

Responses of grassland specialist and generalist beetles to management and landscape complexity

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ABSTRACT

We tested the influence of grazing intensity and effect of landscape complexity on grassland specialist and generalist beetles of three beetle families, i.e. Carabidae, Chrysomelidae, and Curculionidae, on extensively and intensively grazed cattle pastures in three regions of the Hungarian Great Plain. In every region we investigated seven pairs of grazed grasslands. On each field, samples were taken along two 95-m-long transects; one transect at the edge and the other one 50 m away from the edge in the grassland interior (altogether 84 transects). Carabids (Carabidae) were sampled using funnel traps for three 2-week sampling periods during spring and early summer. Leaf-beetles (Chrysomelidae) and weevils (Curculionidae) were surveyed by sweep netting in May and June 2003. Analysing the grazing intensity and landscape complexity effects on generalist and specialist beetles with linear mixed models, grazing effect was detected only on specialist leaf-beetle species richness with more species in the extensively grazed sites. Landscape complexity had contrasting effects on specialist and generalist species. Habitat generalists were more and negatively affected by increasing grassland coverage (reduced heterogeneity) than specialists. At species level analyses on four species out of 21, landscape effects were shown, which suggested that landscape composition might have strong effects on the species composition of the beetle assemblages. Our results suggest that conservation of biodiversity in agricultural systems (such as in managed Central European grasslands) requires a landscape perspective besides investigating management effects.

Keywords

Grazing management, carabid, leaf-beetle, weevil, Carabidae, Curculionidae, Chrysomelidae.

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INTRODUCTION

As a consequence of the reduction of natural and seminatural habitats and the increasing use of external inputs such as fertilizers and pesticides, agricultural intensification is one of the major causes of biodiversity loss (Donald *et al.*, 2002; Benton *et al.*, 2003; Kleijn & Sutherland, 2003; Bengtsson *et al.*, 2005; Tscharrntke *et al.*, 2005). Permanent landscape elements, such as grasslands and woodland fragments, play a crucial role in maintaining biodiversity in cultivated landscapes by providing habitats or refuges for many species (Duelli, 1997; Jeanneret *et al.*, 2003; Woodcock *et al.*, 2005). The biodiversity of grasslands mainly depends on management, especially cutting and grazing. Arthropod species richness and abundance are reduced by intensive grazing and mowing (e.g. Dennis *et al.*, 1998; Kruess & Tscharrntke, 2002; Knop *et al.*, 2005). As important arthropod taxa in terms of their species richness and abundance in grassland ecosystems,

beetles could be a suitable taxon to investigate the effect of grazing intensity. Contradictory results showed that beetles can benefit from extensive grazing in terms of both species richness and abundance in Germany (Coleoptera, Kruess & Tscharrntke, 2002), may not be influenced by grazing management in Sweden (Carabidae, Söderström *et al.*, 2001), and are positively affected by grazing intensity in the Swiss Alps (Carabidae, Grandchamp *et al.*, 2005).

To understand the negative and positive effects of agricultural land use for the conservation of biodiversity, the consideration of different spatial scales is needed, e.g. the field scale and the landscape scale (Tscharrntke *et al.*, 2005). The surroundings of agricultural habitats may strongly affect ground beetle (Carabidae) diversity and abundance (Duelli & Obrist, 2003; Jeanneret *et al.*, 2003; Dauber *et al.*, 2005), suggesting that the landscape scale has to be taken into account when analysing the distribution of these assemblages. Large-scale features, interacting with local factors,

