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High mobility reduces beta-diversity among orthopteran communities – implications for conservation

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Abstract. 1. The analysis of β-diversity, i.e. species turnover, across space is central to a wide array of ecological and evolutionary topics, also providing critical information to conservation planning. Although dispersal limitation has been demonstrated to play an important role in determining insect community structure, very little research has been done to test whether mobility might affect the diversity distribution of species across multiple spatial scales.

2. We considered orthopterans (*Ensifera* and *Caelifera*) inhabiting hay meadows to test whether species mobility modifies β-diversity patterns across three nested spatial scales (1-m^2 plots within meadow, 1000-m^2 meadows within landscape, and 19.6-km^2 landscapes within a region) and along a gradient of management intensity.

3. Orthopteran community composition varied most significantly over broader spatial scales. Larger proportion of regional γ-diversity was mainly composed of β-diversity at the landscape scale, whereas this proportion was smaller at the plot and meadow scale.

4. Mobility, but not management, strongly modified β-diversity patterns. Sedentary species contributed to a greater proportion of β-diversity across all the investigated scales compared with mobile species.

5. Measures currently included in most agri-environment schemes have only focused on the extensive management at the field scale. Our results imply that orthopteran diversity would benefit from maintaining extensively managed meadows scattered throughout the whole region, as the loss of species-rich isolated grassland patches due to abandonment or eutrophication might cause severe reductions of the regional species pool. Increasing connectivity might be also considered as a complementary measure to increase species occupancy and population persistence, particularly for sedentary species.

Key words. Additive partitioning, agri-environment scheme, Alps, dispersal ability, grassland, habitat management, hay meadow, insect conservation, Orthoptera, species turnover.

Introduction

Management intensification has been recognised amongst the main causes of the current decline of grassland insect diversity. However, intensification exerts its influence at multiple spatial scales (Marini *et al.*, 2009a). The management of single fields

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might have an effect at small spatial scale by altering habitat quality, but also at larger spatial scale by modifying landscape composition and configuration (Tscharntke *et al.*, 2005).

The partitioning of γ-diversity into α-diversity and β-diversity components (Lande, 1996) provides an analytical framework to investigate how species diversity varies across multiple spatial scales (Gering *et al.*, 2003) and environmental gradients (e.g. Gabriel *et al.*, 2006; Klimek *et al.*, 2008). In particular, β-diversity, which quantifies the change or turnover, in species across space is central to a wide array of ecological and evolutionary topics, also providing critical information to conservation planning (McKnight *et al.*, 2007; Novotny, 2009). Although the number of species in a local community (α-diversity) often contributes to the relative conservation importance of single areas, it is the species turnover between sites that might indicate the optimal spatial arrangement of conservation areas (Summerville *et al.*, 2003).

Insects are important components of grassland biodiversity, and interact with the landscape by dispersal. Mobility appears as a strong predictor of widespread success or decline of insect populations (Kotiaho *et al.*, 2005). In general poor dispersers seem to be more prone to extinction and range contractions imposed by several human-induced processes such as fragmentation or eutrophication (Reinhardt *et al.*, 2005; Öckinger *et al.*, 2009, 2010; Bommarco *et al.*, 2010; Ekroos *et al.*, 2010; Marini *et al.*, 2010). As mobility might be important in shaping species occupancy patterns (Kunin & Gaston, 1993; Nieminen *et al.*, 1999; Cowley *et al.*, 2001; Gaston & Blackburn, 2003), we expected that this trait should also modify species turnover across space. For instance, the proportion of species shared between two sites often decreases as the distance separating them increases, i.e. distance decay of similarity (Nekola & White, 1999; Morlon *et al.*, 2008). This pattern can be partly explained by increasing dissimilarity in environmental features with increasing distance (effects of niche-based processes) (Loreau, 2000) and partly by landscape configuration that dictates the dispersal rates of organisms between sites (effects of dispersal-based processes) (Nekola & White, 1999). In the latter case, a prediction that arises from the metapopulation theory suggests that species with higher mobility should have high levels of occupancy for their abundance (Hanski, 1999; Gaston & Blackburn, 2003). This should affect species spatial turnover by reducing β-diversity due to the larger exchange of individuals between populations. However, very little research has been done to test whether mobility might affect the diversity distribution of species across multiple spatial scales (but see Summerville *et al.*, 2006; Ekroos *et al.*, 2010).

