hay-making (one cut and very low amounts of fertilizer), and livestock grazing (low stocking rates and no fertilizer). In agricultural grassland, vegetation structure and microclimate are probably the most important determinants controlling diversity of Orthoptera (Van Wingerden, Van Kreveld & Bongers 1992; Ingrisch & Köhler 1998; Gardiner *et al.* 2002). Environmental temperature is particularly important for Orthoptera, as they require a range of physical conditions to meet the demands of the different stages of the life cycle and physiological processes (Willott 1997). In contrast, the effect of landscape structure is less well studied. Recent studies have detected a non-significant influence of habitat configuration (Wettstein & Schmid 1999; Stoner & Joern 2004) while, for example, Batári *et al.* (2007) found significant relationships between landscape composition and the occurrence of several Orthoptera species.

The interactions of local- and landscape-scale factors present a significant challenge for determining which factors influence changes in the resident community (Mazerolle & Villard 1999), with important implications for conservation planning. In particular, a large number of possible direct and indirect effects must be uncovered to improve our understanding of the underlying dynamics between landscape-scale factors and local attributes (Stoner & Joern 2004). Hence the aim of this study was to determine the marginal effects of grassland management and landscape composition, and their potential interactions, on local diversity patterns of vascular plants and Orthoptera in Alpine hay meadows.

We addressed the following questions. (i) What is the influence of grassland management regime on vascular plant and Orthoptera diversity? (ii) Does landscape composition affect both taxonomic groups and, if yes, does its effects interact with management? Our analyses further aimed to provide useful information for the assessment of well-targeted agri-environment schemes in the Italian Alpine meadows.

Materials and methods

STUDY AREA

The study was carried out in 2006 in three neighbouring administrative districts located in the southern part of the Trento Province, north-east Italy: Low Valsugana, High Valsugana and Val Lagarina (Fig. 1). The geology was heterogeneous, comprising calcareous and siliceous bedrocks. The mean annual temperature at the minimum altitude considered (601 m a.s.l.) was *c.* 10·5 °C, while it was *c.* 7·0 °C at the maximum altitude (1273 m a.s.l.). The mean annual rainfall was *c.* 1000 mm. All the selected meadows were located in highland areas, where the agricultural landscape context was characterized by
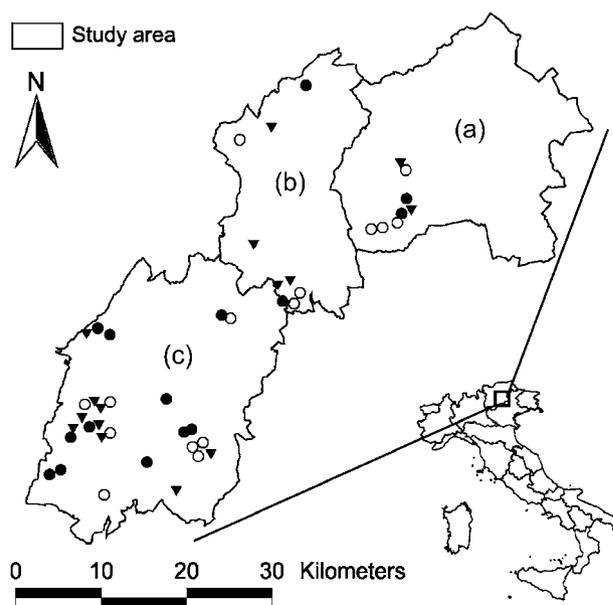

Fig. 1. Location of the study area [three administrative districts: (a) Low Valsugana, (b) High Valsugana and (c) Val Lagarina] showing the 45 hay meadows grouped by management regime. Different symbols indicate the three management groups: black circles, extensive; white circles, low intensive; inverted triangles, intensive.

mixed forests interposed with hay meadows and urban elements. The level of urbanization was relatively low in comparison with the more urbanized areas in the large valleys.

SITE SELECTION

A total of 45 grassland hay meadows was selected in the survey area based on management practices and landscape composition. The aim of the sampling was to obtain a selection of hay meadows balanced for management regime and landscape composition. We considered management regime in three strata, based on fertilizer nitrogen (N) and cutting frequency: (i) extensive meadows without fertilization or with a very low level (0 < N application < 25 kg N ha^{-1} year^{-1}, cutting once in July); (ii) low intensive hay meadows (50 < N application < 100 kg N ha^{-1} year^{-1} and cutting twice in June and August); (iii) intensive meadows (200 < N application < 300 kg N ha^{-1} year^{-1} and cutting twice in June and August). The three management regimes received a mean fertilization N of 6·1 (SD = 13·3), 66·2 (SD = 26·7) and 222·9 (SD = 59·9) kg N ha^{-1} year^{-1}, respectively.