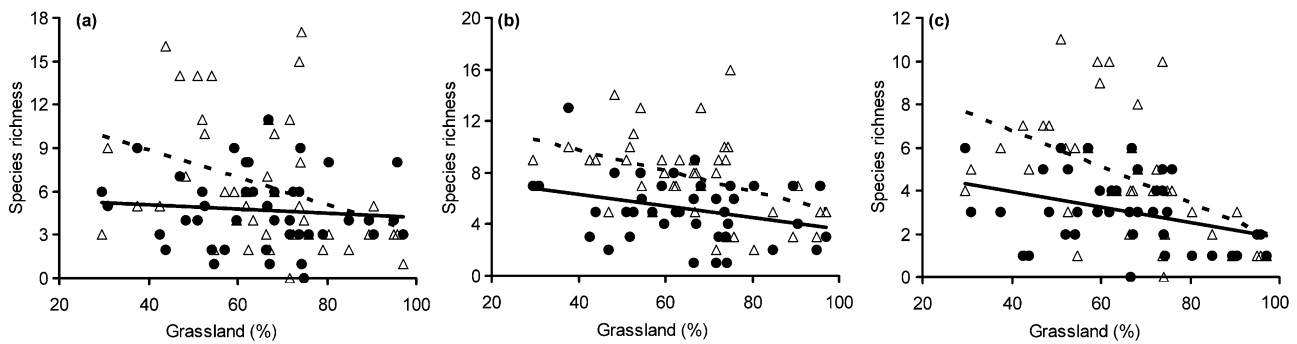


Figure 1 Correlation between the percent cover of grassland within 500 m buffer area of study sites and species richness of specialist and generalist beetles (filled circles indicate habitat specialist; open triangles indicate habitat generalist). (a) Carabids, (b) leaf-beetles, and (c) weevils. Solid line indicates correlation for specialist and dashed line indicates correlation for generalist.

could confound the effect of management practices on biodiversity at local scale (Clough *et al.*, 2005).

We studied extensively and intensively grazed pastures in three regions of the Hungarian Great Plain. The three regions differed in landscape structure (from simple through intermediate to complex). Our aims were to test for the influence of grazing intensity and the effect of landscape on grassland specialist and generalist species belonging to three beetle families: the Carabidae, Chrysomelidae, and Curculionidae.

METHODS

Study area and design

Seven pairs of seminatural grasslands with high and low grazing pressure were selected in the vicinity of each other in each of three distinct biogeographical regions of the Hungarian Great Plain (altogether 21 pairs of fields, equivalent to 42 sample fields, split between three biogeographical regions). The three regions differ in their landscape structure, although grasslands are the most extensive land-use type (over 60%) in every region (Batáry *et al.*, 2007). The first study region was the Heves biogeographical region partly covered by Heves Landscape Protection Area in Eastern Hungary (for geographical location of study areas see Fig. 1 in Báldi *et al.*, 2005) and was dominated by a mosaic-complex of dry and wet alkali grasslands and marshes on solonetz soil. This region had the simplest landscape structure (simple region), containing the largest, least fragmented grassland patches. The second region was situated parallel to the Danube river, in the Kiskunság National Park, had a more complex landscape structure, and contained secondary Pannonic alkali steppe vegetation on solonchak soils (intermediate region). The third region (also in the Kiskunság National Park) was more heterogeneous, with several marshy patches and woodlots in the grasslands, resulting in the most complex landscape structure (complex region). Most (86%) of our intensively grazed sites, and all of the extensively grazed pastures were unfenced. All sites have been grazed by cattle for at least 5 years from early spring until late autumn. The cattle density was < 0.5 cows per hectare on extensive, and > 1 cow per hectare on intensive fields. None of the fields

were fertilized or cut. For a more detailed area description, see Báldi *et al.* (2005). On each field, samples were taken along two 95-m-long transects: one along the edge and another, parallel to the first one, 50 m apart from the edge in the grassland interior. The extensive field and intensive field in a pair had the same soil type and groundwater level and were situated in similarly structured landscapes, therefore the effects of confounding environmental variables were minimized. We had a total of 84 transect sites.