In this study, orthopterans inhabiting hay meadows were chosen as a model system to test how mobility modifies β-diversity patterns across multiple spatial scales and along a gradient of management intensity. We considered three nested spatial scales (1-m^2 plots within meadow, 1000-m^2 meadows within landscape, and 19.6-km^2 landscapes within a region), corresponding to three different scales at which local stakeholders might apply conservation measures in managed grasslands, i.e. management guidelines at the field scale or managing the whole landscape at the regional scale. We tested the hypothesis that high mobility reduces β-diversity due to a homogenising effect of dispersal. As the different spatial scales have also been chosen to match the scales at which conservation measures are normally applied, our results will provide relevant information to manage grasslands for orthopteran conservation.

Materials and methods

Study area

The field survey was carried out in 2007 in the Province of Trento (6200 km^2), in north-eastern Italy. In 2007, the area covered by hay meadows was c. 16 000 ha. In this study, only montane meadows managed for hay production for at least 20 years (permanent meadows) were included. Meadows were fertilised with liquid or farmyard manure and only mown. The meadows are typically small (less than one ha), spatially scattered and interspersed with other management units belonging to different farms. The landscape was mainly composed of a grassland-forest mosaic.

Sampling design

To identify diversity pattern at different spatial scales, a nested sampling design was applied (Fig. 1). Based on official data of the Agriculture Department of the Province of Trento, we brought together information on meadow and topography in a GIS. Then, four classes of management intensity were defined. The four classes were defined on the basis of topographic slope, mowing frequency, soil fertility and sward height (proxy for productivity). The four classes varied from flat, high-productive intensively managed meadows to steep, low-productive, extensively managed meadows (Table 1). Both management intensity and slope are known as important factors affecting α-diversity of orthopterans in hay meadows (Marini *et al.*, 2009a). For each management class, 11 non-overlapping landscape sectors were selected (2.5-km radius) (Fig. 1a, macroscale). Then, within each landscape, three meadows belonging to the same management class were sampled (Fig. 1b, mesoscale). In total, 44 meadow triplets were sampled across the whole study region. We tried to keep the distance between the landscape sectors and the meadows within the sectors more or less equal. The landscapes were also selected to obtain an interspersed distribution of the different management classes. This would reduce potential biases due to different distances between sites belonging to different management classes. The elevation was similar between meadows at the mesoscale (i.e. the three meadows within each landscape had similar elevation), whereas it varied between landscapes from a minimum of 240 to a maximum of 1380 m. However, there was no significant difference in mean elevation between the four management classes (Table 1). Overall, 132 meadow parcels were sampled across the whole study region. The meadow size ranged from 1.2 to 4.5 ha. A plot of 25 × 40 m (1000 m^2) was placed in each meadow, where we carried out the surveys. Within each meadow, orthopteran diversity was sampled using 24 1-m^2 plots (Fig. 1c, microscale) (see below for more details).

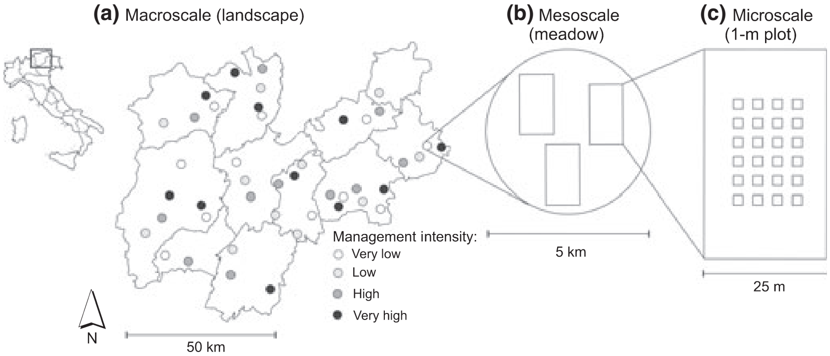

Fig. 1. Nested sampling design performed at three spatial scales: (a) macroscale (landscape), (b) mesoscale (meadow) and (c) microscale (1-m^2 plot). We sampled 11 landscapes for each management classes. The three meadows within each landscape belonged to the same management class.

