



# The influence of grassland management on ground beetles (Carabidae, Coleoptera) in Swiss montane meadows

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## Abstract

Effects of grassland management type and intensity on carabid species richness, number of individuals and species composition were studied in the Swiss Prealps. Carabids were censused in 2001 and 2002 in 21 mown and 20 grazed meadows by means of pitfall traps.

Mean species richness was significantly higher in mown plots than in grazed plots and species composition was significantly different between these two management types. Additionally, different species characteristic for mown and grazed plots were found. These results suggest that mown meadows and grazed meadows represent two habitat types for carabid beetles.

Within both habitats, management intensity was quantified by fertilizing intensity, the number of cuts, cattle density and/or grazing intensity. The relationship between management intensity and the number of individuals and species was positive. Higher fertilizing intensity was the most important factor for higher species richness and had a significant influence on species composition in both habitats. Other variables positively related to the number of individuals, were the number of cuts in mown meadows and grazing intensity and altitude in grazed meadows. Additionally to fertilizing intensity, cattle density was positively related to the number of species in grazed meadows. These results illustrate that in the extensive management systems found in the Swiss Alps and Prealps, even intensively managed meadows can sustain high carabid diversity and abundance.

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## 1. Introduction

Compared to areas in the plain, Swiss alpine and prealpine grasslands are managed extensively. Grazed

meadows are usually browsed by cows during almost the whole vegetation period, i.e. from May to October, and fertilized with dung and manure. In addition, they are mown once in autumn. Hay meadows are fertilized with dung and manure and grazed during a few days in autumn. The number of cuts, varying between one and four times per year, and the intensity of autumn grazing are dependent on the productivity, i.e. are generally

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correlated with altitude and fertilizing intensity (Boltshauser, 2001). Currently, two trends are observed in the Alps: agricultural use of accessible grassland is further intensified; whereas, remote areas are abandoned for economical reasons (Pezzatti, 2001).

So far, the effects of different management types on species richness have been studied for various arthropods, such as grasshoppers (Wingerden et al., 1991; Dolek, 1994; Radlmair and Laussmann, 1997), butterflies (Kruess and Tscharrntke, 2002a,b), bugs (Di Giulio et al., 2001) and carabids (Rushton et al., 1989; Blake et al., 1996; Heydemann et al., 1998; Pfiffner and Luka, 2003; see also Brose, 2003). These studies show the general trend that higher arthropod species richness and abundance are favoured by organic farming in comparison to conventional methods.

Carabids are appropriate indicators for different types of open habitats (Eyre and Luff, 1990) and there is great potential for their use in assessing environmental quality (Eyre et al., 1996). Nevertheless, only few analyses on the effects of management on carabid species richness and assemblages have been performed in grazed meadows and notably in mown meadows. So far, it has been found that extensive grazing maintains high biodiversity (Morris, 1967; Thierry and Kelka, 1998) and favours rare carabid species (Walther et al., 1996). Intensive grazing, on the other hand, may strongly reduce carabid species richness (Luff and Rushton, 1989; Gardner et al., 1997; Heydemann et al., 1998).

The aim of this study is to explore the impact of management practices in montane grasslands in the Swiss Prealps on carabids. Specifically, the following questions were addressed:

- (1) Does management type (mowing or grazing) have an effect on the number of individuals, species richness and composition?
- (2) Are there species characteristic for each management type?
- (3) Is there an effect of management intensity on the number of individuals, species richness and composition within management types?

The data presented in this paper are part of the Swiss carabid data of the BioAssess project, an EU-funded project, which aims at developing a set of indicators that can be used as a tool for the rapid

assessment of biodiversity in a given habitat (Watt et al., 2004).

## 2. Material and methods

The Swiss study region was situated around Sörenberg (Entlebuch, Cantons of Lucerne and Obwalden) in the Swiss Prealps. In 2001 the UNESCO (United Nations Educational, Scientific and Cultural Organization) has accredited the Entlebuch as Biosphere reserve in Switzerland.

Within the study region, four square study-sites of 1 km<sup>2</sup> (1 km × 1 km) each were established. They consist of a mosaic landscape also including peatbogs dominated either by forest, grazed or mown meadows. Each study-site contained 16 plots situated at the intersections of a regular grid (mesh size 200 m). The 64 plots of these four study-sites were classified according to different habitat and/or management types: 18 forest plots, 2 peat bog plots, 21 mown meadow plots, 20 grazed meadow plots and 3 plots which were mown and grazed. For the analyses of this paper, the data of the 21 mown plots (altitude ranging from 919 to 1369 m a.s.l.) and the 20 grazed plots (930–1364 m a.s.l.) were considered (Table 1).

In each plot, four plastic cups (8 cm in diameter, 10.5 cm depth) were buried flush with the ground 4–5 m apart in a square. The traps were partly filled with a mixture of water and propylene glycol as a catching and preservation fluid. A plastic cover prevented the trap fluid from being diluted by rain. The traps were emptied every fortnight from early May to early September in 2001 and 2002. All four traps of one plot were pooled

Table 1

Total and mean number of individuals and species, and mean fertilizing and grazing intensity in the mown and grazed plots in the Swiss meadows studied

	Mown plots	Grazed plots	Total
Number of plots	21	20	41
Total number of individuals	5980	3399	9379
Mean number of individuals	288	170	229
Total number of species	62	63	74
Mean number of species	16.3	13.7	15
Mean fertilizing intensity <sup>a</sup>	7929	10262	9067
Mean grazing intensity <sup>b</sup>	–	1.8	–

<sup>a</sup> kg dung/ha/year.

