

Agricultural management, vegetation traits and landscape drive orthopteran and butterfly diversity in a grassland–forest mosaic: a multi-scale approach

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Abstract. 1. Most ecological processes at the population and community level act on multiple spatial scales. We identified the influence of grassland management, vegetation traits and landscape on orthopteran and butterfly diversity in 44 meadows located in a forest-dominated region in the Italian Alps. The meadows were sampled in landscapes characterised by different proportions of woody vegetation and grasslands quantified at 11 spatial scales (95–3000 m).

2. We applied a multi-scale approach to investigate the scale-dependent effects of landscape. Then, we built generalised linear models (Poisson and log-link function) to test simultaneously vegetation traits and landscape variables on insect species richness.

3. High fertilisation and cutting frequency created tall, species-poor plant communities. This change reduced orthopteran diversity by providing an unsuitable sward structure, and butterfly diversity by creating disturbed plant communities with low species richness and abundance of flowering forbs and host plants.

4. The proportion of woody vegetation had a strong positive effect on the richness of both groups at the smallest spatial scale (95 m), indicating the importance of undisturbed vegetation in the surrounding of mown meadows. The effect tended to disappear with increasing spatial extent.

5. A multi-scale approach was necessary to identify the effects of landscape factors in this study system. Conservation measures should endorse the maintenance of species-rich, sparse and short plant communities by reducing organic fertilisation and cutting frequency. However, these schemes should also promote the presence of undisturbed woody vegetation in the immediate surrounding landscape or at least should prevent the complete mowing of large areas.

Key words. Alps, cutting frequency, fertilisation, forest, hay meadows, herbivores, insect conservation, sward structure.

Introduction

Most ecological processes at the population and community level act on multiple spatial scales (Steffan-Dewenter *et al.*, 2002). The movement and the spatial distribution of species are often strongly affected by both the composition and configuration of the surrounding landscape (Debinski *et al.*, 2001). As a result,

observed patterns of local assemblage diversity are often the outcome of the interaction between habitat patch suitability and landscape context (Krauss *et al.*, 2005; Öckinger, 2008).

Although insects constitute a large component of biodiversity in temperate grassland ecosystems, knowledge is still limited as to effective measures for the conservation of several taxonomic groups (Leather *et al.*, 2008). Most studies that have investigated local and landscape effects on invertebrates in grasslands have focused particularly on fragmented patches embedded in intensive cropland-dominated systems (e.g. Bergmann *et al.*, 2004; Sjödin *et al.*, 2008). However, in many marginal mountain

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areas, characterised by forest-dominated landscapes, recent changes in land use have also caused strong declines in insect diversity (Knop *et al.*, 2006; Steck *et al.*, 2007; Marini *et al.*, 2009). Thus, there is an urgent need to determine the effects of both grassland management and landscape on insect communities over a wide range of spatial scales (Bergmann *et al.*, 2008; Cozzi *et al.*, 2008), as this lack of ecological knowledge is currently constraining the design of effective conservation policies.

In this study, we considered orthopterans and butterflies inhabiting hay meadows in grassland–forest mosaics in the Italian Alps. While orthopterans are generalist herbivores with low mobility, butterflies are relatively more specialised and mobile organisms. At the local scale, there is an increasing consensus that high fertiliser inputs, cutting frequency or grazing intensity reduces invertebrate diversity in managed grasslands (Schwab *et al.*, 2002; Littlewood, 2008; Marini *et al.*, 2008). High nutrient inputs are supposed to be particularly detrimental for several sward-dwelling taxa, as they cause a deterioration of habitat quality by altering sward structure, microclimate, food resources and host-plant availability (Schwab *et al.*, 2002). In cut meadows, high defoliation frequency further reduces insect diversity due to direct mortality (Gerstmeier & Lang, 1996; Gardiner & Hill, 2006; Braschler *et al.*, 2009) or indirect effects via resource and habitat alterations (Gardiner & Hassall, 2009).