Table 1. Comparison of mean values of our three indicators of management intensity and topographic slope between the four management intensity classes.

	Management intensity				
Sampled meadows ($n = 132$)	Very high ($n = 33$)	High ($n = 33$)	Low ($n = 33$)	Very low ($n = 33$)	P[‡]
Number of cuts per year	2.5	2.3	2.0	1.8	< 0.01
Soil Olsen P (mg kg^{-1})*	68.5	67.0	51.1	41.2	< 0.01
Vegetation height (cm)[†]	33.0	33.3	25.9	22.7	< 0.01
Meadow slope (°)	2.5	7.9	14.0	19.0	< 0.01
Elevation (m)	829	891	843	883	n.s.

[*] Exchangeable Olsen P_2O_5 (P) (Olsen *et al.*, 1954) measured on eight samples taken at a depth of 0–20 cm, after removing the organic layer, and bulked prior to analyses.

[†] Vegetation height was measured using a drop-disc method (Stewart *et al.*, 2001).

[‡] *P*-value from a one-way ANOVA.

Orthopteran surveys

We sampled Orthoptera (*Ensifera* and *Caelifera*) by visiting the 132 meadows during the periods of maximum activity and density of the species (between end of July and the end of August). Surveys took place between 10.00 and 17.00 h on warm sunny days that did not follow a day of high rainfall. In each meadow, orthopteran species richness and abundance was determined by using a 'box quadrate' with high sides (Gardiner *et al.*, 2005). We used a white quadrate sampler that is a box with open top and bottom, with a side length of 1.0 m, and a height of 0.75 m. Within each meadow, 24 samplings were carried out by laying the box down rapidly in a vertical position, and therewith capturing all the individuals within the sampler. The nomenclature follows Fontana *et al.* (2005).

Mobility

As a measure of mobility of the orthopteran species, we used the index developed by Reinhardt *et al.* (2005) for Germany. This classification includes the following three classes: sedentary, intermediate disperses, and mobile species (Table 2). All apterous and brachypterous species were classified as sedentary, whereas species flying readily were assigned as mobile. For species showing wing dimorphism, we adopted the most common form. We acknowledge that mobility is not a fixed trait, and that it may differ between and within populations depending on habitat spatial configuration and population history (Poniatowski & Fartmann, 2008). However, we used broad mobility classes, assuming that the degree of intra-specific variation was small compared with the variation between mobility classes (see also Öckinger *et al.*, 2009; Marini *et al.*, 2010). To further reduce potential bias, intermediate dispersers (whose classification typically was more problematic than the sedentary and mobile species) were excluded from the analyses. This allowed us to focus on the contrast between mobile and sedentary species. The species not reported by Reinhardt *et al.* (2005) were classified on the basis of information on taxonomic affinities, body size, and wing development (Fontana *et al.*, 2002). Using these criteria, we located, for each of the twelve non-classified species, the most taxonomically similar one included in Reinhardt *et al.* (2005) for Germany, and then we assigned it the same value. We also classified species either as habitat specialists or generalists following Reinhardt *et al.* (2005), to test whether sedentary species were more likely to be habitat specialists than mobile species. Within our Orthoptera species pool, we found that habitat specialisation and mobility were independent life-history traits (Fisher's exact test, $P = 0.448$).

Table 2. Species list (from the most to the least frequent species), mobility, and habitat specialisation classification (according to Reinhardt *et al*., 2005), species occupancy (occ. %) at the mesoscale (% of the 132 meadows occupied), and total abundance in the four management intensity classes.