<sup>b</sup> Livestock unit/ha.

for one sample per plot. The contents of the traps were conserved in 70% alcohol until they were determined. The carabid beetles were identified to species level using the keys in Trautner and Geigenmüller (1987) and in Freude et al. (1976). Some traps were trampled by cattle or pushed out of the ground by high ground water level. This led to a 0.5% reduction in sample size, i.e. number of carabids. All statistical analyses were performed with the pooled dataset of both years.

Furthermore, the following explanatory variables were recorded on plot-level: fertilizing intensity (kg dung/ha/year), cattle density (livestock unit/ha), number of days grazing (per year), grazing intensity (livestock unit/ha) and number of cuts (per year). These indices were calculated for each plot based on information provided by farmers and/or landowners. In addition, altitude (m a.s.l.) and openness (percentage of the surface not covered by trees within a 56 m radius) were measured for each plot. Degree of openness was computed on the base of aerial photographs.

### 3. Analyses

Mann–Whitney *U*-tests were used to test effects of management type (mowing versus grazing) on number of individuals and species. Because of a possible confounding effect of altitude on the outcome of these tests, it was also tested if altitude differed between mown and grazed plots. However, the difference was not significant (Mann–Whitney *U*-test,  $p = 0.083$ ).

Regression models were applied to determine which variables affected the number of individuals and species richness within each management type. A stepwise backward and forward selection strategy provided by the function ‘stepAIC’ in the package ‘MASS’ in the program R (R Development Core Team, 2003) was used to find the most parsimonious regression explaining variation of the number of individuals or species richness. For the analysis of the carabid data in mown meadows, the following variables were available: altitude, openness, fertilizing intensity, and the number of cuts per year. In grazed meadows the variables altitude, openness, fertilizing intensity, cattle density, the number of days grazing, and grazing intensity were available.

A detrended correspondence analysis (DCA) was performed to explore whether mown and grazed

meadows contained different carabid assemblages. A Mann–Whitney *U*-test on the site scores of the first DCA axis was used to test for effects of management type on carabid species assemblages. In a second step, a canonical correspondence analysis (CCA) revealed which variables influenced species composition within both management types. The forward selection procedure of CANOCO was used to find a minimal model of variables explaining the species data. The explanatory variables were the same variables used in the regressions. Statistical significance of variables was tested by Monte Carlo permutation tests (999 permutations). The forward selection was stopped when the additional effect of the last variable selected was not significant (5% level). In all ordinations, the down-weighting option of CANOCO was applied (DCA and CCA). The original species scores confirm to the number of individuals per species and plot.

The indicator value (IndVal) approach after Dufrière and Legendre, 1997 was applied to find typical species of grazed and mown meadows. The indicator value of a species is the product of its group specificity ( $A_{ij}$ ) and its group fidelity ( $B_{ij}$ ):  $\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100$ .  $A_{ij}$  is the mean number of occupied plots of species  $i$  across sites in group  $j$  divided by the sum of the mean number of occupied plots of species  $i$  over all groups, while  $B_{ij}$  is the number of sites in group  $j$ , where species  $i$  is present divided by the total number of sites in group  $j$ . IndVal is maximum (100%) when all plots occupied by a species are found in one group and when that species occurs in all plots of that group. Following Dufrière and Legendre, 1997, statistical significance of the resulting IndVal was evaluated for each species by a random re-allocation procedure of sites (999 permutations) among the three groups.

Mann–Whitney *U*-tests and all regressions were calculated with R 1.8.1 (R Development Core Team, 2003), ordinations were computed with CANOCO 4.5 (ter Braak and Smilauer, 2002) and indicator values were calculated with IndVal 2.0 (Dufrière and Legendre, 1997).

### 4. Results

A total of 9379 individuals belonging to 74 species were caught in all mown and grazed plots (Table 1,

Appendix A). The most abundant species in all 41 plots were *Pterostichus melanarius* (26.6% of total catch), *Poecilus versicolor* (14.8%) and *Agonum mülleri* (12.1%). All other species had an occurrence of less than 10% of total catch. Considering mown and grazed plots separately, *P. melanarius* and *P. versicolor* were the most abundant species in both habitats, while *A. mülleri* had an occurrence of more than 10% only in mown plots. Two Red List species (Marggi, 1994), *Elaphrus cupreus* and *Elaphrus uliginosus* occurred in both habitats, one species in mown plots only (*Trechoblemus micros*) and one in grazed plots (*Carabus convexus*) only (Appendix A).

In the mown plots, traps contained nearly twice as many individuals as in the grazed plots (5980 versus 3399 individuals, Table 1), but total species richness was the same for both habitat types (62 versus 63 species).

Mean number of individuals did not differ significantly between mown and grazed plots (288 versus 170,  $p = 0.26$ ). The large mean number of individuals in mown plots were largely due to two outliers with 1058 and 892 individuals. *P. cupreus* and *P. melanarius*, respectively, reached high abundances there. Without these outliers, the mean number of individuals in mown plots dropped to 215.