Beetle sampling

In 2003, ground beetles (Carabidae) were sampled using funnel traps (10 cm diameter). Funnel traps are up to three times more efficient per centimetre trap diameter in catching ground beetles than cup traps (Obrist & Duelli, 1996). Two funnel traps, 10 m apart from each other, were placed along the edge of the grassland and two in the interior transects of each field and were opened for three 2-week sampling periods (5–19 May; 19 May to 2 June; 17 June to 1 July) during spring and early summer. For each pair of extensively and intensively grazed fields, the adjacent habitats to the edge were similar. During evaluation, only one of the traps from each transect was used, because several traps were destroyed by cows. Leaf-beetles (Chrysomelidae) and weevils (Curculionidae) were surveyed by sweep-netting twice, in May and June 2003. All sampling was done along the 95-m-long transects, both in the edge and in the field interior. One sweep net sampling consisted of 3 × 20 sweeps with a heavy-duty sweep net (38 cm internal diameter, 7215HS, BioQuip, Rancho Dominguez, CA, USA). The voucher specimens are stored in the Hungarian Natural History Museum. All beetles of these families caught by funnel trapping or sweep-netting were identified to species level (Ádám, 1996; Podlussány, 1996; Vig, 2003).

Lövei & Sunderland (1996) found that habitat choice of many carabids is so specific that they could be used to characterize habitats. Therefore, we divided the species into habitat specialist and generalist, because specialist species usually react in a different way to factors than generalist species (Magura *et al.*, 2000; Söderström *et al.*, 2001; Kruess & Tscharncke, 2002). The division to specialist (vs. generalist) was based on known associations with open areas, but among open areas, the grassland was where the

species most frequently occurred (see Appendix S1 in Supplementary Material). Categorization was based on the published literature (Ádám, 1996; Podlussány, 1996; Vig, 2003).

Landscape data

We used aerial photographs (Institute of Geodesy, Cartography and Remote Sensing; Air project 2000; 0.5 m/pixel resolution) to map land-use types (grassland, forest, cropland, marsh, built-up area, and water) of each fields in a buffer of 500 m radius. The percentage cover of grassland within a radius of 500 m around the study fields was used as a simple measure of landscape complexity as in other study (Purtauf *et al.*, 2005). This landscape variable was similar in all the three regions (simple: $71.8 \pm 14.5\%$, intermediate: $61.7 \pm 10.1\%$, complex: $62.7 \pm 13.6\%$; one-way ANOVA: $F_{2,41} = 1.627$, $P = 0.210$), but can be different between sites (cover of grassland within a radius of 500 m around the study fields ranged from 30% to 97%). Grassland coverage correlated strongly and negatively with three other important landscape measurements, patch density, length of boundaries, and Shannon diversity of land-use types, which reflect landscape complexity (Spearman correlations, total patch density: $R = -0.489$, $P = 0.001$; total length of boundaries: $R = -0.536$, $P = 0.001$; land-use diversity: $R = -0.860$, $P = 0.001$).

Statistical analysis

Effects on species richness and abundance of grassland specialist and generalist beetles of management (extensive or intensive grazing regime) and prevalence of grassland habitat within the landscape (grassland percentage) were analysed in linear mixed models using the Restricted Maximum Likelihood method. Management was used as fixed factor, region and pair of fields were used as random factor, and landscape complexity (grassland percentage) was a covariate. The normality of the distribution of the raw dependent variables was assessed using QQ-plots, and data were log-transformed when necessary. We made similar models at species level, but with nested logistic regression analyses, because none of the abundant species' density was normal. To do this we converted the abundance data to presence-absence data. Species occurring in less than 13 or more than 26 of the total 42 fields were excluded from the analyses. The calculations were made using the R software package (R Development Core Team, 2004).

RESULTS

Our data set consisted of 8212 individuals of 290 species, including 98 carabid species with 2790 individuals, 93 leaf-beetle species with 4156 individuals, and 99 weevil species with 1266 individuals. Generalist abundance and species richness were higher in all taxa except the weevils, where specialists were more abundant (Table 1).