As meadows for hay production are subject to regular disturbance related to the periodic removal of the standing biomass and thus to fluctuations in resource availability and habitat stability (Johst *et al.*, 2006), emigration and immigration to and from the surrounding landscape are expected to play an important role in shaping local invertebrate communities (Debinski *et al.*, 2001). On the one hand, suitable grassland patches surrounded by hostile habitats are more prone to species loss due to population isolation (Hanski, 1998). On the other hand, the presence of refugia at the landscape scale can enhance local species richness because richer communities can persist as immigration from the surrounding landscape might compensate for any reproductive deficit (Moquet & Loreau, 2003). However, a landscape perspective in insect conservation in grassland–forest mosaics is still largely overlooked. The application of a multiple-scale approach is urgently needed to gain insights into the interactions between patch suitability and landscape influences on insect diversity. A previous study (Marini *et al.*, 2008) has demonstrated a negative effect of both intensive grassland management and degree of urbanisation on orthopteran species richness. However, that study did not identify the alteration of sward structure and food quality behind this insect diversity loss and did not consider the role of the composition of the surrounding landscape across a wide range of spatial extents. Particularly, woody vegetation has been recently demonstrated to be a very important factor at least for several butterfly species inhabiting grassland–forest mosaics (Bergmann *et al.*, 2004, 2008; Cozzi *et al.*, 2008).

Hence, in the present study the following hypotheses were tested: (i) an increasing intensity of grassland management creates a shift in grassland vegetation from short, species-rich communities to tall, thick and species-poor communities. This change should affect orthopterans (Stoner & Joern, 2004), due to changes in sward structure, and butterflies due to reduction in food resources and host plants; (ii) undisturbed woody vegetation

in the surrounding landscape enhances local diversity in grasslands by providing alternative food resources and suitable habitats for source communities, which can compensate for the mortality and emigration due to local management disturbance, particularly mowing (Debinski *et al.*, 2001; Bergmann *et al.*, 2008). As conservation measures currently applied for insect diversity in temperate grasslands are mainly based on management practices applied at the field scale, our multiscale study might provide an important contribution to a landscape perspective in insect conservation science.

Materials and methods

Study region

We carried out the study in 2007 in the 11 administrative districts of the Trento Province (northeast Italy) (Fig. 1a). The province extends over an area of *c.* 6200 km². Forest covered half of the total area, open natural areas *c.* 20% (mainly mountain peaks), hay meadows *c.* 5%, and urban elements *c.* 2.5%. The hay meadows in the study area were located mainly in two different landscape contexts: (i) relatively highly urbanised flat valleys, where the agricultural and dairy farming activities were concentrated; here the agricultural landscape was characterised by hay meadows, and forage crops; and (ii) little urbanised steeper mountain slopes mainly covered by forests, and secondarily by hay meadows. In this study, we included meadows managed for hay production for at least 20 years (permanent meadows). All the meadows were only cut and were fertilised in spring and autumn with farmyard manure or liquid manure. Mineral fertiliser was applied rarely between the cuts as nitrogen–phosphorus–potassium ternary fertilisers (mostly 20-10-10) or ammonium nitrate (34-0-0). The surveyed hay meadows included in this study belonged to the *Arrhenaterion elatioris* phytosociological alliance (Ellenberg, 1996).

Sampling design

Based on official data of the Agriculture Department of the Province of Trento, we brought together information on topography, meadow location and land cover in a geographical information systems (GIS) environment. The aim of the sampling was to survey hay meadows with different intensity of management in landscapes characterised by different proportions (from low to high) of grasslands and woody vegetation (shrubs and forests). Overall, we sampled 44 meadow parcels across the whole study region (Fig. 1a). The field size ranged from 1.2 to 4.5 ha. In each meadow we placed a plot of 25 × 40 m (1000 m²), where we carried out the surveys.