Mean species richness was found to be significantly higher in mown plots than in grazed plots (16.3 versus 13.7,  $p = 0.04$ ).

Site scores of the first DCA axis for mown and grazed plots were significantly different ( $p = 0.009$ ), indicating that carabid assemblages in mown and grazed meadows are different (Fig. 1).

In total, there were nine species with an IndVal score higher than 50 (Table 2). Seven of these were indicators for mown plots, two for grazed plots.

For mown plots, the stepwise variable selection strategy resulted in a model with number of cuts and fertilizing intensity, which explains best the number of individuals ( $R_{adj}^2 = 45.9\%$ , Table 3). Both number of cuts and fertilizing intensity were positively related to the number of individuals. However, fertilizing intensity seemed to be the more important variable, because the variance explained by this variable (indicated by the sum of squares) was always clearly higher than the variance explained by the number of cuts, independent of the fitting order. As altitude was

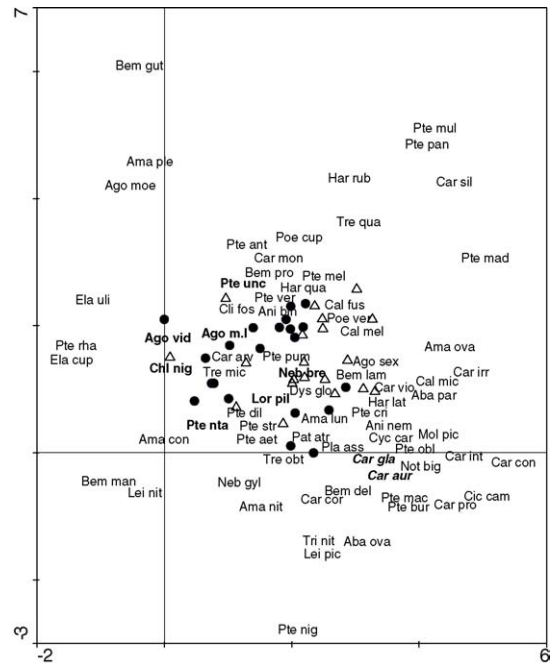


Fig. 1. Detrended correspondence analysis (DCA) ordination diagram of the carabid communities of grazed and mown plots in the Swiss meadows studied in relation to axis 1 and 2: (Δ) grazed plots; (●) mown plots. Species names written in italics are considered as indicators for grazed meadows, in bold for mown meadows. For abbreviations of species names see Appendix A.

significantly correlated with the number of cuts (Spearman rank correlation  $p = 0.002$ ), but not with fertilizing intensity (Spearman rank correlation  $p = 0.46$ ), it was tested if the number of cuts could be replaced by altitude in the final regression model. However, this was clearly not the case, since altitude was far from significance ( $p = 0.35$ ) in such a model. Fertilizing intensity was again positively and the only variable significantly related to species richness of mown plots ( $R_{adj}^2 = 42.8\%$ , Table 3).

For grazed plots, the best model explaining the number of individuals contained the variables grazing intensity and altitude ( $R_{adj}^2 = 62.7\%$ ), which were both positively related to the number of individuals. Grazing intensity explained far more of total variance than altitude, regardless of the fitting order. Moreover, altitude was only significant if fitted after grazing intensity. Species richness was positively related to fertilizing intensity and cattle density ( $R_{adj}^2 = 31.2\%$ ). Again, fertilizing intensity seemed to be the more

Table 2  
Indicator species of mown and grazed plots in the Swiss meadows studied

Species name	Mown plots		Grazed plots		IndVal (%) <sup>b</sup>
	Number of individuals	Number of plots <sup>a</sup>	Number of individuals	Number of plots <sup>a</sup>	
<i>Agonum mülleri</i>	<b>1015</b>	<b>18</b>	120	11	76.2 <sup>c</sup>
<i>Agonum viduum</i>	<b>163</b>	<b>17</b>	30	5	67.8 <sup>c</sup>
<i>Pterostichus nigrita</i>	<b>276</b>	<b>17</b>	63	12	65.3 <sup>c</sup>
<i>Chlaenius nigricornis</i>	<b>272</b>	<b>16</b>	55	7	62.8 <sup>c</sup>
<i>Pterostichus unctulatus</i>	<b>164</b>	<b>14</b>	26	9	57.2 <sup>c</sup>
<i>Nebria brevicollis</i>	<b>300</b>	<b>15</b>	93	8	53.9 <sup>c</sup>
<i>Loricera pilicornis</i>	<b>87</b>	<b>15</b>	35	8	50.2 <sup>c</sup>
<i>Carabus glabratus</i>	50	7	<b>134</b>	<b>16</b>	62.4 <sup>c</sup>
<i>Carabus auronitens</i>	17	7	<b>78</b>	<b>14</b>	57.7 <sup>c</sup>
Total		21		20	

Bold values indicate for which habitat type the species are considered as indicators.

<sup>a</sup> Number of plots in which the species occur.

<sup>b</sup> Indicator value after Dufrêne and Legendre (1997).