				Management intensity			
Species	Mobility	Specialisation	Occ. (%)	Very high	High	Low	Very low
Chorthippus dorsatus	Mobile	Generalist	87.9	249	583	44	498
Chorthippus parallelus	Mobile	Generalist	86.4	446	539	352	61
Glyptobothrus biguttulus	Mobile	Generalist	60.6	27	239	241	151
Stauroderus scalaris	Mobile	Generalist	28.8	2	11	43	11
Euthystira brachyptera	Intermediate	Specialist	27.3	18	8	94	73
Gryllus campestris	Sedentary	Specialist	23.5	2	11	18	2
Decticus verrucivorus	Sedentary	Specialist	20.5	1	5	23	22
Omocestus rufipes	Sedentary	Generalist	18.2	2	1	81	172
*Ruspolia nitidula**	Mobile	Generalist	16.7	21	21	22	34
Stenobothrus lineatus	Intermediate	Specialist	15.9	1	2	37	35
Pholidoptera griseoptera	Sedentary	Generalist	15.2	2	7	17	2
Bicolorana bicolor	Mobile	Specialist	11.4	4	7	1	2
Platycleis grisea	Intermediate	Specialist	10.6	1		15	6
Glyptobothrus brunneus	Mobile	Specialist	9.8	12	21	12	3
Glyptobothrus mollis	Mobile	Specialist	9.1	4	1	16	3
Tetrix tenuicornis	Sedentary	Specialist	8.3	1	2	5	1
Dirshius haemorrhoidalis	Sedentary	Specialist	7.6		7	5	15
Tettigonia cantans	Intermediate	Generalist	7.6	1	2	2	11
*Eucorthippus declivus**	Mobile	Specialist	6.8	21	1	36	1
Gomphocerus rufus	Intermediate	Generalist	6.8	1	1	9	35
Phaneroptera falcata	Mobile	Specialist	5.3			6	9
Oedipoda caerulea	Mobile	Specialist	4.5			4	4
Omocestus viridulus	Intermediate	Generalist	4.5	4	1		1
Tetrix subulata	Mobile	Specialist	4.5	2		12	3
*Parapleurus alliaceus**	Intermediate	Specialist	3.8	6	3	1	
Tetrix bipuctata	Sedentary	Specialist	3.8			3	3
Arcyptera fusca	Sedentary	Generalist	3			8	9
*Leptophyes boscii**	Intermediate	Specialist	3			3	2
Pholidoptera falcata	Sedentary	Specialist	2.3		1		3
Roeseliana roeseli	Sedentary	Specialist	2.3	3	1		
Tettigonia viridissima	Mobile	Generalist	2.3			3	
*Kisella irena**	Sedentary	Specialist	1.5			1	1
Nemobius sylvestris	Sedentary	Specialist	1.5		2	1	
*Pachytrachis striolatus**	Sedentary	Specialist	1.5			5	
Pholidoptera aptera	Sedentary	Generalist	1.5			1	1
*Tetrix bolivari**	Sedentary	Specialist	1.5				2
*Xiphidion discolor**	Intermediate	Specialist	1.5			2	
*Barbitistes serricauda**	Sedentary	Specialist	0.8				1
Calliptamus italicus	Intermediate	Specialist	0.8				12
*Calliptamus siciliae**	Intermediate	Specialist	0.8			4	
*Ephippiger vicheti**	Sedentary	Specialist	0.8				1
Glyptobothrus apricarius	Mobile	Specialist	0.8				5
Leptophyes albovittata	Mobile	Specialist	0.8			1	
Psophus stridulus	Sedentary	Specialist	0.8			1	
*Tettigonia caudata**	Intermediate	Specialist	0.8	1			

*Species not included in Reinhardt *et al*. (2005) were classified according to Fontana *et al*. (2002).

Scales and additive partitioning of species diversity

We additively decomposed the total observed γ-diversity into diversity components within and among sampling units (α- and β-diversity, respectively) separately for each management classes at the micro-, meso- and macroscale (Fig. 1). Within the context of this study, orthopteran species richness was used as a measure of species diversity. At the microscale, α-, β- and γ-components of diversity were calculated in 3168 1 m^2 plots (792 for each management class, respectively); at the mesoscale in 132 meadow parcels (33 for each management classes), and at the macroscale in 44 landscape sector (11 for each management class). The α-diversity (within-unit diversity) was the average number of species found in a sampling unit (plot, meadow, and landscape). The γ-diversity was the total number of species found in the pooled sampling units. For the three spatial scales, β-diversity (between-unit diversity) was calculated by subtracting α from γ (Gering *et al*., 2003). As α- and β-diversity components were expressed in the same units of species richness, their contribution to total observed γ-diversity can be compared directly.