Orthopteran and butterfly recordings

We recorded Orthoptera (Ensifera and Caelifera) by visiting the 44 meadows twice, during the periods of maximum activity and density of the species. The first period was at the end of July, and the second at the end of August. Surveys took place between

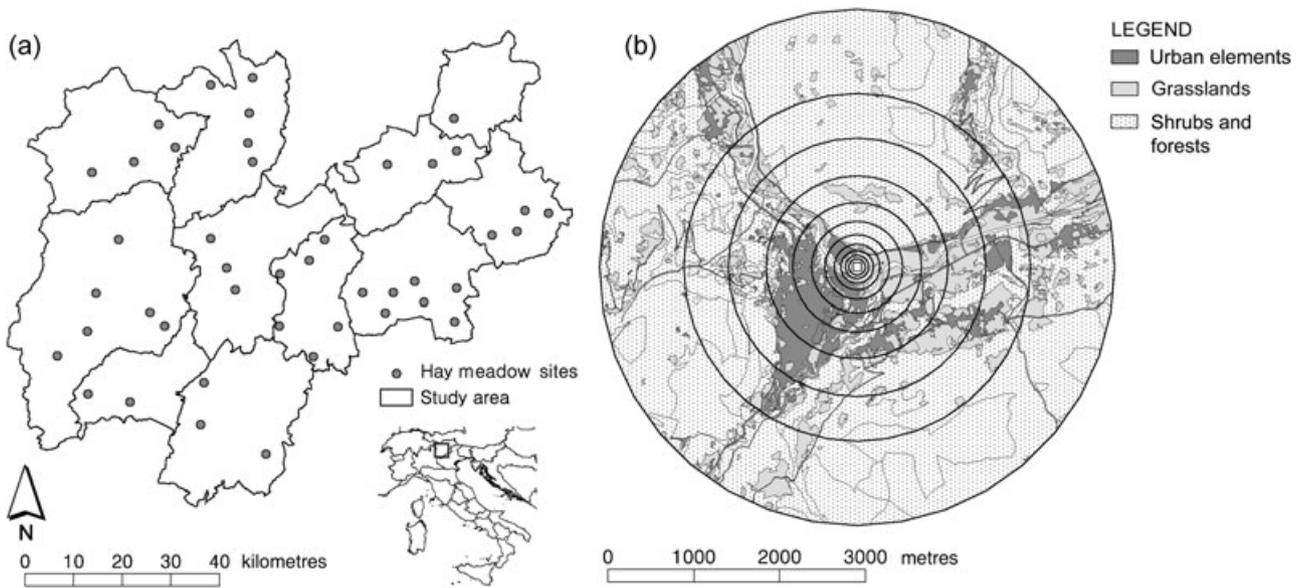


Fig. 1. (a) Location of the study area in the Italian Alps and distribution of the 44 hay meadows sites studied; and (b) example of digital map of one of the 44 landscape sectors. The circle radii represent the 11 spatial scales of 95, 135, 190, 265, 375, 530, 750, 1060, 1500, 2120 and 3000 m around the hay meadow site at which landscape composition was quantified.

10.00 hours and 17.00 hours on warm sunny days that did not follow a day of rainfall. In each meadow, we determined orthopteran species richness and abundance using a 'box quadrat' with high sides (Gardiner *et al.*, 2005). We used a white quadrat sampler, a box with open top and bottom, and with a side length of 1 m and a height of 0.75 m. Within each meadow, we carried out 12 samplings per visit by laying the sampler down rapidly in a vertical position, and therewith capturing all the individuals within. After the survey, we released the individuals that did not require laboratory identification. We assessed the appropriate number of samples within site by analysing species accumulation curves with a preliminary sampling in 12 meadows with high species diversity.

We sampled diurnal Lepidoptera (Hesperioidea and Papilionidea), hereafter labelled as butterflies, using an area transect survey (Debinski *et al.*, 2001). Within each meadow, we patrolled a fixed rectangular area of 1000 m² (25 × 40 m) in a serpentine way for 15 min. We identified and counted all of the butterflies within reach of a net. This method was more suitable than a linear transect survey due to the small dimension of our meadow parcels (Balmer & Erhardt, 2000). Surveys took place between 10.30 hours and 17.00 hours in sunny (cloud cover below 25%) and warm conditions (air temperature above 18°C). We repeated the sampling five times from the first half of May to the end of August. In each meadow, we alternated the sequence of surveys to avoid any systematic effect of time of day. Due to bad weather conditions, we could sample butterflies in only 40 hay meadows.