Within each of these management strata, we selected 15 sites in landscapes characterized by different proportions (from low to high) of urban elements, grassland and forests. Between the three groups of management regimes, there was no significant difference in mean values of landscape composition variables (Table 1). To reduce the effect of altitude on the diversity patterns of the two taxonomic groups, only sites situated between 600 and 1300 m a.s.l. were considered. All investigated sites were spatially independent (distance from the nearest site > 1 km).

VASCULAR PLANTS AND ORTHOPTERA

Vascular plant diversity was estimated once before the first cut and once before the second cut. If meadows were cut only once a year, the second sampling was carried out when the second sward regrowth occurred. To avoid bias in estimates of plant species diversity as a result of the internal variability of vegetation within management units, a vegetation sampling plot of 10 × 10 m was established randomly in a homogeneous stand of vegetation in each meadow. Within the management unit, we avoided sampling zones containing

anomalous areas (e.g. organic fertilizer deposits, small rock outcrops, paths and trees). The use of a single sampling plot produced standardized data of both species richness (Zechmeister *et al.* 2003) and composition (Schwab *et al.* 2002) in hay meadow vegetation. Edge effects were reduced by excluding a 10-m buffer zone from the management unit boundaries. Within each vegetation sampling plot, vascular plants were recorded to species level, and the percentage of biomass was estimated visually using the Van der Maarel (1979) abundance scale. We also recorded the cover of bare ground before the first cut. Plant species richness was the cumulative number of species found in each sampling unit during the two visits. Nomenclature was according to Wisskirchen & Haeupler (1998).

Orthoptera (Ensifera and Caelifera) were sampled by visiting the meadows twice, during the periods of maximum activity and density of the species. The first period was at the end of July (19–27) and the second at the end of August (23–29) to ensure detection of species with different phenological patterns. Surveys took place between 10:00 and 17:00 on warm sunny days that did not follow a day of high rainfall. In each meadow, the Orthoptera diversity was determined at two spatial scales. First, Orthoptera species richness was determined using a modified 'timed counts' method (Gardiner, Hill & Chesmore 2005). Within each meadow, centred in the vegetation quadrat, a 400-m^2 plot was established, and the Orthoptera species were recorded during 20 min. The surveys were carried out by the same two operators, who recorded species both by visual sighting and by song identification. Secondly, we determined individual abundance of Orthoptera species by using a white PVC cylinder sampler, open top and bottom, with a radius of 32·5 cm and a height of 80 cm. The relatively small diameter was selected because of the high Orthoptera density (up to 10·0 individuals m^{-2}). This method corresponds to a modified 'box quadrat' method with high sides (Gardiner, Hill & Chesmore 2005). Within each 400-m^2 plot, we carried out 12 samplings at random by leaning the cylinder rapidly in a vertical position, and so capturing all the individuals within the cylinder. Orthoptera were only rarely observed escaping underneath the sampler, while escape from the top was avoided by capturing instead of counting the individuals. We used this sampling technique instead of others (e.g. net sweeping transect and open quadrats) to enable recording of those species that spend most of the time in the lowest

Table 1. Descriptive statistics (means ± SD) of the three grassland management regimes. Comparisons of the means were conducted using one-way ANOVA

	Extensive	Low intensive	Intensive	*F*	*P*
Management unit area (m^2)	7102 ± 5884	9265 ± 8573	8556 ± 6314	1·35	0·27
Altitude (m a.s.l.)	988·6 ± 246·8	873·0 ± 182·3	930·9 ± 201·6	0·75	0·48
Slope (degree)	9·52^a ± 5·35	6·84^b ± 3·57	4·81^b ± 3·55	4·65	0·02
Annual mean temperature (°C)	8·87 ± 1·43	9·27 ± 0·97	9·05 ± 1·12	0·41	0·66
Radiation of May (kWh m^{-2})	172·01 ± 12·00	170·80 ± 11·17	176·29 ± 8·48	1·11	0·33
Proportion in a 500-m radius					
Urban elements (%)	6·52 ± 7·22	6·25 ± 8·60	8·22 ± 8·44	0·26	0·81
Grassland (%)	34·06 ± 18·17	36·38 ± 18·77	42·00 ± 13·01	0·88	0·42
Forest (%)	56·95 ± 21·40	55·15 ± 19·37	4 8·67 ± 17·58	0·75	0·48
Vegetation traits					
Competitor component (%)*	32·81^a ± 12·62	38·7^{ab} ± 10·73	44·7^b ± 14·7	3·24	0·05
Stress-tolerant component (%)*	45·24^a ± 14·43	31·6^b ± 11·32	20·7^c ± 09·5	17·20	< 0·01
Ruderal component (%)*	22·20^a ± 7·31	29·9^b ± 8·31	34·8^b ± 10·1	8·13	< 0·01
Bare-ground cover (%)†	9·40^a ± 4·97	2·67^b ± 3·72	0^c	27·43	< 0·01

