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Ground beetles (Coleoptera: Carabidae) in anthropogenic grasslands in Germany: effects of management, habitat and landscape on diversity and community composition

Biegaczowate (Coleoptera: Carabidae) łąk antropogenicznych w Niemczech: wpływ użytkowania, środowiska i krajobrazu na różnorodność i skład gatunkowy

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ABSTRACT: Grasslands are of great importance for the conservation and maintenance of biodiversity in agricultural landscapes. In order to sustain grasslands and their associated biodiversity, we need to widen our knowledge of the role of grassland management and the amount of grassland cover in a landscape. The aim of our study was to correlate the variability of community composition and diversity of carabid beetles in anthropogenic grasslands with management, habitat conditions, landscape composition and plant species richness. Since the condition of grassland biodiversity is often solely evaluated on the basis of species richness of vascular plants, we also wanted to assess whether plants could indicate the diversity of carabid beetles in grasslands. Therefore, we sampled carabid beetles on 29 grassland sites with low to high management intensity and a great variation of abiotic conditions in Central Germany. The diversity of carabid beetles was the highest in grasslands of medium management intensity and was positively affected by a high cover of crops in the surrounding landscape. Both the landscape and soil moisture had an impact on activity density of carabids but depended on the trophic group of the beetles. There was no connection between plant species richness and carabid diversity. The results of our study suggest that plant species richness as a sole indicator of grassland biodiversity might not be sufficient. Nevertheless, moderate management intensity which supports high plant species richness can also increase carabid diversity. We therefore conclude that moderate management intensity is crucial to provide highest biodiversity of carabid beetles in grasslands. Due to landscape effects on carabid communities, we suggest that besides management of single fields, the composition and structure of the whole landscape should be taken into consideration in order to sustain a rich species pool of carabid beetles in agricultural landscapes

KEYWORDS: Carabidae, grassland, management intensity, trophic groups, habitat, landscape.

Introduction

Grasslands are of great importance for the conservation and maintenance of biodiversity in agricultural landscapes of Central Europe (WALLISDEVRIES et al. 2002; DUELLI, OBRIST 2003). Changes in agricultural production systems affect both spatial cover and management intensity of grasslands. While areas favoured for crop production will undergo further intensification with decreasing the cover of grassland, the areas marginal in agricultural production will undergo further ‘extensification’, often associated with abandonment of land use and therefore also decreasing the cover of grassland (GIBON 2005). So both the intensification and abandonment of management can lead to habitat degradation of grasslands and in turn to a loss of biological diversity (VICKERY et al. 2001, SPIEGELBERGER et al. 2006). In order to sustain grasslands and their associated biodiversity, we need to increase our knowledge of the role of grassland management and amount of grassland cover in a landscape and find suitable indicators for the evaluation of grassland condition.

At present the condition of grassland biodiversity is often solely evaluated based on species richness of vascular plants (e.g. HARPOLE, TILMAN 2007; LORENZO et al. 2007; PÄRTEL et al. 2007); mostly due to the fact that plant species richness is an easily assessed indicator. Based on findings for vascular plants, moderate management intensity – particularly a reduction of nitrogen fertilisation on meadows and stocking rates on pastures – is suggested to support high plant species richness (e.g. KLIMEK et al. 2007; DIETSCHI et al. 2007; SPIEGELBERGER et al. 2006).

Yet the total biodiversity of grasslands includes a much higher number of taxa such as ground dwelling arthropods, many of which are not primarily associated with plants. It is still an open question whether inferences obtained from plant surveys can be assigned to other taxa as well and whether plants could function as biodiversity indicators in grasslands. The aim of our study was to correlate the variability of community composition and diversity of carabid beetles in anthropogenic grasslands with management, habitat conditions, composition of the surrounding landscape and finally, plant species richness. As carabid beetles of different trophic groups should respond to plant diversity and management intensity in different ways (PURTAUF et al. 2005), feeding preferences of the species were considered. We expect phytophagous species to be positively affected by higher plant diversity providing higher food resources. Other trophic groups might also prefer areas of high plant richness providing a diverse habitat structure but most carnivorous carabids should favour simpler habitat structure (caused by higher management intensity) which facilitates searching for food and hunting. Following the medium disturbance theory (CONNELL 1978), the highest diversity should be archived by intermediate management intensity.