<sup>c</sup>  $p \leq 0.05$ .

important variable. In contrast to fertilizing intensity, cattle density was significantly related to altitude (Spearman rank correlation  $p = 0.006$ ). However, replacing cattle density in the final model for species richness by altitude, revealed no significant effects of altitude ( $p = 0.13$ ).

By means of forward selection strategy to find the best CCA model, two models explaining the same amount of variation of the species assemblages of mown plots were detected. The first model included openness ( $p = 0.002$ ) and altitude ( $p = 0.06$ ) and explained 19.7% of the variation of species assemblages, while the second model contained openness ( $p = 0.002$ ) and number of cuts ( $p = 0.014$ ) and explained 20%. This indicates that altitude and number of cuts were strongly correlated ( $r = -0.74$ ). However, fertilizing intensity had a significant effect on species assemblages ( $p = 0.017$ ), if fitted as the second variable after altitude had been included.

In grazed plots, altitude ( $p = 0.009$ ), grazing intensity ( $p = 0.002$ ) and fertilizing intensity ( $p = 0.015$ ) were included into the best model revealed by the forward selection strategy. These three variables explained 30.6% of the variation of species assemblages. Fertilizing intensity also had a significant effect on species assemblages when included as the first variable ( $p = 0.01$ ) or as the second variable after altitude had been included ( $p = 0.025$ ).

## 5. Discussion

The lower mean number of species in grazed plots (same results in Gutiérrez et al., 2004), despite the same total number of species in both habitats demonstrated that grazed meadows were a more variable habitat to carabids than mown meadows. Both management types, mowing and grazing, have different effects on grasslands. While mowing leads to a rather homogeneous structure of the sward, grazing creates a spatially heterogeneous structure caused by non-random habitat-use of cattle and by different activities, like trampling and dung deposition (van Wieren, 1995). Obviously, carabids were affected differently by constant disturbance (trampling) than by distinct disturbance events (mowing) and different species reacted differently to both disturbance types. This led to communities which were different despite many species occurring in both habitats. Furthermore, mown plots and grazed plots contained distinct indicator species. Indicators for mown plots were more numerous than for grazed plots and were mainly species of open habitats. Indicator species of grazed plots and almost all further species with higher occurrence in grazed plots were forest specialists (Maggi, 1992). However, the proximity of the forest was high but in the same range in both habitats (unpublished data). Due to lower variability of the habitat and lower heterogeneity in mown meadows, a

Table 3

Results of multiple regression analyses for the relationship between several explanatory variables and the number of individuals and species in the Swiss meadows studied

Habitat	Dependent variable	Explanatory variables	d.f.	Sum sq <sup>f</sup>	F-ratio	
Mown plots	log 10 (individuals) <sup>g</sup>	Cuts <sup>a</sup>	1	6.30	6.98*	
		Fertilizer <sup>b</sup>	1	10.22	11.33**	
		Residuals	18	16.24		
		Fertilizer <sup>b</sup>	1	12.82	14.21**	
		Cuts <sup>a</sup>	1	3.69	4.09+	
		Residuals	18	16.24		
	Species	Fertilizer <sup>b</sup>	1	291.73	15.98***	
		Residuals	19	346.94		
		log 10 (individuals) <sup>g</sup>	Altitude <sup>c</sup>	1	0.003	0.009
			Grazing <sup>d</sup>	1	11.12	33.93***
Residuals	17		5.57			
Grazing <sup>d</sup>	1		8.71	26.58***		
Altitude <sup>c</sup>	1		2.41	7.35*		
Residuals	17		5.57			
Species	Fertilizer <sup>b</sup>	1	87.30	5.55*		
	Density <sup>e</sup>	1	79.91	15.08*		
	Residuals	17	267.32			
	Density <sup>e</sup>	1	56.67	3.6+		
	Fertilizer <sup>b</sup>	1	110.55	7.03*		
	Residuals	17	267.33			

As the significance of some explanatory variables is dependent on the fitting order in some models, both models are shown.

<sup>a</sup> Number of cuts/year.

<sup>b</sup> Amount of organic fertilizer.

<sup>c</sup> Altitude in m a.s.l.

<sup>d</sup> Grazing intensity (livestock unit/ha/year).

<sup>e</sup> Cattle density (livestock unit/ha).

<sup>f</sup> Sum of squares.

<sup>g</sup> log 10-transformed number of individuals.

+  $p \leq 0.1$ .

\*  $p \leq 0.05$ .

\*\*  $p \leq 0.01$ .

\*\*\*  $p \leq 0.001$ .

typical carabid assemblage is more likely to be found there. In pastures, carabids of close forest patches dominated as no typical community could establish.

Within mown plots, fertilizing intensity had a positive effect on species richness and the number of individuals. Such an effect was not expected, since fertilizer input usually has a negative influence on carabid abundance, e.g. in crop fields (Pffner and Luka, 2003). In grazed plots, cattle density or grazing intensity were the most important variables affecting species richness and the number of individuals (Luff and Rushton, 1989; Dennis et al., 1997). However,

fertilizing intensity also influenced carabid species richness there.