Data analysis

To test if the proportion of β-diversity (% of γ-diversity within the same spatial scale) components differs between management classes and between mobile and sedentary species at micro-, meso- and macroscale, General Linear Mixed Models were used (SAS Proc Mixed, Littell *et al*., 1996) with mobility and management as fixed effects. The random structures were defined to account for sampling nestedness. At the microscale, meadow identity nested within landscape sectors was included as a random factor, and at the mesoscale, landscape sector was included as a random factor. The ratio β/γ (arcsine($\sqrt{}$)-transformed) within each spatial scale (i.e. β-micro/γ-micro, β-meso/γ-meso, and β-macro/γ-macro) were used as response variables.

Results

Overall, 45 orthopteran species were found (27 *Caelifera* and 18 *Ensifera*) in the 132 meadows. Fifteen species were mobile, 19 sedentary, and 12 were intermediate dispersers. *Chorthippus parallelus* and *C. dorsatus* were the most abundant species, followed by *Glyptobothrus biguttulus*, *Omocestus rufipes* and *Eutistyra brachyptera*. The total number of species (γ-macro) was higher within the low intensity management classes (Fig. 2). Eighty percent of the overall number of species found was observed in the very low intensity management class, whereas only 50% was found on very intensively managed meadows. The species found in the very high intensity class was almost completely nested in the species pool found in the very low intensity class, i.e. no species were strictly associated with the intensively managed meadows. Considering all the species together, the proportion of β-diversity of the regional γ-diversity varied between the three spatial scales. β-diversity decreased passing from the macro-, to the meso-, and microscale (the mean values are indicated in Fig. 2).

The patterns in species turnover within scale (% of β- of γ-diversity within each scale) varied between sedentary and mobile species. At all three spatial scales, β-components (% of β- of γ-diversity) were larger for sedentary than for mobile species (Table 3), i.e. there was higher species turnover between plots, meadows and landscapes. At micro- and macroscale, but not at the mesoscale, there were also non-significant tendencies to lower β-diversity with decreasing intensity of management. The interaction between mobility and management class was not significant at any of the investigated spatial scales.

Discussion

Our study indicates that the three investigated scales contributed differently to the partitioning of the regional γ-diversity along our management gradient and that orthopteran community composition varied most significantly over broader spatial scales. Mobility strongly modified β-diversity patterns of orthopterans, where sedentary species contributed to a greater proportion of β-diversity across different scales compared with mobile species. The orthopteran communities inhabiting intensively managed meadows were strongly nested and were a subset of those inhabiting extensively managed meadows.

Scales and partitioning of the total γ-diversity

Larger proportion of total γ-diversity (overall number of species in the study area) was composed of β-diversity at the macroscale (landscape), whereas this proportion was smaller at the microscale (plot) and mesoscale (meadow). The observed β-diversity patterns at each scale was probably the result of both environmental heterogeneity, species niche differentiation (Loreau, 2000) and dispersal limitation processes (Nekola & White, 1999). Separating these factors for explaining species distribution across scale is difficult, although we did test for certain important environmental variables such as slope and management intensity. We surmise from our results that mobility and dispersal processes are important at all scales, but perhaps especially important determinants for beta-diversity at small and intermediate scales. The distance between sampling units was more or less constant within each scale of analysis, although it increased passing from a few metres between 1-m plots, to 0.5–1.5 km between meadows and to several kilometres between landscape sectors. The large β-diversity at the macroscale compared with the meso- and microscale concurs with the distance decay of similarity hypothesis (Nekola & White, 1999; Morlon *et al*., 2008). Longer distances between landscapes than between meadows might increase dispersal limitation and therefore lead to different species pool adapted to local conditions. These results generally confirm the observations of several previous studies that indicate that insect community composition varies most significantly over broader spatial scales, even when total species richness does not (e.g. Summerville *et al*., 2003, 2006).