Explanatory variables

For each meadow, we quantified three sets of explanatory variables: (i) agricultural management, (ii) vegetation-trait, and

(iii) landscape variables (Table 1). For agricultural management, we determined the number of cuts (CUT) and the amount of fertiliser nitrogen (N) by interviewing the farmers, and the soil fertility measured as exchangeable Olsen P₂O₅ (P).

As we expected that insect diversity should be affected by grassland management via indirect effects related to changes in plant communities, we quantified several vegetation traits known as important drivers of insect diversity. Vegetation traits were determined once before the first cut. We randomly established two vegetation sampling plots of 4 × 4 m in the 1000 m² plot with a separation of 10 m, where we carried out the surveys. We measured vegetation height (VEG) using a drop-disk method (Stewart *et al.*, 2001), and the percentage of bare ground cover was visually estimated (GAP). We carried out eight measures per plot and then we averaged the values. Considering food quality for orthopterans, we determined the content of crude protein (CP) (Kjeldhal) of the herbage (strip of 0.1 × 10 m per meadow). We further estimated the overall plant species richness (PLA), the species richness of forbs (FORB) and the relative abundance (percentage of biomass estimated visually) of flowering forbs (FORB%). Species richness was obtained by cumulating the species found in the two plots while the abundance was obtained by averaging the values measured in the two plots. As we used butterfly species richness as response variable, PLA can be considered a good indicator of the species richness of host plants (i.e. almost each plant species was a host plant for one or more butterfly species). We further measured altitude (ALT) and slope (SLO) of the meadows.

The landscape variables were derived from a detailed vector-based land-use map (Servizio Urbanistica, Provincia di Trento). Three classes of land use were defined: (i) grassland (GRA), (ii) woody vegetation (shrubs, forests, and partially open forest-grassland areas) (FOR), and (iii) other land uses. The first two

Table 1. Descriptive statistics of the explanatory variables considered for each of the 44 (40 for butterflies) hay meadows in the Italian Alps.

Name	Description and unit	Mean	SD	Min	Max
Agricultural management					
P	Olsen phosphorous in soil (mg kg ⁻¹)	63	33.6	15.7	156.8
N	Fertiliser nitrogen (kg N ha ⁻¹ y ⁻¹)	138	75.6	20	300
CUT	Number of cuts per year	2.2	0.65	1	4
Vegetation traits					
CP	Content of raw protein in the herbage (percentage)	15.3	2.63	8.60	20.9
PLA	Number of plant species	25.8	8.52	14	49
FORB	Number of forbs species	17.4	7.0	8	38
FORB%	Abundance of flowering forbs species (percentage of biomass)	26.8	16.9	2.0	67.0
VEG	Drop-disk sward height (cm)	29.4	8.46	10.5	43.2
GAP	Bare-ground cover (percentage)	6.5	3.9	0	25
Abiotic environment					
SLO	Mean slope of the management unit (degree)	10.98	6.26	1.70	24.42
ALT	Altitude of the management unit (m a.s.l.)	863	283	251	1377
Landscape					
GRA _{750m}	Proportion of grassland area 750 m radius (percentage)	33.9	15.1	5.6	73.6
FOR _{750m}	Proportion of forest area 750 m radius (percentage)	48.9	22.2	7.3	89.3

Table 2. Pearson correlations calculated between all the predictors quantified for the hay meadows studied.