Carabid species richness and abundance are expected to increase up to a certain management intensity but decrease again towards highly intensive agricultural treatments (Intermediate Disturbance Hypothesis, Connell, 1978). Therefore, a lower number of species and individuals in the most intensively managed plots were expected, assuming that management intensity was high in some of the sites. Such an effect has been reported for carabids along urban-to-rural gradients (Niemelä et al., 2002).

Obviously, though, the management intensity in the study region was still low enough not to decrease carabid species richness and abundance. In other areas, especially in lower regions, extensively managed meadows and crops fields contain higher number of species (Heydemann et al., 1998), or number of individuals and species (Hance and Grégoire-Wibo, 1987; Càrcamo et al., 1995; Di Giulio et al., 2001; Pfiffner and Luka, 2003) than intensively managed meadows and crop fields. Up to a certain level, spreading organic fertilizer may thus induce an increase in the number of individuals only (Pietraszko and de Clercq, 1982), or an increase of species richness and of abundance of at least some species in crop fields (Purvis and Curry, 1984; Hance and Grégoire-Wibo, 1987; Humphreys and Mowat, 1994). It is likely that fertilizer application favours carabid beetles because heavily fertilized and stressed plants contain high concentration of amino acids in their phloem (Arndt, 1970). High amount of amino acids favours plant sucking insects (mainly aphids) (Braun and Flückiger, 1985), which again favours carabids, as they abound where their prey abounds. Accordingly, regular input of organic fertilizer favours other soil invertebrates (Bardgett and Cook, 1998; Ryan Megan, 1999), i.e. potential preys for carabids.

Altitude is usually negatively correlated with overall management intensity. Nevertheless, there was an effect of management intensity (fertilizing intensity, number of cuts or grazing intensity) independent of altitude on the number of individuals, species richness, and assemblages.

Although fertilizing intensity was not included in the model for carabid assemblages in mown plots at all, and was only the third most important in grazed plots, the results demonstrated that fertilizing intensity still had a significant influence on the assemblages of both management types. Furthermore, its influence on number of species and individuals was outstanding. This suggests that a wide variety of fertilizing regimes is favourable for carabid diversity on the landscape level.

Managed meadows are very variable habitats within a country or across different countries as management techniques differ considerably. Thus, it is a prerequisite to use absolute values for measuring management intensity as in this study, i.e. amount of fertilizer (expressed in kg dung/ha) or cattle density

(livestock unit/ha). This enables direct comparison of the impacts of management in different agricultural landscapes.

The two most frequent species in this study, *P. melanarius* and *P. versicolor* are among the most common species of Switzerland (Marggi, 1992). *P. melanarius* is a eurytope species occurring in open habitats. It settles even in very intensively managed cultivated areas (Marggi, 1992), urban and other disturbed habitats (Niemelä and Spence, 1991; Grandchamp et al., 2000) and is the most abundant species in many other studies, such as in Hance and Grégoire-Wibo, 1987; Heydemann et al., 1998 and Brose, 2003. Two of the three most frequent species found in all meadows of this study (*P. melanarius* and *A. mülleri*) belonged to the most typical species of arable habitats in England and Central Europe (Kromp, 1999). All indicator species are common species in Northern Switzerland and generally prefer moist habitats. Actually, peatbogs and wet grassland were common in the study area. *Agonum viduum* (indicator for mown plots) occurs in all kinds of humid habitats, *Pterostichus nigrita* (mown), *Chlaenius nigricornis* (mown) and *Loricera pilicornis* (mown) prefer very moist open habitats. *Pterostichus unctulatus* (mown) lives in mulch layer. *Nebria brevicollis* (mown), *Carabus glabratus* (grazed) and *Carabus auronitens* (grazed) are forest species.

It is concluded that carabid diversity is favoured by a certain amount of management intensity in montane grasslands. Nevertheless, it is presumed that this result is due to the traditionally low cow grazing intensity in the Alps, and that diversity is likely to decrease if management intensity is further intensified. Additionally, carabid species richness will be highest if mown and grazed meadows of low and high intensity management co-occur. To understand the complex influence of management on carabids, it is important to actually quantify management intensity and to distinguish between management types, as they have different effects on ground beetles.

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## Appendix A

Number of individuals of all carabid species found in the two habitat types in the Swiss meadows studied