In this study, we asked the following questions: (1) Is plant species richness correlated with carabid diversity? (2) Does moderate management intensity increase the diversity of carabids? (3) How do the management, habitat conditions and landscape composition together affect the carabid diversity and community composition?

Material and Methods

Study area and study sites

The study was carried out within the rural district of Northeim, Lower Saxony (Germany). The district comprises lowland and upland areas with altitudes above sea level ranging from 72 to 527 m. Mean annual precipitation is 645 mm, mean annual temperature is 8.7° C. The land cover is characterized by a large proportion of arable land and forest, interspersed with patchily distributed fragments of grassland. Most of the grassland in the lowland areas is structurally uniform and poor in plant species richness, whereas in the steeper areas, fragments of plant species-rich semi-natural grassland can be found (KLIMEK et al. 2007). We studied 14 mown meadows and 15 mown pastures within the research area, including mesic to wet and neutral to moderately acidic loam, sandy loam and loamy sand soils. The 29 study sites were randomly distributed over the whole district. The management of the sites ranged from low-input to high intensity management. Not-mown pastures were not included. All sites were of approximately similar size (1.6 +/– 1.1 ha) but showed a great rage of site specific conditions (Tab. I). The maximum distance between two sites was 38 km and minimum distance was larger than 1,500 m. The elevation of the study sites varied from 102 to 328 m a.s.l.

Sampling and species determination

Carabids were sampled using pitfall traps (diameter: 85 mm, volume: 500 ml) from 20th to 27th July 2005 and from 03rd to 16th May 2006. The traps were filled with approximately 100 ml of Ethylenglycol-solution (1:2) with a detergent added to reduce surface tension. Each trap was shielded with a 25 × 25 cm acrylic glass pane about 10 cm high to avoid flooding by rain. All the individuals were determined down to species level (TRAUTNER, GEIGENMÜLLER 1987; FREUDE 1976) and characterized according to their feeding type following LUFF (1998), LINDROTH (1985, 1986) and RIBERA et al. (2001). Carabid species were assorted into three trophic groups: carnivorous, mixophagous, and phytophagous (Tab. II).

Tab. I. Range of variation (maximum, minimum, mean) of vegetation, habitat, landscape and management variables of the study sites. LU: livestock units

Zakres zróżnicowania (maksimum, minimum, średnie) roślinności, środowiska, krajobrazu i zróżnicowanie użytkowania stanowisk badawczych. LU: jednostki przeliczeniowe inwentarza

	min.	max.	mean średnio
Vegetation – Roślinność			
plant species richness – bogactwo gatunkowe roślin	5.7	24.3	14.9
Landscape – Krajobraz			
crop cover – pokrycie uprawami (750 m radius – promień)	0	82.0	35.9
grassland cover – pokrycie łąkami (750 m radius – promień)	3.7	32.6	17.3
Habitat – Środowisko			
soil moisture – wilgotność gleby (Ellenberg ind. F-Z – liczba Ellenberga F-Z)	5.1	6.9	5.7
soil pH value – wartość pH gleby (Ellenberg ind. R-Z – liczba Ellenberga R-Z)	4.3	6.8	6.1
insolation – usłonecznienie (SI)	2.7	4.3	3.6
Management – Użytkowanie			
grazing pressure – intensywność wypasu [LU*days/ha]	0	363	76.6
number of mowings / year – ilość koszeń / rok	1	4	2.1
management intensity – intensywność użytkowania	25	125	74.6

Habitat and landscape characteristics

Plant species richness and management data (grazing pressure in the form of livestock units [LU], times of mowing per year) of the study sites were provided by the Research Centre for Agriculture and the Environment in Göttingen (ZLU; see KLIMEK et al. 2007 for a description of the methods used). Habitat conditions were characterized by Ellenberg indicator values for soil moisture (F-Z) and pH-value (R-Z; ELLENBERG et al. 2001) and by microclimate in terms of insolation of the sites. Insolation was calculated as the mean annual intensity of solar radiation (kW m^{-2}) that reaches a position on the earth's surface derived from a Digital Elevation Model using the formula provided by SHARY et al. (2002).