Grazing intensity affected only the species richness of specialist leaf-beetle species, where more species were found at the extensively grazed sites (Table 2). Regarding landscape complexity, significant effects were found in the species richness of generalist

Table 1 Diversity and abundance of specialist and generalist beetles sampled on 21 pairs of extensively and intensively grazed cattle pastures in the Hungarian Great Plain

	Species richness		Abundance	
	Specialist	Generalist	Specialist	Generalist
Carabids	34	64	816	1974
Leaf-beetles	33	60	1656	2500
Weevils	28	71	812	454

Table 2 Linear mixed models on the effects of management (extensive or intensive grazing regime) and landscape (grassland percentage within 500 m buffer area of study sites) on specialist and generalist beetle assemblages of Hungarian grasslands. Stars indicate level of significance

	Management		Landscape	
	F	P	F	P
Species richness				
Specialist carabids	1.794	0.196	0.149	0.704
Specialist leaf-beetles	6.189	0.022*	3.770	0.067(*)
Specialist weevils	0.074	0.789	5.928	0.025*
Generalist carabids	0.156	0.697	5.097	0.036*
Generalist leaf-beetles	2.414	0.137	8.703	0.008**
Generalist weevils	0.003	0.956	15.660	0.001***
Abundance				
Specialist carabids	1.735	0.203	0.103	0.752
Specialist leaf-beetles	1.689	0.209	1.109	0.306
Specialist weevils	0.038	0.847	2.115	0.162
Generalist carabids	2.489	0.131	3.585	0.074(*)
Generalist leaf-beetles	0.292	0.595	5.735	0.027*
Generalist weevils	0.567	0.461	8.179	0.010*

(*) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$.

carabids, generalist leaf-beetles, and specialist and generalist weevils (Table 2). The species richness of grassland specialists was not or weakly negatively related to grassland coverage, while the species richness of generalists correlated negatively, but more strongly with grassland coverage (Fig. 1a,b,c).

The abundance of beetle assemblages was not affected by grazing intensity (Table 2). Landscape effects were shown for generalist species of all taxa (in the case of carabids only marginally significant), grassland coverage correlated negatively with (log-transformed) abundance of generalist species, but not with that of the specialist species (Table 2; Fig. 2a,b,c).

At the species level, logistic regression analyses were performed for ten carabid, seven leaf-beetle, and four weevil species. Management effects were found in the case of one specialist carabid (*Harpalus serripes* Quensel) and specialist weevil species (*Pseudocleonus cinereus* Schrank), with more probable presence on the intensively grazed sites (Table 3). In three species, we showed a significantly negative landscape effect: the presence of

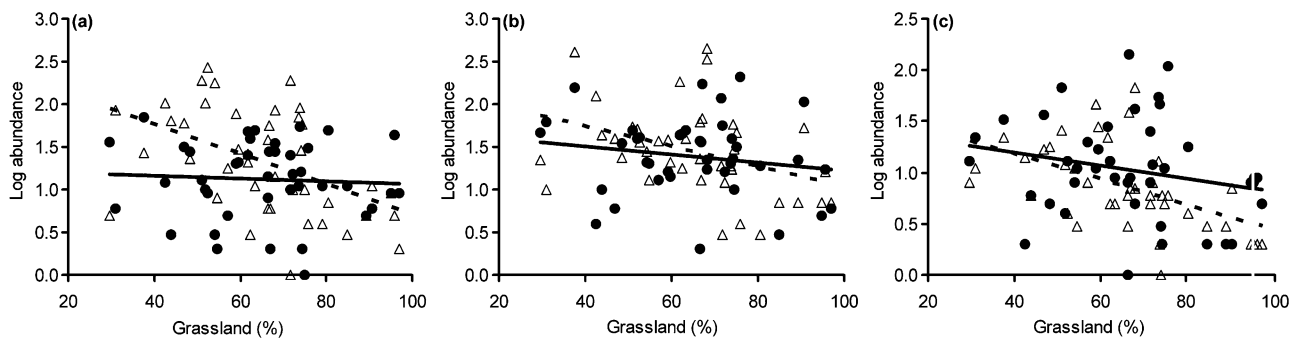


Figure 2 Correlation between the percent cover of grassland within 500 m buffer area of study sites and abundance of specialist and generalist beetles on logarithmic scale (filled circles indicate habitat specialist; open triangles indicate habitat generalist). (a) Carabids, (b) leaf-beetles, and (c) weevils. Solid line indicates correlation for specialist and dashed line indicates correlation for generalist.