Different letters indicate significant differences in mean values according to the Duncan post-hoc test for multiple comparisons (*P* < 0·05).
*Competitor component, stress-tolerant component and ruderal component of the functional signature according to Hunt *et al.* (2004).
†Bare-ground cover estimated before the first cut.

vegetation layer or on the ground (e.g. Tettigoniidae species such as *Decticus verrucivorus*, *Pholidoptera* sp., *Roeseliana roeseli* and Gryllidae species) (Gardiner & Hill 2006a). After sampling, we released the specimens, which did not require laboratory identification. Sampling by both methods was repeated in July and August. The species richness was the accumulated number of species found during the two visits (total of 40 min site^{-1}), while the abundance was the accumulated number of individuals per species in the two PVC sampler surveys (8 m^2 site^{-1}). Nomenclature of Orthoptera was according to Fontana, La Greca & Kleukers (2005).

GRASSLAND MANAGEMENT AND LANDSCAPE COMPOSITION

Grassland management variables (amount of fertilizer N and cutting frequency) were obtained from interviews using a standardized questionnaire. The total amount of fertilizer N was calculated by summing up organic and mineral N. The concentration of N for the different organic fertilizers was retrieved from Walther *et al.* (1994). All investigated meadows were only cut, and were mainly fertilized with farmyard or liquid manure.

At the landscape scale, we quantified the area of land-use classes surrounding each grassland site. Landscape composition variables were measured by calculating a circular buffer with a 500-m radius around the geographical centre of each meadow. This choice of spatial extent was considered relevant for both vascular plants (Söderström *et al.* 2001; Krauss *et al.* 2004; Tscharntke *et al.* 2005) and most European Orthoptera species, whose population dynamics may operate at this spatial scale (Ingrisch & Köhler 1998). The landscape variables were derived from a detailed vector-based land-use map (SIAT, Servizio Urbanistion e Tutela del Territorio, Trento, Italy). We defined the following five classes of land use: (i) urban elements (houses, streets and other urban land uses); (ii) grassland; (iii) forest; (iv) water bodies (lakes and rivers); (v) other land uses. Before further analyses, we checked the accuracy of the land-use classes within the buffers using aerial photographs (IT2000, SIAT, Rervizio Urbanistion e Tutela del Territorio, Trento, Italy) to avoid eventual classification errors. Then we calculated the proportion of the different land-use classes within the buffers. All the analyses were carried out using ArcGIS 8.3 (ESRI, Redland, CA). In the statistical analyses, we focused on the three landscape composition variables proportion of grassland (GRA), forest (FOR) and urban elements (URB), as these represented the dominant land-use classes in our study area (Table 1). As GRA was highly negatively correlated with FOR (Spearman's rank correlation index = –0·88, $n = 45$, $P < 0·01$), this latter variable was excluded from further analyses to exclude redundant information caused by strong collinearity between covariates (Quinn & Keough 2002). The two variables GRA and URB were not significantly correlated (Spearman's rank correlation index = 0·25, $n = 45$, $P = 0·10$).

DATA ANALYSIS

To examine the marginal effects of grassland management and landscape composition on species richness of vascular plants and Orthoptera, we applied analysis of covariance (ANCOVA with type III sum of squares) using management regime (MAN) as factor (categorical variable) and GRA and URB as covariates. Following the statistical hypothesis testing scheme proposed by Avois *et al.* (2000), ANCOVA was used to test the main effects of MAN, GRA and URB as well as the first- and second-order interactions. To meet assumptions of ANCOVA, we checked the variables for normality and variance homogeneity. Further, we analysed scatterplots to check linearity of the relationships between the covariates and species richness (Quinn & Keough 2002). Only URB was log-transformed. The ANCOVA was repeated separately for both species richness of vascular plants and Orthoptera.

The relationship between species composition, management regime and landscape composition was also analysed by means of redundancy analysis (RDA) as implemented in the CANOCO package (version 4.5; Ter Braak & Smilauer 2002). Vascular plant species that were found only once in the 45 meadows were excluded from the ordination. The vascular plant abundance data were not transformed, while the Orthoptera abundance was log-transformed to reduce the effect of the most abundant species (Lepš & Šmilauer 2003). RDA was calculated using the same set of explanatory variables as in the ANCOVA model. The model building started with the inclusion of the management regime, which was preliminarily transformed into three dummy variables. Then a forward manual selection procedure was performed with the landscape composition variables ($P < 0·05$). All the analyses were tested for significance using a Monte Carlo permutation test (MCP; Ter Braak & Šmilauer 2002) with 1000 randomizations. The variation explained by the full model was then partitioned into pure management, pure landscape composition and shared component between the two sets (Borcard, Legendre & Drapeau 1992).