	ORT	BUT	[P]	[N]	CUT	CP	PLA	[FORB]	FORB%	VEG	GAP	GRA _{95m}	GRA _{530m}	GRA _{1500m}	FOR _{95m}	FOR _{530m}	
ORT																	
BUT	0.59																
[P]	—	—															
[N]	-0.45	-0.66	0.66														
CUT	—	—	0.47	0.57													
CP	—	-0.45	0.41	—	—												
PLA	0.54	0.70	-0.50	-0.74	-0.45	-0.48											
[FORB]	0.62	0.70	-0.48	-0.74	-0.51	-0.44	0.94										
FORB%	—	—	—	—	—	—	—	0.42									
VEG	-0.56	-0.72	—	0.70	—	0.42	-0.73	-0.72	—								
GAP	0.47	0.50	—	-0.52	0.60	—	-0.74	-0.73	—	-0.55							
GRA _{95m}	—	-0.50	—	—	—	0.46	—	—	—	—							
[GRA _{530m}]	—	—	—	—	0.62	—	—	—	—	—	0.50						
[GRA _{1500m}]	—	—	—	—	0.51	—	—	—	—	—	—	0.70					
FOR _{95m}	0.61	0.79	—	-0.44	—	-0.55	0.58	0.56	—	-0.61	—	-0.66	-0.45	—			
[FOR _{530m}]	—	0.47	—	—	-0.55	—	—	0.36	—	-0.43	—	—	-0.76	-0.65	0.61		
[FOR _{1500m}]	—	—	—	—	-0.52	—	—	—	—	—	—	—	-0.65	-0.83	0.41	0.75	

Only the significant correlations are shown ($P < 0.01$, $n = 40$). Variables excluded from the generalised linear model analysis were indicated in square brackets. Variable abbreviations are according to Table 1.

classes together covered a large proportion of the landscape sectors considered in this study. Before further analyses, we checked the accuracy of land-use classes using aerial photographs to avoid classification errors. Around the geographical centre of the sampling plot within each meadow, 11 nested spatial scales were considered by measuring the landscape composition within windows of varying radii (95, 135, 190, 265, 375, 530, 750, 1060, 1500, 2120, and 3000 m). Each increment in scale doubled the surrounding area from 0.028 (95 m) to 28.3 km² (3000 m) (Fig. 1b). We did not have any overlap between our landscape sectors.

Data analysis

Our response variables were the species richness of orthopterans and butterflies calculated as the cumulative number of species found during the two and the five sampling visits, respectively. Preliminarily, we computed a Pearson correlation analysis on the available predictors to evaluate the degree of collinearity and to show the simple relations between our response variables and each predictor (Table 2). Therefore, the explanatory variables were reduced to a smaller number of partially independent factors using their correlation coefficients. In case of highly correlated variables

(Pearson correlation coefficient > 0.6), only one of them was used in the multiple model. Thus, among the vegetation-trait variables, we omitted from further analyses the number of forbs as they were highly correlated with the overall number of species.

As landscape variables quantified at nested spatial scales were highly correlated, we selected only that scale which best explained the variation for each species group for use in further analyses (Steffan-Dewenter *et al.*, 2002; Cozzi *et al.*, 2008). To evaluate the spatial scale, we performed a simple Poisson regression (generalised linear models with Poisson error distribution and log-link function) between each landscape variable and species richness of orthopterans and butterflies at the eleven spatial scales.

Then, we used multiple Poisson regression to test simultaneously the influence of vegetation traits, cutting frequency (indicator of disturbance) and landscape variables on insect species richness. Along with the main effects, we tested also the interaction between PLA × FOR_{95m} for butterfly and VEG × FOR_{95m} for orthopterans to detect a potential interactive effect of landscape composition with habitat quality. We tested our variables using a Wald χ^2 test implemented in the 'car' package for R version 2.6.2 (Fox, 2002). During model building, we tested also quadratic terms to detect non-linear relations. We applied a backward deletion using analysis of deviance to build our minimum adequate model. We started with a complex model containing all the linear and quadratic terms and the two interactions, then we simplified the model removing one by one the non-significant terms (Crawley, 2007). We ran the analyses with the 'glm' function implemented in 'stats' package in R. As the presence of spatial autocorrelation in model residuals can lead to misleading parameter estimates, we computed Moran's I on the model

residuals. As none of the models presented in this study had significant Moran's I, we did not use explicit spatial models.

Results

The total number of orthopteran species sampled was 32, with 1516 individuals recorded. The mean orthopteran species richness per site was four, with a minimum of one and a maximum of 11. The mean orthopteran density was 34 individuals per site, with a minimum of two and a maximum of 139. The total number of butterfly species sampled was 60, with 1644 individuals recorded. The mean butterfly species richness per site was eight, with a minimum of one and a maximum of 22. The mean butterfly density was 41 individuals per site, with a minimum of four and a maximum of 96.