Species name	Red List status <sup>a</sup>	Abbreviation	Mown 21 <sup>b</sup>	Grazed 20 <sup>b</sup>	Total 41 <sup>b</sup>
<i>Abax ovalis</i> (Duft., 1812)		Aba ova	3	1	4
<i>Abax paralleipedus</i> (Pill.Mitt., 1783)		Aba par	129	262	391
<i>Agonum moestus</i> (Duftschm., 1812)		Ago moe	34	55	89
<i>Agonum mülleri</i> (Hbst., 1784)		Ago m.l	1015	120	1135
<i>Agonum sexpunctatum</i> (L., 1758)		Ago sex	4		4
<i>Agonum viduum</i> (Panz., 1797)		Ago vid	163	30	193
<i>Amara convexior</i> Steph., 1828		Ama con	3		3
<i>Amara lunicollis</i> Schdte., 1837		Ama lun	4	3	7
<i>Amara nitida</i> Sturm, 1825		Ama nit	25	1	26
<i>Amara ovata</i> (F., 1792)		Ama ova		2	2
<i>Amara plebeja</i> (Gyll., 1810)		Ama ple	6	8	14
<i>Anisodactylus binotatus</i> (F., 1787)		Ani bin	5	1	6
<i>Anisodactylus nemoralis</i> Müll., 1764		Ani nem		1	1
<i>Bembidion deletum</i> Serv., 1821		Bem del		1	1
<i>Bembidion guttula</i> (F., 1792)		Bem gut		1	1
<i>Bembidion lampros</i> (Hbst., 1784)		Bem lam	5	3	8
<i>Bembidion mannerheimi</i> Sahlb., 1827		Bem man	2		2
<i>Bembidion properans</i> (Steph., 1828)		Bem pro	9		9
<i>Calathus fuscipes</i> (Goeze, 1777)		Cal fus	86	45	131
<i>Calathus melanarius</i> (Ill., 1798)		Cal mel	34	24	58
<i>Calathus micropterus</i> (Duft., 1812)		Cal mic	1	10	11
<i>Carabus arvensis</i> Hbst., 1784		Car arv	45	71	116
<i>Carabus auronitens</i> F., 1792		Car aur	17	78	95
<i>Carabus convexus</i> F., 1775	3	Car con		3	3
<i>Carabus coriaceus</i> L., 1758		Car cor		1	1
<i>Carabus glabratus</i> Payk., 1790		Car gla	50	134	184
<i>Carabus intricatus</i> L., 1761		Car int		8	8
<i>Carabus irregularis</i> F., 1792		Car irr		2	2
<i>Carabus monilis</i> F., 1792		Car mon	171	24	195
<i>Carabus problematicus</i> Hbst., 1786		Car pro	1	20	21
<i>Carabus silvestris</i> Panz., 1796		Car sil	5	53	58
<i>Carabus violaceus</i> L., 1758		Car vio	4	8	12
<i>Chlaenius nigricornis</i> (F., 1787)		Chl nig	272	55	327
<i>Cicindela campestris</i> L., 1758		Cic cam		1	1
<i>Clivina fossor</i> (L., 1758)		Cli fos	33	8	41
<i>Cychrus caraboides</i> (L., 1758)		Cyc car		7	7
<i>Dyschirius globosus</i> (Hbst., 1784)		Dys glo	2	5	7
<i>Elaphrus cupreus</i> Duft., 1812	2	Ela cup	5	26	31
<i>Elaphrus uliginosus</i> F., 1775	1	Ela uli	6	2	8

(Continued)

Species name	Red List status <sup>a</sup>	Abbreviation	Mown 21 <sup>b</sup>	Grazed 20 <sup>b</sup>	Total 41 <sup>b</sup>
<i>Harpalus latus</i> (L., 1758)		Har lat	2	2	4
<i>Harpalus quadripunctatus</i> Zett., 1828		Har qua	1		1
<i>Harpalus rubripes</i> (Duft., 1812)		Har rub	1	2	3
<i>Leistus nitidus</i> (Duft., 1812)		Lei nit	2	1	3
<i>Leistus piceus</i> Fröl., 1799		Lei pic	1		1
<i>Loricera pilicornis</i> (F., 1775)		Lor pil	87	35	122
<i>Molops piceus</i> (Panz., 1793)		Mol pic	5	6	11
<i>Nebria brevicollis</i> (F., 1792)		Neb bre	300	93	393
<i>Nebria gyllenhalii</i> (Ström, 1768)		Neb gyl	12	1	13
<i>Notiophilus biguttatus</i> (F., 1779)		Not big		1	1
<i>Patrobilus atrorufus</i> (Ström, 1768)		Pat atr	62	86	148
<i>Platynus assimilis</i> (Payk., 1790)		Pla ass	54	157	211
<i>Poecilus cupreus</i> (L., 1758)		Poe cup	272	10	282
<i>Poecilus versicolor</i> (Sturm, 1824)		Poe ver	707	678	1385
<i>Pterostichus aethiops</i> (Panz., 1797)		Pte aet	1		1
<i>Pterostichus anthracinus</i> (Ill., 1798)		Pte ant	114	6	120
<i>Pterostichus burmeisteri</i> Heer, 1841		Pte bur	10	38	48
<i>Pterostichus cristatus</i> (Duft., 1820)		Pte cri	1		1
<i>Pterostichus diligens</i> (Sturm, 1824)		Pte dili	30	17	47
<i>Pterostichus madidus</i> (F., 1775)		Pte mad	2	70	72
<i>Pterostichus melanarius</i> (Ill., 1798)		Pte mel	1601	890	2491
<i>Pterostichus multipunctatus</i> (Dej., 1828)		Pte mul	4	20	24
<i>Pterostichus niger</i> (Schall., 1783)		Pte nig	7		7
<i>Pterostichus nigrita</i> (Payk., 1790)		Pte nta	276	63	343
<i>Pterostichus oblongopunctatus</i> (F., 1787)		Pte obl		59	60
<i>Pterostichus panzeri</i> (Panz., 1850)		Pte pan	3	24	27
<i>Pterostichus pumilio</i> (Dej., 1828)		Pte pum	27	12	39
<i>Pterostichus rhaeticus</i> Heer, 1837		Pte rha	6	2	8
<i>Pterostichus strenuus</i> (Panz., 1797)		Pte str	26	9	37
<i>Pterostichus unctulatus</i> (Duft., 1812)		Pte unc	164	26	282
<i>Pterostichus vernalis</i> (Panz., 1796)		Pte ver	45	6	79
<i>Trechoblemus micros</i> (Hbst., 1784)	4	Tre mic	1		1
<i>Trechus obtusus</i> Er., 1837		Tre obt	6	9	16
<i>Trechus quadristriatus</i> (Schrk., 1781)		Tre qua	1	2	3
<i>Trichotichnus nitens</i> (Heer, 1838)		Tri nit	10		10
		Total	5980	3399	9379