Table 3 Results of the nested logistic regressions using presence–absence data of beetle species as dependent variable, management (extensive or intensive grazing regime) was a categorical variable, while landscape (grassland percentage within 500 m buffer area of study sites) was a covariate. Stars indicate level of significance

Species	Family	Management		Landscape	
		F	P	F	P
<i>Harpalus anxius</i> Duftschmid	Carabidae (specialist)	0.089	0.769	2.516	0.129
<i>Harpalus flavicornis</i> Dejean	Carabidae (specialist)	0.738	0.401	0.101	0.754
<i>Harpalus rubripes</i> Duftschmid	Carabidae (specialist)	0.324	0.576	1.119	0.304
<i>Harpalus serripes</i> Quensel	Carabidae (specialist)	10.790	0.004***	0.073	0.790
<i>Harpalus subcylindricus</i> Dejean	Carabidae (specialist)	0.412	0.529	0.038	0.848
<i>Ophonus azureus</i> F.	Carabidae (specialist)	0.076	0.786	3.005	0.099(*)
<i>Pterostichus macer</i> Marsham	Carabidae (specialist)	0.679	0.420	1.279	0.272
<i>Calathus melanocephalus</i> L.	Carabidae (generalist)	0.118	0.735	0.022	0.884
<i>Harpalus rufipes</i> De Geer	Carabidae (generalist)	0.135	0.718	1.175	0.292
<i>Microlestes minutulus</i> Goeze	Carabidae (generalist)	0.142	0.711	4.680	0.044*
<i>Chaetocnema aridula</i> Gyllenhal	Chrysomelidae (specialist)	2.463	0.133	0.093	0.764
<i>Labidostomis longimana</i> L.	Chrysomelidae (specialist)	0.000	0.995	0.594	0.450
<i>Chaetocnema tibialis</i> Illiger	Chrysomelidae (generalist)	0.532	0.475	0.241	0.629
<i>Gonioctena fornicata</i> Bruggemann	Chrysomelidae (generalist)	2.996	0.099(*)	2.398	0.138
<i>Longitarsus pratensis</i> Panzer	Chrysomelidae (generalist)	0.329	0.573	0.973	0.336
<i>Phyllotreta atra</i> F.	Chrysomelidae (generalist)	0.107	0.747	0.017	0.898
<i>Phyllotreta vittula</i> Redtenbacher	Chrysomelidae (generalist)	0.408	0.531	2.801	0.111
<i>Eusomus ovulum</i> Germar	Curculionidae (specialist)	1.809	0.195	10.959	0.004***
<i>Pseudocleonus cinereus</i> Schrank	Curculionidae (specialist)	659907	0.001***	1709	0.001***
<i>Sitona humeralis</i> Stephens	Curculionidae (generalist)	0.243	0.628	11.102	0.004***
<i>Sitona puncticollis</i> Stephens	Curculionidae (generalist)	0.177	0.679	0.600	0.448

(*) $P < 0.1$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.005$.

one generalist carabid species (*Microlestes minutulus* Goeze), one specialist weevil species (*Eusomus ovulum* Germar), and one generalist weevil species (*Sitona humeralis* Stephens) decreased with increasing grassland coverage (Table 3). While in the case of one specialist weevil (*P. cinereus* Schrank) the probability of presence increased with grassland cover.

DISCUSSION

The beetle species recorded in the present study represent a significant part of the Hungarian carabid, leaf-beetle, and weevil

fauna (about 19% of carabids [Ádám, 1996], 16% of leaf-beetles (Podlussány, 1996), and 8% of weevils; (Vig, 2003)]. Around one third of the sampled species are grassland specialists, which means that cattle-grazed pastures play an important role in maintenance of grassland specialized beetle fauna in Hungary. Magura *et al.* (2001) in their forest study found that 39% of the species are forest specialist, which is slightly higher than our case.