Furthermore, the plant species were classified using the C (competitor), S (stress-tolerant) and R (ruderal) plant functional types according to Hodgson *et al.* (1999). For each vegetation plot, a functional signature was derived using the Excel spreadsheet-based tool proposed by Hunt *et al.* (2004). This C-S-R signature is a three-part index that indicates the proportion of the three strategies in a plant community.

Results

SITE CHARACTERISTICS

Management unit area, altitude, annual mean temperature, radiation and landscape composition variables did not differ between the three management regimes (Table 1). As extensively managed meadows were very rarely located on flat areas, the extensive meadows had a significantly steeper slope than low intensive and intensive meadows (Duncan test, $P < 0·05$). The functional signatures of the vegetation differed significantly between the management regimes. The extensive regime was mainly characterized by stress-tolerant species, while along with increasing management intensity the ruderal and competitor species increased. Moreover, the higher percentage of bare-ground area within the vegetation sampling plots of the extensive meadows indicated the presence of more vegetation gaps (Table 1).

VASCULAR PLANTS

Overall 189 vascular plants were recorded in the 45 meadows: 30 monocotyledons and 159 were dicotyledons. Most of the vascular plant species were common mesophilous species adapted to Alpine hay meadows. In the 15 extensively managed meadows, 161 plant species were found (77 exclusively), while only 89 (four exclusively), and 92 (nine exclusively) were

Fig. 2. Box-plots of (a) vascular plant and (b) Orthoptera species richness in the three grassland management regimes. The boundaries of the box indicate the 25th and 75th percentile, whiskers indicate the 90th and 10th percentiles, the solid and the dashed lines the median and the mean, respectively.
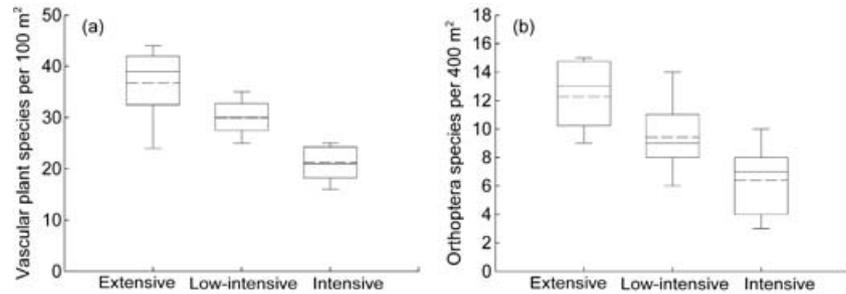

Table 2. Results of ANCOVA for vascular plants and Orthoptera in 45 hay meadows considering management regime (MAN) as a factor and percentage of landscape elements (grassland, GRA; urban elements, URB) within a 500-m radius buffer as covariates. Results refer to the ANCOVAs testing the main effects assuming slope homogeneity

Source of variation*	d.f.	Vascular plants				Orthoptera			
		SS	F	P	Slope	SS	F	P	Slope
MAN	2	1645·4	28·25	< 0·01		200·8	18·14	< 0·01	
GRA	1	15·9	0·55	0·46		29·5	5·80	0·02	−0·051
URB	1	24·4	0·84	0·37		32·1	5·33	0·02	−0·110
MAN × URB	–	–	–	NS		–	–	NS	
MAN × GRA	–	–	–	NS		–	–	NS	
URB × GRA	–	–	–	NS		–	–	NS	
MAN × GRA × URB	–	–	–	NS		–	–	NS	
Error	40	1164·4	–	–		221·3	–	–	

*All non-significant interaction terms were removed from the final model using a backward procedure. For details on ANCOVA computations and abbreviations of variables see the Materials and Methods.

found in the low intensive and intensive management regimes, respectively. Plant species richness of all management regimes averaged 29·2 100 m^{-2}, with a minimum of 16 and a maximum of 51. ANCOVA revealed that the plant species richness was significantly related to local management, while landscape composition variables were not significant (Table 2). The species richness increased with decreasing management intensity (Fig. 2a).

The RDA model confirmed that solely MAN was significantly related to plant species composition (sum of all eigenvalues = 0·183, MCP, $P < 0·01$). Landscape variables did not affect plant species composition. The first two canonical axes explained 13·2% and 5·2% of the total variation, respectively (Fig. 3a). The ordination diagram clearly demonstrated that the extensive management of meadows was most suitable for many stress-tolerant plant species adapted to low-input management, such as *Arabis ciliata* and *Primula veris*. The grasses that dominated these meadows were *Bromus erectus* and *Festuca rupicola*. The intensive meadows were dominated by tall grasses (e.g. *Alopecurus pratensis*, *Poa trivialis*, *Phleum pratense* and *Elymus repens*) and competitive forbs (e.g. *Heracleum sphondylium* and *Rumex obtusifolius*) related to high-input management. The low intensive meadows were characterized by several species with intermediate ecological characteristics, such as *Helictotrichon pubescens* and *Crepis biennis*, which could be found in both nutrient-limited and fertile meadows.