<sup>a</sup> 1 = Critically endangered, 2 = endangered, 3 = threatened, 4 = nearly threatened (after Marggi, 1994).

<sup>b</sup> Number of plots.

## References

- Arndt, U., 1970. Konzentrationsänderungen bei freien Aminosäuren in Pflanzen unter dem Einfluss von Fluorwasserstoff und Schwefeldioxid. Staub-Reinhalt. Luft 30, 256–259.
- Bardgett, R.D., Cook, R., 1998. Functional aspects of soil animal diversity in agricultural grasslands. Appl. Soil Ecol. 10, 263–276.
- Boltshauser, M., 2001. Agrarforschung 8, Grundlagen für die Düngung im Acker- und Futterbau 2001. Bundesamt für Landwirtschaft, Bern, Switzerland.
- Blake, S., Foster, G.N., Fisher, G.E.J., Ligertwood, G.L., 1996. Effects of management practices on the carabid faunas of newly established wildflower meadows in southern Scotland. Ann. Zool. Fennici 33, 139–147.
- Braun, S., Flückiger, W., 1985. Increased population of the aphid aphid-pomi at a motorway. The effect of exhaust-gases. Environ. Pollut. Ser. A 39 (2), 183–192.
- Brose, U., 2003. Regional diversity of temporary wetland carabid beetle communities: a matter of landscape features or cultivation intensity? Agric. Ecosyst. Environ. 98, 163–167.
- Cárcamo, H.A., Niemelä, J., Spence, J., 1995. Farming and ground beetles: effects of agronomic practice on populations and community structure. Can. Entomol. 127, 123–140.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.