Agricultural management strongly affected vegetation traits (Table 2). Increasing fertiliser N and cutting frequency strongly decreased the number of plant species. Particularly, the number and the abundance of flowering forbs species declined with increasing management intensity. The sward height increased with N and cutting frequency, i.e. the vegetation of the intensively managed meadows was dominated by tall and competitive plant species, particularly by grasses. The crude protein content in sward was correlated with N inputs positively, providing better food quality for herbivores.

The Poisson regression between species richness of the two taxonomic groups and the proportion of woody vegetation and grasslands at the 11 spatial scales indicated a scale-dependent effect of the two landscape variables (Fig. 2). The scale for the

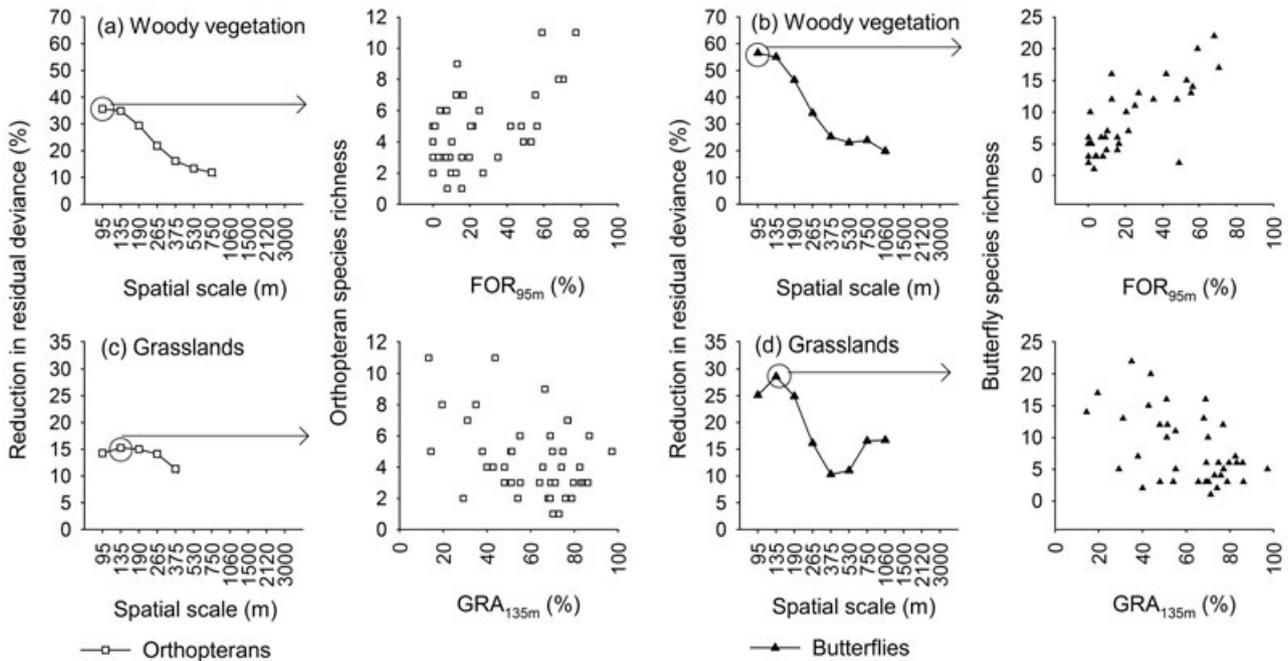
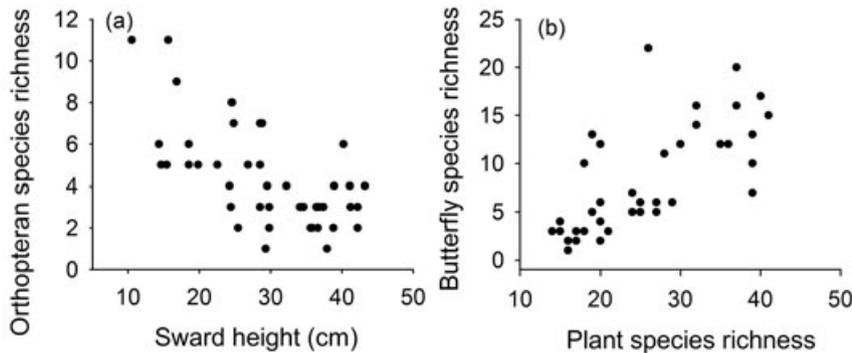