ORTHOPTERA

In the 45 meadows, we observed a total of 49 Orthoptera species, 26 of which were Ensifera and 23 were Caelifera species. In the 15 extensive meadows, 36 species were found (10 exclusively), while only 25 (five exclusively) and 19 (two exclusively) were found in the low intensive and intensive management regimes, respectively. Orthoptera species richness of all management regimes averaged 9·35 400 m^{-2}, with a minimum of 2 and a maximum of 17. The ratio between Ensifera species richness and the overall species richness considering all 45 sites was 0·38, and it did not vary between the three management regimes. In ANCOVA models, MAN was significantly related to the number of species (Table 2). Species richness decreased significantly from the extensive meadows to the low intensive meadows, reaching the lowest value in the intensive meadows (Fig. 2b). Although the measured proportion of urban elements in the surrounding landscape was relatively low (proportions ranged from 0% to *c*. 40% in the 500-m radius buffer), this covariate was significantly negatively related to species richness. Furthermore, GRA was a significant covariate, which was negatively related to the number of species (Fig. 4). However, the partitioning of the SS in the ANCOVA model indicated that the management regime was the main determinant of Orthoptera species richness (Table 2). The landscape composition variables GRA and URB did not interact with management regime, indicating independence between any effects.
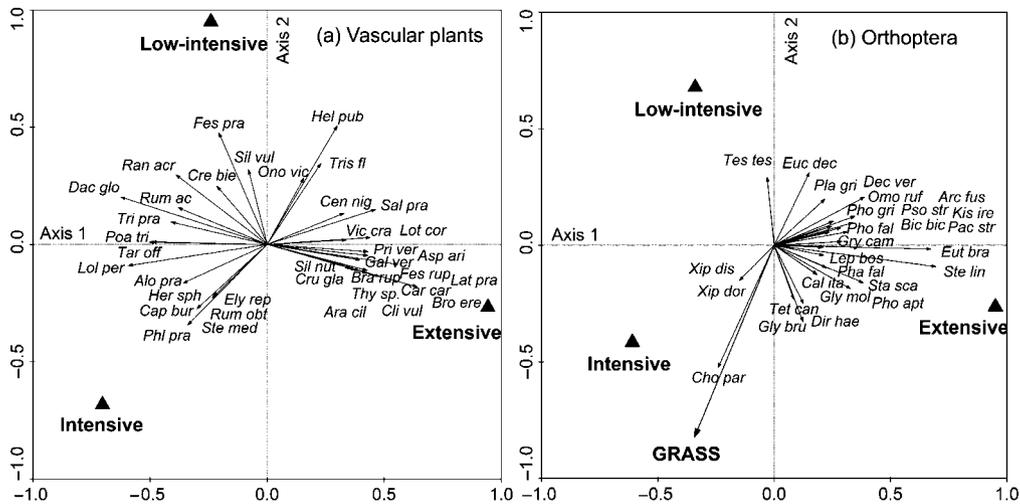
Fig. 3. Redundancy analysis (RDA) diagrams of (a) vascular plant and (b) Orthoptera species occurring in the 45 hay meadows. In the diagram, nominal variables are represented by triangles, and continuous variables as vectors. Only vascular plant species ($n = 37$) and Orthoptera species ($n = 27$) with a fit-range above 10% are shown. The models were significant ($P < 0.05$) according to MCP ($n = 1000$). (a) Vascular plants species abbreviations: Alo pra, *Alopecurus pratensis*; Ara cil, *Arabis ciliata*; Asp ari, *Asperula aristata*; Bra rup, *Brachypodium rupestre*; Bro ere, *Bromus erectus*; Cap bur, *Capsella bursa-pastoris*; Car car, *Carex caryophyllea*; Cen nig, *Centaurea nigrescens*; Cli vul, *Clinopodium vulgare*; Cre bie, *Crepis biennis*; Cru gla, *Cruciata glabra*; Dac glo, *Dactylis glomerata*; Ely rep, *Elymus repens*; Fes pra, *Festuca pratensis*; Fes rup, *Festuca rupicola*; Gal ver, *Galium verum*; Hel pub, *Helictotrichon pubescens*; Her sph, *Heracleum sphondylium*; Lat pra, *Lathyrus pratensis*; Lol per, *Lolium perenne*; Lot cor, *Lotus corniculatus*; Ono vic, *Onobrychis viciifolia*; Phl pra, *Phleum pratense*; Poa pra, *Poa pratensis*; Poa tri, *Poa trivialis*; Pri ver, *Primula veris*; Ran acr, *Ranunculus acris*; Rum ace, *Rumex acetosa*; Rum obt, *Rumex obtusifolius*; Sil nut, *Silene nutans*; Sil vul, *Silene vulgaris*; Ste med, *Stellaria media*; Tar off, *Taraxacum officinale* Sect. *Ruderalia*; Thy sp. *Thymus* sp.; Tri pra, *Trifolium pratense*; Tris fl, *Trisetum flavescens*; Vic cra, *Vicia cracca*. (b) Orthoptera species abbreviations: Arc fus, *Arcyptera fusca*; Bic bic, *Bicolorana bicolor*; Cal ita, *Calliptamus italicus*; Cho par, *Chorthippus parallelus*; Dec ver, *Decticus verrucivorus*; Dir hae, *Dirshius haemorrhoidalis*; Euc dec, *Euchorthippus declivus*; Eut bra, *Euthystira brachyptera*; Gly bru, *Glyptobothrus brunneus*; Gly mol, *Glyptobothrus mollis*; Gry cam, *Gryllus campestris*; Kis ire, *Kisella irena*; Lep bos, *Leptophyes bosci*; Omo ruf, *Omocestus rufipes*; Pac str, *Pachytrachis striolatus*; Pha fal, *Phaneroptera falcata*; Pho apt, *Pholidoptera aptera*; Pho gri, *Pholidoptera griseoaptera*; Pla gri, *Platycleis grisea*; Pso str, *Psophus stridulus*; Sta sca, *Stauroderus scalaris*; Ste lin, *Stenobothrus lineatus*; Tes tes, *Tessellana tessellata*; Tet can, *Tettigonia cantans*; Xip dis, *Xiphidion discolor*; Xip dor, *Xiphidion dorsalis*.
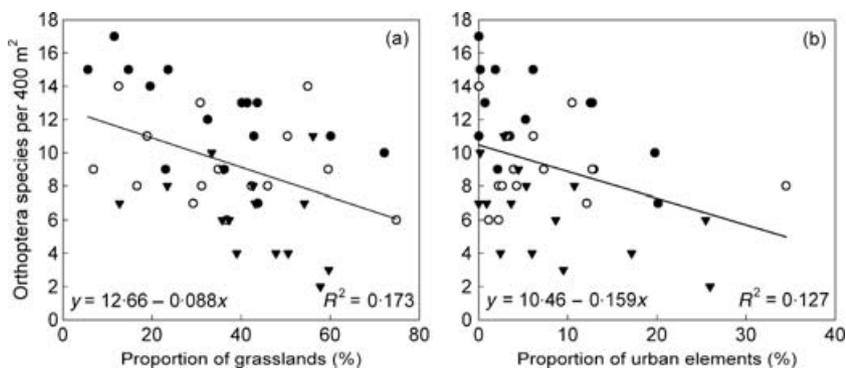