- Dennis, P., Young, M.R., Howard, C.L., Gordon, I.J., 1997. The response of epigeal beetles (Col: Carabidae, Staphylinidae) to varied grazing regimes on upland *Nardus stricta* grasslands. *J. Appl. Ecol.* 34, 433–443.
- Di Giulio, M., Edwards, P.J., Meister, E., 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *J. Appl. Ecol.* 38, 310–319.
- Dolek, M., 1994. Der Einfluss der Schafbeweidung von Kalkmagerrasen in der südlichen Frankenalb auf die Insektenfauna (Tagfalter, Heuschrecken). Haupt, Bern, Stuttgart, Wien-Landschaft, 97 pp.
- Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol. Monogr.* 67, 345–366.
- Eyre, M.D., Luff, M.L., 1990. A preliminary classification of European grassland habitats using carabid beetles. In: Stork, N. (Ed.), *Ground Beetles: Their Role in Ecological and Environmental Studies*. Intercept Publications, Andover, pp. 227–236.
- Eyre, M.D., Lott, D.A., Garside, A., 1996. Assessing the potential for environmental monitoring using ground beetles (Coleoptera: Carabidae) with riverside and Scottish data. *Ann. Zool. Fennici* 33, 157–163.
- Freude, H., Harde, K.W., Lohse, G.A., 1976. Die Käfer Mitteleuropas, Band 2. Goecke & Evers, Krefeld.
- Gardner, S.M., Hartley, S.E., Davies, A., Palmer, S.C.F., 1997. Carabid communities on heather moorlands in northeast Scotland: the consequences of grazing pressure for community diversity. *Biol. Conserv.* 81, 275–286.
- Grandchamp, A.-C., Niemelä, J., Kotze, J., 2000. The effects of trampling on carabid assemblages of ground beetles (Coleoptera, Carabidae) in urban forests in Helsinki. *Finland Urban Ecosyst.* 4, 321–332.
- Gutiérrez, D., Menéndez, R., Méndez, M., 2004. Habitat-based conservation priorities for carabid beetles within the Picos de Europa National Park, northern Spain. *Biol. Conserv.* 115, 379–393.
- Hance, Th., Grégoire-Wibo, C., 1987. Effects of agricultural practices on carabid populations. *Acta Phytopathol. Entomol. Hung.* 22, 147–160.
- Heydemann, B., Hofmann, W., Irmeler, U., 1998. Der Einfluss der Beweidung auf die Wirbellosenfauna im Grünland. *Faun-Oekol. Mitt. Suppl.* 24, 45–71.
- Humphreys, I.C., Mowat, D.J., 1994. Effects of some organic treatments on predators (Coleoptera: Carabidae) of cabbage root fly, *Delia radicum* (L.) (Diptera: Anthomyiidae), and on alternative prey species. *Pedobiologia* 38, 513–518.
- Kromp, B., 1999. Carabid beetles in sustainable agriculture: a review on pest control efficacy, cultivation impacts and enhancement. *Agric. Ecosyst. Environ.* 74, 187–228.
- Kruess, A., Tscharrntke, T., 2002a. Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conserv. Biol.* 16, 1570–1580.
- Kruess, A., Tscharrntke, T., 2002b. Contrasting responses of plants and insect diversity to variation in grazing intensity. *Biol. Conserv.* 106, 293–302.
- Luff, M.L., Rushton, S.P., 1989. The ground beetle and spider fauna of managed and unimproved upland pasture. *Agric. Ecosyst. Environ.* 25, 195–205.
- Marggi, W.A., 1992. Faunistik der Sandlaufkäfer und Laufkäfer der Schweiz. *Documenta Faunistica Helvetiae*, Teil 1 und 2. CSCF, Neuchâtel, Switzerland.
- Marggi, W.A., 1994. Rote Liste der gefährdeten Laufkäfer und Sandlaufkäfer der Schweiz. In: Duelli, P. (Ed.), *Rote Liste der Tierarten in der Schweiz*. Bundesamt für Umwelt, Wald und Landschaft, pp. 55–59.
- Megan, R., 1999. Is an enhanced soil biological community, relative to conventional neighbours, a consistent feature of alternative (organic and biodynamic) agricultural systems? *Biol. Agric. Hortic.* 17, 131–144.
- Morris, M.G., 1967. Differences between the invertebrate faunas of grazed and ungrazed chalk grasslands. *J. Appl. Ecol.* 4, 459–474.
- Niemelä, J., Spence, J.R., 1991. Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. *Oikos* 62, 351–359.
- Niemelä, J., Kotze, J., Venn, S., Penev, L., Stoyanov, I., Spence, J., Hartley, D., Montes de Oca, H., 2002. Carabid beetle assemblages (Coleoptera Carabidae) across urban-rural gradients: an international comparison. *Landscape Ecol.* 17, 387–401.
- Pezzatti, M.G., 2001. Einfluss der Erschliessung auf die Agrarstrukturen im Alpenraum. *Agrarwirtschaft und Agrarsoziologie* 1, 9–33.
- Pfiffner, L., Luka, H., 2003. Effects of low-input farming systems on carabids and epigeal spiders – a paired farm approach. *Basic Appl. Ecol.* 4, 117–127.
- Pietraszko, R., de Clercq, R., 1982. Influence of organic matter on epigeic arthropods. *Med. Fac. Landbouww. Rijksuniv. Gent* 47 (2), 721–728.
- Purvis, G., Curry, J.P., 1984. The influence of weeds and farmyard manure on the activity of Carabidae and other ground-dwelling arthropods in a sugar beet crop. *J. Appl. Ecol.* 21, 271–283.
- Radlmair, S., Laussmann, H., 1997. Auswirkungen extensiver Beweidung und Mahd von Moorstandorten in Süddeutschland auf die Heuschreckenfauna (Saltatoria). *Verh. Ges. Ökol.* 27, 199–205.
- R Development Core Team, 2003. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>.
- Rushton, S.P., Luff, M.L., Eyre, M.D., 1989. Effects of pasture improvement and management on the ground beetle and spider communities of upland grasslands. *J. Appl. Ecol.* 26, 489–503.
- ter Braak, C.J.F., Smilauer, P., 2002. CANOCO Reference manual and CanoDraw for Windows user guide: Software for Canonical Community Ordination (version 4.5). Microcomputer Power, Ithaca, NY, USA.
- Thieri, J., Kelka, H., 1998. Beweidung als geeignetes Mittel zur Bergwiesenpflege?—Erfahrungen nach 25jähriger Beweidung einer Bergwiese im Harz. *Natur und Landschaft* 73 (2), 64–66.
- Trautner, J., Geigenmüller, K., 1987. Tiger beetles, ground beetles. Josef Margraf, Germany.
- van Wieren, S.E., 1995. The potential role of large herbivores in nature conservation and extensive land use in Europe. *Biol. J. Linn. Soc.* 56 (Suppl.), 11–23.

- Walther, C., Beinlich, B., Plachter, H., 1996. Die Bedeutung intensiv beweideter Kalkmagerrasen (Mesobromion) Südwestdeutschlands für Laufkäfer (Carabidae), Heuschrecken (Saltatoria) und Tagfalter (Lepidoptera: Rhopalocera, ZygenidaeHesperidae). *Verh. Ges. Oekol.* 26, 355–362.
- Watt, A., Fuller, R., Chamberlain, D., van Swaay, C., Scheidegger, C., Stofer, S., Fernández-González, F., Niemelä, J., Lavelle, P., Dubs, F., Sousa, J.P., Koch, B., Ivits, E., Sanz, P.G., Bolger, T., Korsos, Z., Vanbergen, A., 2004. Biodiversity assessment—final report of the BioAssess project. Submitted to Research DG DI-2 Biodiversity and Global Change.
- Wingerden, W., Musters, J., Kleukers, R., Bongers, W., Biezen, J., 1991. The influence of cattle grazing intensity on grasshopper abundance (Orthoptera: Acrididae). *Proc. Exp. Appl. Entomol.*, N. E. V. Amsterdam 2, 28–34.