Because landscape composition could affect carabid diversity (DAUBER et al. 2005), we calculated a percentage cover of grassland and arable land in 750 m around each study site from a digital land use map with the help of ArcView 3.2 GIS software (ESRI, Redlands, Cal.). We expected a high

Tab. II. Species recorded during this study, the total number of individuals (**A**), percentage of study sites were species could be detected (**B**) and a trophic group (**C**): c – carnivorous, m – mixophagous, p – phytophagous, ? – no classification possible

Gatunki zarejestrowane podczas badań, całkowita liczba osobników (**A**), udział procentowy stanowisk badawczych, gdzie gatunek był obecny (**B**) i grupa troficzna (**C**): c – drapieżne, m – wszystkożerne, p – roślinożerne, ? – sklasyfikowanie niemożliwe

Carabid species Gatunek	**A**	**B**	**C**
1	2	3	4
Abax parallelepipedus (PILLER et MITTERPACHER, 1783)	2	6.9	c
Acupalpus meridianus (LINNAEUS, 1761)	1	3.4	c
Agonum mülleri (HERBST, 1784)	37	48.3	c
Agonum piceum (LINNAEUS, 1758)	1	3.4	c
Agonum sexpunctatum (LINNAEUS, 1758)	6	10.3	c
Agonum viduum (PANZER, 1796)	65	13.8	c
Agonum viridicupreum (GOEZE, 1777)	2	3.4	c
Amara aenea (DE GEER, 1774)	26	24.1	p
Amara communis (PANZER, 1797)	8	17.2	p
Amara eurynota (PANZER, 1797)	2	3.4	p
Amara familiaris (DUFTSCHMID, 1812)	23	41.4	p
Amara lunicollis SCHIÖDTE, 1837	3	10.3	p
Amara montivaga STURM, 1825	7	13.8	p
Amara ovata (FABRICIUS, 1792)	4	3.4	p
Amara plebeja (GYLLENHAL, 1810)	15	27.6	p
Amara similata (GYLLENHAL, 1810)	6	13.8	p
Anchomenus dorsalis (PONTOPPIDAN, 1763)	8	6.9	c
Anisodactylus binotatus (FABRICIUS, 1787)	7	20.7	c
Asaphidion flavipes (LINNAEUS, 1761)	3	10.3	c
Badister sodalis (DUFTSCHMID, 1812)	2	3.4	?
Bembidion biguttatum (FABRICIUS, 1779)	32	20.7	c
Bembidion gilvipes STURM, 1825	6	6.9	c
Bembidion guttula (FABRICIUS, 1792)	4	10.3	c
Bembidion lampros (HERBST, 1784)	67	62.1	c
Bembidion lunulatum (FOURCROY, 1785)	3	6.9	c

1	2	3	4
Bembidion obtusum (SERVILLE, 1821)	3	6.9	c
Bembidion properans (STEPHENS, 1829)	45	31.0	c
Bembidion quadrimaculatum (LINNAEUS, 1761)	5	10.3	c
Bembidion tetracolum SAY, 1823	3	10.3	c
Calathus fuscipes (GOEZE, 1777)	16	17.2	c
Carabus auratus LINNAEUS, 1761	972	41.4	c
Carabus auronitens FABRICIUS, 1792	1	3.4	c
Carabus granulatus LINNAEUS, 1758	250	62.1	m
Carabus irregularis FABRICIUS, 1792	1	3.4	c
Carabus nemoralis O. F. MÜLLER, 1764	117	72.4	m
Carabus violaceus LINNAEUS, 1758	1	3.4	m
Claenius nigricornis (FABRICIUS, 1787)	17	10.3	c
Clivina fossor (LINNAEUS, 1758)	42	51.7	m
Dyschirius globosus (HERBST, 1784)	24	13.8	c
Harpalus affinis (SCHRANK, 1781)	6	10.3	m
Harpalus anxius (DUFTSCHMID, 1812)	1	3.4	p
Harpalus latus (LINNAEUS, 1758)	9	13.8	p
Harpalus rufipes (DE GEER, 1774)	4	13.8	p
Harpalus tardus (PANZER, 1796)	2	3.4	p
Loricera pilicornis (FABRICIUS, 1775)	17	34.5	c
Microlestes maurus (STURM, 1827)	8	3.4	c
Nebria brevicollis (FABRICIUS, 1792)	3	3.4	c
Notiophilus aquaticus (LINNAEUS, 1758)	1	3.4	c
Notiophilus biguttatus (FABRICIUS, 1779)	2	6.9	c
Notiophilus palustris (DUFTSCHMID, 1812)	7	17.2	c
Oodes helopioides (FABRICIUS, 1792)	8	6.9	c
Platynus assimile (PAYKULL, 1790)	6	10.3	c
Poecilus cupreus (LINNAEUS, 1758)	609	89.7	m
Poecilus versicolor (STURM, 1824)	2284	89.7	c
Pterostichus anthracinus (PANZER, 1795)	15	10.3	c
Pterostichus burmeisteri HEER, 1841	12	27.6	c
Pterostichus madidus (FABRICIUS, 1775)	1	3.4	c
Pterostichus melanarius (ILLIGER, 1798)	316	75.9	c