Fig. 4. Best-fit linear regression (pooled regression, $n = 45$) of species richness of Orthoptera vs. (a) proportion of grassland (%) and (b) proportion of urban elements (%) in a 500-m radius. Different symbols indicate the three management groups: black circles, extensive; white circles, low intensive; inverted triangles, intensive.

In contrast to vascular plant species composition, the Orthoptera species composition responded significantly to both management regime and proportion of grassland (sum of all eigenvalues = 0.161, MCP, $P < 0.05$). Variation partitioning revealed that the local variable MAN and the landscape variable GRA had significant pure effects on Orthoptera composition, accounting for 70.8% and 22.4% of the total variation explained, respectively. The shared component was negligible, accounting for 6.8% of the total variation explained. Generally, most Orthoptera species benefited from extensive management (Fig. 3b). The communities found in the extensive meadows were dominated by *Stauroderus scalaris*,

Stenobothrus lineatus and *Euthystira brachyptera*, frequently associated with several Ensifera species (e.g. *Pholidoptera griseoaptera*, *Pachytrachis striolatus* and *Platycleis grisea*), which showed larger abundances compared with the other two management regimes. A few species, such as *Tessellana tessellata*, were related to low intensive management. The assemblages found in the intensive meadows were mostly dominated by small Caelifera species such as *Chorthippus parallelus*, *Glyptobothrus brunneus* and *Glyptobothrus mollis*, which formed species-poor communities with high population densities. Ensifera species had very low individual abundances in the intensive meadows. *Chorthippus parallelus* was the most

frequent species in the 45 meadows and appeared to benefit from the intensive management. The two hygrophilous species *Xyphidion discolor* and *Xyphidion dorsalis* were found exclusively in intensive meadows. Overall, excluding the behaviour of *Chorthippus parallelus*, Ensifera and Caelifera species were enhanced by the decreasing intensity of management in a similar manner.

Regarding the landscape variables, a few Caelifera species were positively affected by the proportion of grassland in the surrounding landscape, while most of the species were negatively affected. *Chorthippus parallelus* abundance presented the most pronounced positive response to the proportion of grassland.