Fig. 2. Scale-dependent effect of the landscape variables on orthopteran and butterfly species richness. We report the drop in residual deviance (percentage) of the significant Poisson regressions (log-link function) between species richness and proportion of woody vegetation and grasslands at the 11 scales. For each predictor we report also the scatterplot for the scale with the largest drop in residual deviance (marked with a circle).

Table 3. Summary of the explanatory variables' influence on orthopteran ($n = 44$) and butterfly ($n = 40$) species richness resulting from the Poisson regression analysis. Variables were tested using a Wald χ^2 test as implemented in the 'car' package (Fox, 2002).

Variables	b	SE	d.f.	Wald χ^2	P	Drop in residual deviance
Orthopterans						54.0%
VEG	-0.0299	0.009700	1	9.5084	< 0.01	
FOR _{95m}	0.0066	0.003439	1	3.7184	0.05	
Butterflies						66.4%
FOR _{95m}	0.0144	0.002852	1	25.474	< 0.01	
PLA	0.0297	0.008042	1	13.666	< 0.01	

*Variable names are according to Table 1.

**Fig. 3.** Scatterplots of the species richness of (a) orthopterans and (b) butterflies vs. the significant vegetation traits included in the multiple Poisson regression model.

proportion of woody vegetation with the largest drop in residual deviance was 95 m, with similar patterns for orthopterans and butterflies. Butterflies showed a more pronounced response to the presence of woody vegetation, while orthopterans were less affected. Both groups responded to this factor positively. The proportion of grasslands had less explanatory power and affected insect species richness negatively. The best scale for both groups was 135 m.

Considering the multiple Poisson regression testing the vegetation traits and landscape variables on orthopterans, the minimum adequate model retained VEG and FOR_{95m} (Table 3). The variables included in the model caused a drop in residual deviance of 54.0%. Orthopteran species richness was related to sward height negatively (Fig. 3a) and to forest positively. For butterflies, the minimum adequate model retained PLA and FOR_{95m} causing a drop in residual deviance of 66.4%. Both plant species richness and forest affected the number of species positively (Fig. 3b).

Discussion

Effects of grassland management via vegetation alteration

The detrimental influence of intensive grassland management on insect diversity was mainly related to indirect effects via the modification of important vegetation traits such as sward structure, food quality and plant species richness. Although highly fertilised meadows provided better food resources for

orthopterans due to greater N-tissue concentration, we did not find any positive effect of crude protein on species richness. Our results demonstrate that sward structure is much more important than food quality in managed grasslands. Many experimental studies report a strong positive effects of N addition on orthopteran performance (e.g. Ritchie, 2000). However, they did not take into account the effects of the associated alteration of vegetation structure and microclimate occurring in natural systems. Orthopteran diversity may benefit from low-input fertilisation as the less dense and tall structure provides more suitable microhabitats (Marini *et al.*, 2008). The low temperature within the tall sward strongly limits the above-ground stages, controlling all of the key physiological processes (e.g. feeding and reproduction) and thus determining orthopteran performance and fitness (Willott & Hassall, 1998). The negative relation with sward height was opposite to that found by Gardiner *et al.* (2002) in pastures, as grazing tends to create short turfs with increasing intensity. The low level of disturbance (cutting frequency) of the meadows sustained higher species richness, while the greater disturbance by frequent cutting regimes may have led to higher mortality due to injuries from blades and machine movements (Gerstmeier & Lang, 1996; Gardiner & Hill, 2006). Mowing is supposed to be one of the most detrimental factors reducing orthopteran species richness in managed grasslands (Braschler *et al.*, 2009).