1	2	3	4
Pterostichus niger (SCHALLER, 1783)	9	13.8	c
Pterostichus nigrita (PAYKULL, 1790)	31	13.8	c
Pterostichus oblongopunctatus (FABRICIUS, 1787)	2	6.9	c
Pterostichus strenuus (PANZER, 1796)	6	20.7	c
Pterostichus vernalis (PANZER, 1795)	68	65.5	c
Trechoblemus micros (HERBST, 1784)	1	3.4	?
Trechus secalis (PAYKULL, 1790)	3	10.3	?
Zabrus tenebrioides (GOEZE, 1777)	1	3.4	p

cover of crops to provide more generalist open land species, whereas a high grassland cover should support more specialised grassland species. In contrast, a low cover of crops and grassland indicates a high amount of surrounding forest which should increase the number of forest carabid species.

Grazing pressure and times of mowing per year are indices for management intensity. To compare management intensity of mown pastures and meadows we determined the maximum land use impact for each management form. The maximum grazing pressure, specified as livestock-units multiplied with grazing days per hectare was 363 and maximum number of mowing was 4 times (Tab. I). We calculated the percentage of maximum grazing pressure and the times of mowing for each study site and added both parts. To detect a supposed non-linear impact of management intensity, we defined three intensity classes: "low intensity" ranged from management intensity up to 60%, "medium intensity" from >60 to 90% and "high intensity" comprised grasslands of management intensity >90%. All classes comprise a comparable number of study sites.

Statistical analyses

Carabid species number and activity density were cumulated for each site over both sampling periods. Carabid diversity is described with the Shannon-index and evenness. The impact of plant species richness, habitat characteristics, management intensity and landscape on carabid diversity and evenness as well as on species richness and activity density of each trophic group was analyzed separately using General Regression Models (GRM; forward stepwise procedure). GRM implements stepwise and best-subset regression for Analysis of Covariance (ANCOVA) design with categorical and continuous predictor variables (StatSoft Inc., 2001).

Mean plant species richness (plant), Ellenberg indicators for moisture (F-Z) and pH value (R-Z), insolation (SI) and grassland and crop cover in 750m surrounding were included in the models as continuous variables. The management intensity was included as a categorical variable (low, medium, high). As the study was conducted in a small geographical area with moderate differences in altitude, no impact of geographic position and altitude of the study sites on the observed species richness or community composition of carabid beetles was expected. Therefore, we did not include altitude or geographical location as explanatory variables in our statistical models.

To determine an impact of the explanatory variables on community composition we conduct Principal Components Analyses (PCA) with dominance data of species found on more than 25% of the investigated grasslands and the environmental variables. To permit the interpretation of the PCA results, environmental parameters were added to the analysis as supplementary variables so they did not influence the ordination of species data.

The data were tested for normal distribution and were log-transformed prior to statistical analysis whenever necessary. Parameters calculated as percentage were ArcSin transformed (angular transformation) prior to statistical analyses. All the analyses were performed using the STATISTICA 7.0 software package (STATISTICA software V 7.0, StatSoft Inc., Tulsa, USA).

Results

In total, we found 66 carabid species with 5,269 individuals (Tab. II). Species richness ranged from 7 to 21 on the investigated grasslands. Out of the total, 42 species were carnivorous, ranging from 4 to 13; 7 were mixophagous species, ranging from 1 to 6 and 14 were phytophagous, ranging from 0 to 6. Species number was highest under medium management intensity. Of the 55 species occurring in medium-intensity managed grasslands, 10 species were solely found here (Fig. 1).