At the microscale (1-m plot), we found low species turnover between plots within meadows. Although plots within meadow may vary in microclimate and vegetation architecture, orthopteran species usually exploit the whole meadows and do not respond to environmental heterogeneity at such fine spatial scale (Ingrisch & Köhler, 1998). At the mesoscale (meadow), the relatively low level of β-diversity can be a consequence of our sampling design in which meadows with similar slope and management were selected within a landscape of 2.5 km radius. Keeping management constant, the relatively short distances between meadows (0.5–1.5 km) might have contributed to community homogenisation, as this distance range is comparable with orthopteran dispersal. The macroscale (landscape) contributed a large proportion of β-diversity with values up to 90% of

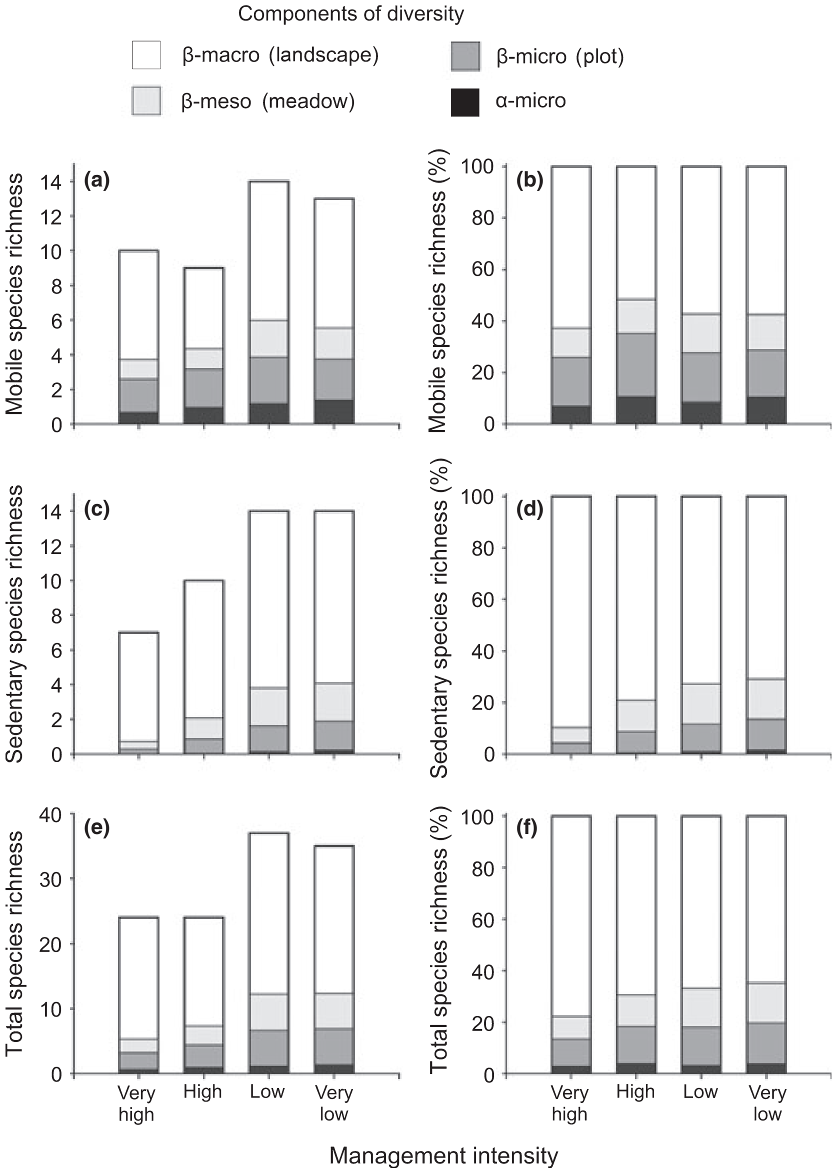

Fig. 2. Additive partitioning of orthopteran species richness at the three spatial scales (microscale: 1-m^2 plot; mesoscale: meadow, macroscale: landscape) within the four management classes. Mean α- and β-components for (a) mobile, (c) sedentary and (e) total species richness. We show also the relative contributions (i.e. % of total γ) of the α-component and β-component in panels (b), (d) and (f).

the total γ-diversity. Landscape may vary a lot in several features such as topography, climate, habitat diversity, or history. All these factors are known to influence local assemblages and composition of orthopteran communities (Schouten *et al.*, 2007; Gardiner & Hassall, 2009; Schirmel *et al.*, 2010). In particular, it is well known that orthopteran communities shift strongly along mountain elevation gradients (Alexander & Hilliard, 1969). As the landscape sectors were located along a relatively extended

Table 3. General linear mixed model results, testing the effects of management and mobility on β-diversity patterns. We tested β-micro (% on γ-micro) at the mesoscale (meadow) (n = 132), (b) β-meso (% on γ-meso) at the mesoscale (landscape) (n = 44), and β-macro (% on γ-macro).