Discussion

GRASSLAND MANAGEMENT

The analyses showed that plant species richness tended to decline with increasing management intensity. These findings conform to several studies, which have found pronounced decreases in species diversity after nutrient enrichment (Gough *et al.* 2000). There is evidence that the combination of above-ground and below-ground competition in highly fertilized meadows reduces species richness because of an interspecific competitive exclusion (Rajaniemi 2002). Intensive management caused a vegetation structure dominated by tall grasses and forbs with competitor or ruderal functional traits (Table 1), which reduce the light availability for smaller plant species (Grime 2001). In contrast, extensively fertilized meadows, where resources such as nutrients and soil moisture are generally limiting, promoted diversity by enabling the co-existence of many stress-tolerant species as a result of niche overlaps. Site conditions such as steep slope may also contribute to high plant species richness.

Besides fertilization, the cutting regime of the hay meadows is likely to affect plant diversity patterns. Principally, hay cutting has a short-term effect by removing above-ground biomass periodically, and so influencing plant dispersal, competition and germination conditions. In observational studies, the effect of cutting frequency *per se* remains controversial, because cutting frequency is highly confounded by the history of fertilizer applications and length of growing season (Zechmeister *et al.* 2003). However, experimental long-term monitoring studies have confirmed the positive effect of hay-making once a year (September or alternating July and September), while hay-making twice a year has shown a unimodal relationship on plant species richness after fertilization cessation (Bakker, Elzinga & de Vries 2002).

Analogously, Orthoptera species richness declined across the gradient of management intensity. This effect was even more pronounced if species composition (abundance) was considered. The species composition in the intensive meadows comprised only a few Caelifera species, such as *Chorthippus parallelus* and *Glyptobothrus* sp., which were the only species able to develop substantial populations in the intensive meadows. The Ensifera species were all found at very low densities, and

they were probably foraging individuals from surrounding habitats (e.g. hedgerow edges). With a decrease in management intensity, the diversity of the Orthoptera assemblages increased, probably because of higher species turnover, as indicated by the high proportion of exclusive species in the extensively managed areas (> 20% of the overall species).

Although interspecific competition among phytophagous insects is recognized as an important factor controlling local population dynamics in grassland environments (Denno, McClure & Ott 1995; Chase 1996), density-independent factors might better explain the Orthoptera diversity distribution among different grassland types (Stoner & Joern 2004). Fertilization can affect Orthoptera populations in two contrasting ways: (i) highly fertilized meadows may provide a better food resource for Orthoptera because of greater N tissue concentration (Ritchie 2000); (ii) high long-term nutrient inputs create tall, dense and relatively 'cold' swards (Schwab *et al.* 2002), with strong consequences on the Orthoptera communities (Van Wingerden, Van Kreveld & Bongers 1992; Willott & Hassall 1998; Gardiner *et al.* 2002; Gardiner 2006).

Even though no data on food quality were available to assess this important factor in this study, the trophic resources seemed to be important at least for *Chorthippus parallelus*, which appeared to be highly specialized for feeding on intensively managed swards dominated by grasses. This result conforms to studies on the feeding behaviour of this species, which show they prefer to feed on tall and coarse grasses such as *Dactylis glomerata* and *Lolium perenne* (Gardiner & Hill 2004), which were common and abundant species in our intensive meadows. Regarding the sward structure, which was not directly measured because of time constraints, the functional traits of the plant species found and the vegetation cover in the three management regimes clearly differed (Table 1). Orthoptera diversity may benefit from low-input fertilization as the less dense and tall structure created by stress-tolerant plant species provides more suitable microhabitats. These results support the hypothesis that most temperate Orthoptera species require open, thin and relatively dry and warm meadows (Craig *et al.* 1999; Vickery *et al.* 2001; Gardiner *et al.* 2002; Knop *et al.* 2006). A low temperature within the sward strongly limits the above-ground stages of the life cycle, controlling all the key physiological processes (e.g. feeding and reproduction) and thus determining the Orthoptera performance and fitness (Willott & Hassall 1998). Additionally, the tall and dense sward may have led to lower temperatures in the egg environment, which possibly has negative effects on more thermophilous species (Van Wingerden, Musters & Maaskamp 1991; Gardiner 2006). In this context, we suggest that future studies aiming to develop new insights into the relations between grassland management and Orthoptera communities should include accurate measurements of food quality, vegetation structure and within-sward microclimate.