Shannon-diversity of carabids ranged from 0.3 to 2.8 and evenness ranged from 0.15 to 0.92. Shannon-diversity and evenness of carabid beetles increased with increasing crop cover in 750m surrounding (Tab. III). The diversity was also affected by management intensity. The grasslands of intermediate management intensity harboured the highest diversity (Fig.2).

Species richness of carnivorous and phytophagous carabids was only affected by soil moisture. While the richness of carnivorous species was positively affected by soil moisture, phytophagous species were negatively affected (Tab. III). No impact on the richness of mixophagous species could be detected.

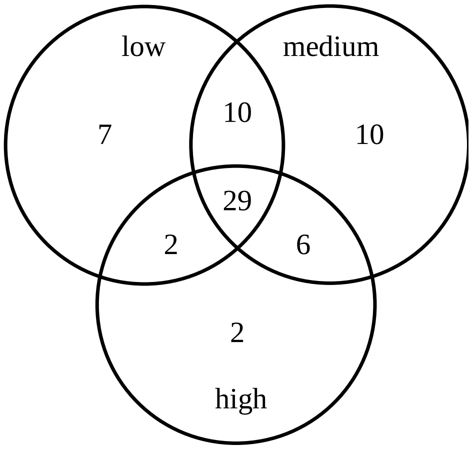

Fig. 1. Number of carabid species on grasslands of different management intensity class and numbers of species shared among the classes

Ryc. 1. Liczba gatunków biegaczowatych na łąkach o zróżnicowanych klasach użytkowania, intensywności użytkowania i ilość gatunków wspólnych dla różnych klas użytkowania

Activity density of the trophic groups was also differentially affected by the tested variables. While no impact on activity density of carnivorous beetles was detectable, mixophagous activity density increased with increasing moisture, whereas phytophagous activity density decreased. Mixophagous activity density also increased with the increasing cover of grassland in the landscape, while phytophagous activity density increased with the increasing crop cover (Tab. III).

The carabid community was dominated by only a few species. *Poecilus versicolor* provided more than 40% of total individuals, *Carabus auratus* nearly 20% and *Poecilus cupreus* more than 10%. Only eight species could be found on more than 50% of the investigated fields. More than a third of the species could not be found on more than 10% of the investigated fields, 17 species could be found only at one grassland site (Tab. II).

The first axis in the PCA accounted for 25.25 % (eigenvalue: 3.79) of the variance in carabid species composition (Fig. 3), the second axis accounted for 13.77 % (eigenvalue 2.07). Correlations of the environmental variables with the PC axis are given as vectors in the biplot (Fig. 3). The first axis was strongest correlated to medium management intensity and soil moisture described by Ellenberg indicator of moisture (F-Z), the second axis strongest to Ellenberg indicator for pH value (R-Z) and plant species richness.

Tab. III. The results of GRM for Carabid diversity and evenness and for species richness and activity density of the trophic groups, F and p-level, percentage of explained variance (VE) and sign of influence (I) for significant variables and R^2 and p for the whole model. Only significant variables are shown. MI – management intensity, F-Z – Ellenberg indicator for moisture, crop – crop cover in 750 m landscape radius, grassland – grassland cover in 750 m landscape radius

Wyniki GRM dla różnorodności gatunkowej biegaczowatych, jednolitości, bogactwa gatunkowego, łowności poszczególnych grup troficznych, F i poziom p-miary rozproszenia, udział procentowy objaśnionych wariancji i wpływ (I) zmiennych istotnych modelu oraz modele R^2 i p dla całego modelu. Przedstawiono tylko zmienne istotne. MI – intensywność użytkowania, F-Z – liczby Ellenberga dla wilgotności, crop – pokrycie uprawami w promieniu terenu wynoszącym 750 m , grassland – pokrycie łąkami w promieniu terenu wynoszącym 750 m

	diversity – różnorodność				evenness – jednolitość			
	F	p	VE	I	F	P	VE	I
MI	4.22	0.026	20.6					
crop	7.51	0.011	18.3	+	8.74	0.006	24.5	+
model R^2	0.43				0.24			
model p	0.002				0.006			
	carnivorous species richness bogactwo gatunkowe drapieżników (lnx+1)				phytophagous species richness bogactwo gatunkowe roślinożerców			
	F	p	VE	I	F	P	VE	I
F-Z	6.32	0.018	19.0	+	6.33	0.018	19.0	–
model R^2	0.19				0.19			
model p	0.018				0.018			
	mixophagous activity density łowność gatunków wszystkożernych (lnx+1)				phytophagous activity density łowność gatunków roślinożernych (lnx+1)			
	F	p	VE	I	F	P	VE	I
F-Z	4.79	0.038	13.3	+	9.98	0.004	23.2	–
crop					6.99	0.014	16.3	+
grassland	5.18	0.031	14.4	+				
model R^2	0.33				0.40			
model p	0.005				0.001			