	(a) Microscale			(b) Mesoscale			(c) Macroscale		
	d.f.	*F*	*P*	d.f.	*F*	*P*	d.f.	*F*	*P*
Mobility	1,73	87.1	< 0.001	1,31	68.6	< 0.001	1,3	40.2	0.008
Management	3,73	2.17	0.099	3,31	0.47	0.71	3,3	8.50	0.056
Management × Mobility	3,73	1.29	0.29	3,31	1.58	0.21	–	–	–

elevation gradient (range: 240–1380 m), the differences in temperature between low- and high-elevation areas might have played an important role in increasing species turnover at the broad spatial scale.

Mobility effect on β-diversity patterns

Mobility, but not management, strongly modified *β*-diversity patterns within each of the investigated scales, reducing species turnover between plot, meadows and landscapes, respectively. High dispersal probably worked as homogenising force at all spatial scales. The lack of management effects indicate that niche-based processes were probably less important than dispersal limitation in shaping *β*-diversity patterns. Dispersal limitation has been demonstrated to play an important role in determining insect community structure, especially in highly disturbed or fragmented systems (Thomas, 2000; Öckinger *et al*., 2009, 2010; Bommarco *et al*., 2010; Marini *et al*., 2010). Summerville *et al*. (2006), using body size as a proxy for mobility, found that species turnover did not vary between small and large species, although they also indicated that this trait might not be a good proxy for species dispersal and occupancy in moths. Our results generally concur with those of Ekroos *et al*. (2010), who found that agricultural intensification decreases *β*-diversity of butterflies as a result of an increasing proportion of habitat generalists and increasing average mobility in the butterfly communities. Highly mobile species are expected to be less affected by barriers, being better able to occupy suitable habitats compared with sedentary species.

Dispersal might also rescue local populations from extinction (Brown & Kodric-Brown, 1977) in habitats that are of low quality for orthopterans due to intensive management (Pulliam, 1988). For instance, local disturbance through management strongly affects orthopteran diversity due to the direct mortality of mowing (Humbert *et al*., 2009), and increased sward height due to fertilisation intensification (Marini *et al*., 2009a). Thus, highly mobile species should be better able to escape and recolonise the meadows after the disturbance related to management, rendering a generally higher regional occupancy. Loss of sedentary species may not affect α-diversity as dramatically as it affects *β*-diversity, because α-diversity often largely consists of common mobile species, whereas *β*-diversity measures diversity responses at larger spatial scales, and is more contingent on sedentary species (Ekroos *et al*., 2010).

Implications for conservation

Mobility has been demonstrated to be one of the strongest predictors of widespread decline of orthopteran populations caused by habitat degradation and loss both at the local (Marini *et al*., 2010) and the biogeographical scale (Reinhardt *et al*., 2005). Low mobility was associated with higher species turnover across space, particularly at the broader spatial scale. Sedentary species are probably the most threatened species by ongoing land-use changes such as intensification and abandonment. Effective conservation of orthopteran specie richness at the regional scale should therefore consider the mobility-dependent response of species diversity. Previous research has demonstrated that eutrophication (Marini *et al*., 2009a), disturbance through mowing (Humbert *et al*., 2009, 2010), and abandonment (Marini *et al*., 2009b) are major drivers of species richness decline of orthopterans in alpine hay meadows. Conservation measures currently included in most agri-environment schemes have, therefore, focused only on the extensive management of grasslands at the field scale (Knop *et al*., 2006; Merckx *et al*., 2009). Our results, however, also indicate that the spatial distribution of these meadows is crucial and that incorporating *β*-diversity might provide complementary information to conservation planning to maintain high species diversity at the regional scale. We therefore suggest maintaining extensive meadows scattered throughout the whole region, as the loss of species-rich isolated grassland patches due to abandonment or eutrophication might cause severe reductions of the regional diversity. Increasing connectivity between meadows might be also considered as a complementary measure to improve species occupancy and population persistence, particularly for sedentary species (Ekroos *et al*., 2010). The inclusion of species mobility in additive partitioning analyses has provided new insights into the processes shaping species diversity, indicating also the relevant scales for optimising future conservation measures.

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