Regarding the cutting regime, Orthoptera species are likely to be affected by mowing in different ways. The greater disturbance by the two-cutting regimes may have led to higher mortality because of injuries from blades and machine movements (Wagner 2004; Gardiner & Hill 2006b). The first cut

probably injures the low-mobile early instars, while the second cut affects the adults negatively (Gardiner 2006). The removal of vegetation shelter could enhance bird predation (Ingrisch & Köhler 1998) and, in some cases, could create overheating conditions (Willott 1997). Furthermore, local communities may be reduced by increased short-term dispersal to adjacent, more favourable habitats because of a lack of resources and sward protection from predation on cut meadows (Guido & Gianelle 2001). *Chorthippus parallelus* appeared to be able to recolonize the meadow microhabitats from adjacent undisturbed areas used as a shelter during hay-making (Thorens 1993), while the low individual abundance of the Ensifera species confirmed their higher susceptibility to a two-cutting regime (Guido & Gianelle 2001). However, a very early first cut before nymph hatching and a late second cut after reproduction might create more favourable thermic conditions in intensively fertilized meadows and might reduce mortality related to mechanical operations (Van Wingerden, Van Kreveld & Bongers 1992; Chambers & Samways 1998; Gardiner 2006).

LANDSCAPE COMPOSITION

The non-significant influence of landscape variables on plant species richness and composition conforms to several studies (Dauber *et al*. 2003; Krauss *et al*. 2004) reflecting that the actual state of meadow vegetation largely depends on local factors. Hence we assume that landscape processes such as dispersal and species-pool limitations (Poschlod, Tackenberg & Bonn 2005) are not relevant determinants compared with local resource competition and disturbance caused by grassland management.

However, the landscape composition variables showed a significant effect on Orthoptera diversity. We found a negative effect of the proportion of urban elements in the surrounding landscape on Orthoptera species richness. To our knowledge, no studies have examined the direct effects of surrounding urbanization on Orthoptera diversity in Alpine grasslands. A large amount of urban areas is likely to increase the proportion of inhospitable habitat for most Orthoptera species within the surrounding landscape of hay meadows. We hypothesize that meadows in urban areas are more prone to pollution (dry and wet deposition), recreational use and random disturbance events (e.g. fires and dumping), with detrimental effects on Orthoptera populations. However, direct causation is difficult to establish, and it remains unclear whether this result may be explained by dispersal limitations, population fragmentation or historical disturbances (e.g. differences in former land use near the villages). Thus further studies are necessary to elucidate the effect of this complex factor.

The Orthoptera species richness and composition were also significantly related to the proportion of grassland in the surrounding landscape. *Chorthippus parallelus* benefited from a large proportion of grassland, while most of the species belonging to Ensifera and Caelifera were affected negatively (Fig. 3). At the landscape scale, an enhanced mortality because of mowing of large areas is suggested to be the main constraint

to high diversity of Orthoptera communities (Gardiner 2006). In contrast, in landscapes with a low proportion of grassland, the local diversity could benefit from the presence of ecotonal habitats such as forest edges, hedgerows and bushes. Small grassland areas possibly accumulated more visiting species from these habitats by providing suitable conditions for foraging and reproduction.

IMPLICATIONS FOR CONSERVATION

We conclude that the extensive management regime (no or a very low level of fertilization and cut once a year) was most suitable for the conservation and promotion of diversity of both vascular plant and Orthoptera species. Intensive management was highly detrimental for both taxonomic groups. Compared with the intensive management regime, the low intensive regime may combine both adequate forage production and biodiversity improvements. For low intensive or intensive meadows, we suggest, as a first approximation, that the first cut should be at the end of May and the second one should be delayed until the middle of September; this should reduce Orthoptera mortality and create more favourable thermic conditions during the above-ground stages (Gardiner 2006). When hay-making, sectors of tall and dense vegetation should be left as a shelter for Orthoptera during the post-cutting period (Van Wingerden, Musters & Maaskamp 1991). The conservation of extensive hay meadows surrounded by a low proportion of urban elements and intensive meadows seemed to be important for Orthoptera, although it was of secondary importance in comparison with local management. According to recent studies, this extensive management regime is also suitable for the conservation of other invertebrate taxa such as bugs (Di Giulio, Edwards & Meister 2001), spiders (Schwab *et al*. 2002), butterflies (Vickery *et al*. 2001) and wild bees (Knop *et al*. 2006). In conclusion, our results indicate that the implementation of well-targeted agri-environment schemes for compensation payments against intensification and abandonment of extensive hay meadows appears to be a promising tool to protect both plant and Orthoptera diversity. In this context, we suggest that the ecological compensation area (ECA) hay meadow agri-environment scheme, already operating in Switzerland, which requires at least one cut every year and no fertilizer application (Knop *et al*. 2006), may also be suitable for the Italian Alpine hay meadows. Moreover, the significant influence of landscape composition on Orthoptera diversity indicates that the effectiveness of measures applied at a field scale may be improved by integration of traditional protected area schemes with farms or groups of farms managed extensively (Whittingham 2007).

Acknowledgements

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