There was a clear differentiation between varying preferences of carabid species to soil moisture. Hygrophilous species like *Carabus granulatus*, *Pterostichus vernalis*, *Clivina fossor*, *Agonum mülleri*, *Loricera pilicornis* and *Poecilus cupreus* were orientated towards higher F-Z. *C. auratus,* a thermophilous species, was orientated opposite. The silvicolous species *Pt. burmeisteri* and *C. nemoralis* were orientated towards a lower cover of open landscapes but increasing forest cover. *Pterostichus melanarius* and *Amara familiaris* were orientated to the second PCA axis, which reflected a high pH value and low plant species richness. Additional to moisture requirements preference to different intensity of management and landscape structure might explain orientation of other species.

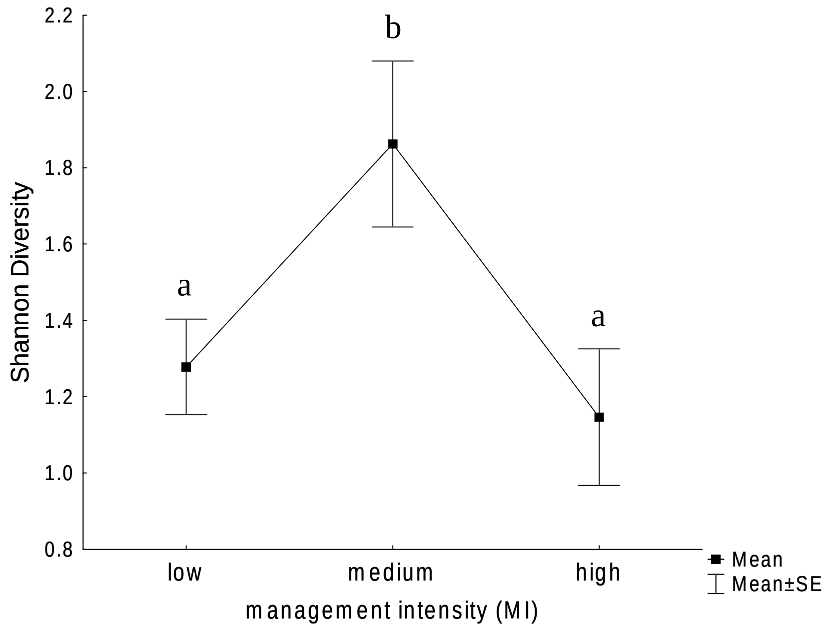

Fig. 2. Mean carabid beetle diversity on grasslands with low, medium and high management intensity. Bars represent standard error. Values with identical letters are not significantly different at the $p < 0.05$ level (Tukey HSD-test)

Ryc. 2. Średnia różnorodność gatunkowa biegaczowatych na łąkach o niskiej, średniej i wysokiej intensywności użytkowania. Grafy obrazują standardowe odchylenie. Wartości oznaczone identycznymi literami nie różnią się znacząco (na poziomie $p< 0.05$, wg. testu HSD Tukey'a)