We found significant grazing effect only on species richness of specialist leaf-beetle species among the three examined beetle taxa. Regarding the abundance of specialist and generalist beetles, no grazing effect was shown. This confirmed the results

of Söderström *et al.* (2001), that there is no grazing effect on ground beetles in Sweden. Other studies examining management effect (low vs. high grazing intensity) on beetle abundance in grasslands are also contradictory. Oliver *et al.* (2005) found no effect in south-eastern Australia (stocking rate varied between six and 20 wethers/ha), while Grandchamp *et al.* (2005) showed positive effect in Switzerland (they compared mown vs. grazed plots, the grazing intensity was 1.8 livestock unit/ha), and Kruess & Tscharrntke (2002) showed negative effect in Germany. However, in the latter case the mean grazing intensity was higher on the extensively grazed pastures (1.4 cattle/ha vs. 5.5 cattle/ha on the intensive pastures) than our intensively grazed grasslands, and the difference between intensive and extensive mean grazing intensity in Kruess & Tscharrntke's (2002) study was larger than in our case. In this sense, one explanation of the general absence of grazing effect of the present study could be that our intensive study sites, which were unfertilized, free of chemicals, and were less intensively grazed than in Western Europe, are close to the extensive sites along a hypothetical intensification gradient. This supports the claims of Tscharrntke *et al.* (2005) that in a landscape where biodiversity is high (in this sense in all of our regions), the effectiveness of agri-environment schemes or effects of management intensity is low. The potential outcome may be that even intensively grazed grasslands could preserve a rich beetle fauna in Hungary, at least at this level of intensive grazing. However, if we move further on the hypothetical intensification gradient (in the direction of abandonment or intensification of grazing management), it can be harmful for the biodiversity as was shown on birds in Hungary by Verhulst *et al.* (2004).

The examined taxa showed different responses to landscape complexity. Habitat generalists were more affected by increasing grassland coverage (reduced heterogeneity) than specialists. The negative effect of grassland coverage on species richness (but not on abundance) of specialist leaf-beetles and weevils could be due to a lower carrying capacity of grasslands resulting from the inverse relationship between grassland cover and diversity of landscape and amount of high productivity of surrounding habitats (mainly fertilized croplands and marshy habitats). Grassland generalist may benefit more from high habitat heterogeneity in large grasslands compared to habitat specialists. This result is consistent with the main findings of Jonsen & Fahrig (1997) that generalist richness and abundance increased with increasing landscape diversity (in our case increasing land-use diversity, patch density, and boundary length) and percentage cover of examined habitat in the landscape does not affect specialist insects. Furthermore, edges are preferred areas for many generalist beetle species (Magura *et al.*, 2001; Kotze *et al.*, 2003). This could perhaps be one mechanism in increasing generalist species richness and abundance.

The results of nested logistic regression suggest that landscape metrics, at least grassland coverage could be an important factor, which may have strong effects on the species composition of the beetle assemblages. Similar to the community level results, we found that generalist species were affected negatively by increasing grassland coverage. Probably these species need heterogeneity at the landscape level. Furthermore, generalist species could originate

from the surrounding matrix, e.g. from croplands (Frampton *et al.*, 1995; Mauremooto *et al.*, 1995; Thomas *et al.*, 1997).

Our results suggest that conservation of biodiversity in agricultural systems (such as in managed Central European grasslands) benefits from a landscape perspective (Bengtsson *et al.*, 2003; Tscharrntke *et al.*, 2005; Marshall *et al.*, 2006). Habitat specificity also seems to be an important factor, because habitat specialists react differently from habitat generalists (Magura *et al.*, 2000; Niemelä, 2001; Steiner *et al.*, 2002; Kotze *et al.*, 2003). Previously, continuous grasslands are being fragmented by croplands and planted forests (i.e. the total cover of grasslands decreases on a landscape scale). Fragmentation of grasslands could affect the specialist species and generalists could invade the remnants of grasslands and later displace the specialist species. Under environmental change, this could lead to a situation where communities will increasingly become dominated by generalist species (Bowers & Harris, 1994).

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article:

Appendix S1 Species lists with total abundances of grassland

specialist and generalist beetles in PDF format. Stars indicate grassland specialist species

This material is available as part of the online article from:
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