The significant effect of plant species richness on butterfly species richness conforms to the findings of Skórka *et al.* (2007), who has found similar results in mountain wetland-forest mosaics. Plant species richness is highly correlated with the abundance of

nectar resources (Krauss *et al.*, 2003). In our study area, the number of forbs and legume species was reduced by increasing management intensity suggesting that butterfly species richness declined due to low presence of nectar resources. Moreover, the probability to find suitable host plant species in plant species poor communities dominated by grasses was much lower than in species-rich meadows.

Effects of woody vegetation in the surrounding landscape

We found a strong scale-dependent effect of the proportion of woody vegetation. The proportion of woody vegetation had the strongest positive effect on richness at the smallest spatial scale considered. Interestingly, the explained variation decreased drastically at scales between 95 m and 365 m, which are smaller than the smallest spatial extent used in most studies investigating the influence of landscape on invertebrate diversity patterns (e.g. Bergmann *et al.*, 2008; Sjödin *et al.*, 2008). Thus, this factor could have been overlooked in several studies considering only larger spatial extents (e.g. Marini *et al.*, 2008).

Although the few studies on the role of landscape on orthopteran communities in grasslands have stressed contrasting results on the importance of composition (e.g. Batáry *et al.*, 2007; Marini *et al.*, 2008) and configuration (e.g. Stoner & Joern, 2004; Diekötter *et al.*, 2007), our study clearly indicates the importance of the presence of woody vegetation in our grassland–forest mosaic. As orthopterans are typically related to open grasslands (Steck *et al.*, 2007), a positive effect of forest cover seems quite surprising. However, orthopterans are prone to high mortality in mown meadows because they cannot readily escape from mechanical hay making (Gardiner & Hill, 2006). Thus, the presence of undisturbed areas dominated by woody vegetation in close proximity might have provided suitable refugia, enabling recolonisation of the meadows after the disturbance probably due to a rescue effect (Guido & Gianelle, 2001). At the landscape scale, increased mortality due to mowing of large areas is suggested to pose the main constraint on sward-dwelling invertebrates attaining high diversities (Gardiner & Hill, 2006; Johst *et al.*, 2006). The conflict between the need to mow meadows in order to maintain them and the detrimental effect of the mowing operations on invertebrates with low mobility might be mitigated by the presence of uncut areas in the close surrounding.

As for orthopterans, the richest sites in butterfly species were those containing a mosaic of grassland, shrub and woodland in the immediate vicinity, which probably enhanced the heterogeneity around the meadows (Weibull *et al.*, 2000; Schneider & Fry, 2001). Most butterfly species avoid open areas as wind speed increases and shelter is an important factor in the landscape (Dover & Settele, 2009). Indeed, several studies have shown that butterfly species richness increases with increasing proportions of shrubs and trees in pastures (Söderström *et al.*, 2001; Bergmann *et al.*, 2004) or in recently abandoned grasslands (Balmer & Erhardt, 2000; Skórka *et al.*, 2007). Although it has also been found that butterflies specialising in open habitats perceive forest as a dispersal barrier, our study shows a strong positive effect of forest (see also Schneider & Fry, 2001; Bergmann *et al.*, 2008; Cozzi *et al.*, 2008). The affinity of many butterfly species for

woodland might be related to their evolutionary history, which was probably connected to grazed half-open forests created by large herbivores (Bergmann *et al.*, 2004).

Conclusions and implications for conservation

Our results indicate that even in non-intensive systems, such as our forest-dominated region, the presence of undisturbed woody vegetation, along with local habitat quality, plays a key role in shaping diversity patterns in disturbed ecosystems such as hay meadows. We suggest that conservation measures applied at the field scale in Alpine hay meadows should promote the maintenance of species-rich, short, and sparse plant communities (see also Schwab *et al.*, 2002; Knop *et al.*, 2006; Marini *et al.*, 2008, 2009). This result should be achieved by reducing organic fertilisation and cutting frequency and by maintaining the traditionally extensively managed hay meadows. However, these schemes should also incorporate some measures to promote the maintenance of undisturbed woody vegetation in the immediate surrounding landscape or at least should prevent the complete mowing of large areas. Hence, future assessments of invertebrate habitat suitability for biodiversity conservation should be conducted at a wide range of spatial scales because insect diversity responds strongly to both local habitat quality and landscape context.

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