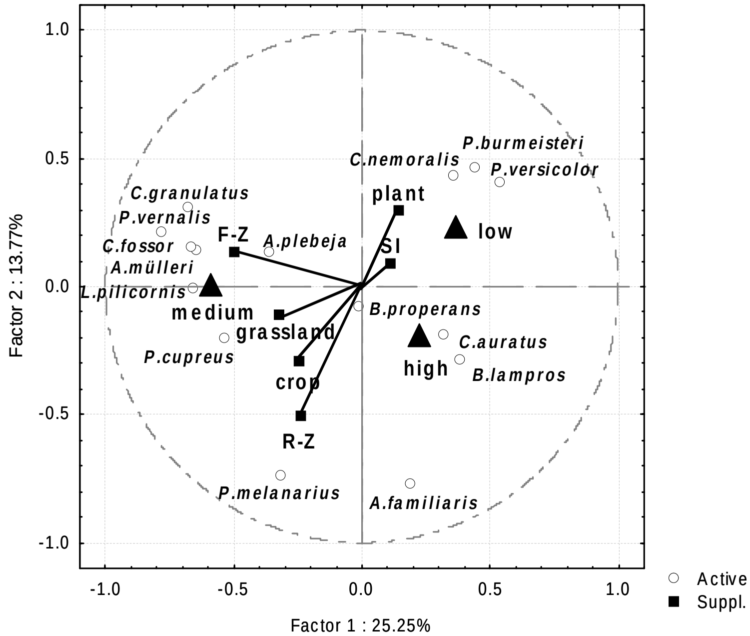

Fig. 3. Ordination diagram showing species scores from the principal component analysis (PCA) of carabid species composition at the 29 study sites. Environmental variables are presented by lines indicating the direction of increasing value. Management intensity classes are indicated by triangles, species are marked with open circles

Ryc. 3. Diagram porządkowy obrazujący wyniki analizy komponentów głównych (PCA) składu gatunkowego biegaczowatych (Carabidae) dla 29 badanych stanowisk. Zmienne środowiskowe są obrazowane przez linie wskazujące kierunek wzrastających wartości. Klasy intensywności użytkowania są oznaczone trójkątami, gatunki pustymi kółkami

Discussion

We found a comparatively high number of carabid species in the grasslands of our study region and a variability of community composition on a single grassland was equally high (Figs. 1 and 3). Carabid diversity was highest on the grassland with medium management intensity. This is in accordance with the medium disturbance theory (CONNELL 1978), which predicts that the presence of specialised grassland species together with generalist and pioneer species will lead to a higher diversity in sites of medium disturbance. Indeed, the total number of carabids and the number of species unique in one of the management classes were higher in medium than in low or high intensity management. Although plant species richness is supposed to be the highest under medium management intensity as well (PÄRTEL et al. 2007), no impact of plant species richness on carabid diversity or any trophic carabid group was found. This indicates that carabid communities respond to a different spectrum of grassland characteristics than plants (compare KLIMEK et al. 2007). Indeed, the surrounding landscape and soil moisture had an additional strong impact on carabid diversity and on species richness and activity density of different trophic croups.

Cutting and mowing grasslands affects habitat conditions like temperature and soil moisture by changing sward height. Intensive management is related to higher disturbance and degradation of hiding places, low management intensity in contrast leads to strong changes in habitat conditions after mowing. Grasslands with medium management intensity should exhibit smaller annual variation in habitat conditions. This should primarily benefit the species sensitive to disturbance. However, many carabid beetles which are typical of agricultural landscapes are adapted to disturbance and even frequently appear in crop fields (PURTAUF et al. 2004a). This explains a high number of species found even in intensively managed grasslands (Fig. 1) and it also explains the positive influence of high land cover of crop fields in the surroundings on the diversity and evenness of carabid beetles. Even though semi-natural habitats like grasslands are important habitats for breeding and hibernation (e.g. WALLIN 1985; PFIFFNER; LUKA 2000; DUELLI, OBRIST 2003), crop fields are a source of high species richness of generalist carabid beetles enhancing carabid diversity and evenness of grasslands (compare PURTAUF et al. 2004b).

In contrast to carnivorous carabids in crop fields, which are strongly affected by the amount of non-crop habitat in the surrounding landscape (PURTAUF et al. 2005), carnivorous beetles in grasslands of our study region were not affected by landscape composition. Instead, we found a landscape impact on activity density of mixophagous and phytophagous carabid beetles. Mixophagous carabid beetles were more numerous in the areas with high cover of grassland. This seems to be remarkable, because many mixophagous species like *Carabus granulatus* and *Poecilus cupreus* prefer crop fields over grasslands (see DAUBER et al. 2005), although they can reach high densities in both habitats. In areas with a high crop cover, some beetles of these species might change habitat from grassland to crops, whereas in areas with a low crop cover, these species remain in the grasslands reaching higher densities there. Most phytophagous species are xerophilous open land species common in both grasslands and crops (KOCH 1989). Because most of these species are able to fly, they can alter between these habitats very fast. A higher cover of arable land is often associated with higher cover of open landscape in total and this might explain the positive impact of crop cover on density of phytophagous carabids.

Besides landscape composition, habitat characteristics and especially soil moisture affected species richness and activity density of different trophic groups of carabid beetles. A strong influence of soil moisture on habitat selection of ground beetles is well known and has been described by several authors (e.g. THIELE 1977; HOLOPAINEN et al. 1995). The differences between the trophic groups are related to the preference of either moist or dry soils by various common species as indicated by the PCA results (Fig. 3). Dominant mixophagous species *Carabus granulatus* and *Poecilus cupreus* for example were positively affected by high soil moisture and even many carnivorous species preferred high soil moisture, but most of these species are not dominant, which explains an impact of soil moisture on the species number but not on activity density. Most species of the phytophagous *Harpalus* spp. and *Amara* spp. in contrast are xerophile, whereas the group of carnivorous carabids contains more hygrophilous species (KOCH 1989).

The results of our study suggest that plant species richness as a sole indicator of grassland biodiversity might not be sufficient. Nevertheless, moderate management intensity which supports high plant species richness can also increase carabid beetle diversity. We therefore conclude that moderate management intensity is crucial to provide the highest biodiversity of carabid beetles on grasslands in agricultural landscapes. The effects of landscape composition on carabid diversity and composition of trophic groups found indicate a strong interaction between grasslands and other landscape elements such as crop fields and forests. Therefore we suggest that besides management of single fields, the composition and structure of the whole landscape should be taken into consideration in order to sustain a rich species pool of carabid beetles in agricultural landscapes.

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STRZESZCZENIE

Łąki mają duże znaczenie dla zachowania i utrzymania bioróżnorodności w krajobrazie rolniczym. Po to, by zachować zasady zrównoważonej gospodarki krajobrazem i związaną z nim bioróżnorodność, nieodzowny jest ciągły rozwój wiedzy o roli sposobu użytkowania łąk oraz udziale łąk w ogólnym pokryciu terenu. Celem prowadzonych badań było wykazanie czy istnieje korelacja zróżnicowania składu gatunkowego chrząszczy z rodziny biegaczowatych z typem gospodarowania, warunkami siedliskowymi, strukturą krajobrazu i bogactwem gatunkowym roślin w środowisku łąk antropogenicznych.

Jako że bioróżnorodność łąk jest często oceniana jedynie na podstawie bogactwa gatunkowego roślin naczyniowych, postanowiono ocenić czy rośliny mogą być jednocześnie wskaźnikiem zróżnicowania gatunkowego biegaczowatych w tym środowisku. Dlatego w rejonie środkowych Niemiec dokonano odłowu biegaczowatych na 29 stanowiskach wytyczonych na łąkach różniących się intensywnością użytkowania i warunkami abiotycz-nymi.

Zróżnicowanie zgrupowań biegaczowatych było największe na łąkach o średnio intensywnym użytkowaniu i zależało od wielkości udziału upraw rolnych w pokryciu otaczającego terenu. Oba czynniki: krajobraz i wilgotność gleby miały wpływ na łowność biegaczowatych uzależnioną również od grup troficznych do których należały chrząszcze. Nie stwierdzono zależności pomiędzy bogactwem gatunkowym roślin a zróżnicowaniem gatunkowym biegaczowatych. Wynik przeprowadzonych studiów zatem sugeruje, że bogactwo gatunkowe roślin nie jest miarodajnym wskaźnikiem bioróżnorodności łąk. Jednakże, umiarkowana intensywność użytkowania z połączeniu z wysokim bogactwem gatunkowym roślin może wpływać na wzrost różnorodności gatunkowej również biegaczowatych.

Dlatego stwierdzono, że umiarkowana intensywność użytkowania jest kluczowa dla zachowania najwyższej bioróżnorodności chrząszczy z rodziny biegaczowatych bytujących w środowiskach łąkowych. Mając na uwadze wpływ krajobrazu na zgrupowania biegaczowatych, by zachować cały potencjalny skład gatunkowy biegaczowatych w zrównoważonym gospodarowaniu łąkami pod uwage należy brać kompozycję i strukturę otaczającego krajobrazu rolniczego.

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