



# Carabid communities in the spatio-temporal mosaic of a rural landscape

Tobias Purtauf<sup>\*</sup>, Jens Dauber, Volkmar Wolters

*Department of Animal Ecology, Justus Liebig University, Heinrich-Buff-Ring 26-32 (IFZ), D-35392 Giessen, Germany*

## Abstract

The effect of landscape dynamics on carabid communities was investigated using a chronosequence of managed grassland sites. A total of 52 carabid species was found. Species richness was significantly higher in early than in later stages of grassland succession. The change from an arable land to a grassland carabid community was almost complete 10 years after the conversion to grassland. The accompanying change in the dominant feeding mode indicates a marked shift in the functional structure of the carabid community from arable land to grassland. Correlation analysis revealed a positive response of phytophagous species to dense and species-rich grassland vegetation that was only loosely related to grassland age.

Invasion of grassland species was largely confined to the early stages of carabid succession. On the other hand, loss of species continued until the latest stage of the chronosequence, though many species preferring arable land had already vanished a short time after the conversion to grassland. The species turnover was independent of the dispersal abilities of the carabid species involved. This is probably due to the high spatial connectivity of suitable habitats in the small-scale landscape mosaic of the Lahn-Dill-Bergland.

It is concluded that the variety of land use (arable land versus grassland) contributes considerably more to the species richness of carabids at the landscape level than the simultaneous availability of grassland sites of different age, provided that areas converted to grassland are allowed to persist for at least 10 years. The missing invasion of additional species into later stages of grassland succession can partly be explained by the premature state that is maintained at the older sites by management.

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*Keywords:* Rural landscape; Managed grassland; Species richness; Carabidae; Space-for-time-substitution; Colonisation

## 1. Introduction

Many European landscapes have been exposed to intensification of agriculture since the end of the Second World War. In contrast to this general trend, however, large areas of Europe are still covered by low-intensity farming systems (McCracken et al., 1994). These areas are hot spots of European biodi-

versity (Bignal and McCracken, 1996) that are threatened by major changes of land use resulting from abandonment in regions where conditions are unfavourable for arable farming ('marginal landscapes' sensu Baldock et al., 1996). The study presented here was carried out in such a marginal landscape: the Lahn-Dill-Bergland (Central Hesse, Germany). This region has been exposed to successive abandonment of arable farming during the last five decades. The accompanying increase of managed grassland has created a complex spatio-temporal pattern of grassland sites of different age. Though it seems to be

<sup>\*</sup> Corresponding author. Fax: +49-641-993-5709.

E-mail address: [tobias.purtauf@allzool.bio.uni-giessen.de](mailto:tobias.purtauf@allzool.bio.uni-giessen.de) (T. Purtauf).

axiomatic that the succession induced by the sequential conversion of arable land into grassland strongly impacts communities via changes in colonisation patterns, maturation of populations or the probability of local extinction (Walker and Chapin, 1987), little is known about the consequences of these processes on species richness at the landscape level.

The present study focussed on carabid communities in a chronosequence of grassland sites of different age. The underlying approach is ‘space-for-time-substitution’, i.e. an approach that has been successful where general trends are to be generated by extrapolation of a temporal trend from a series of different age samples (Pickett, 1989). Understanding the response of individual populations and species to landscape processes is one of the major challenges to conservation ecology in cultivated landscapes (Dunning et al., 1992; Collinge, 2001). Studies that increase our knowledge of temporal changes in species composition and diversity following land-use change (e.g. after the conversion of arable land into grassland) should enhance sustainable conservation efforts in changing landscapes (Harrison and Fahrig, 1995; Zedler, 2000). Carabid communities are well suited for this type of study because they have proven to respond sensitively to both land-use change and environmental changes associated with succession (Burel and Baudry, 1994; Fournier and Loreau, 1999). However, only a few studies have focussed on the long-term development of carabid communities in grassland (see e.g. Schnitter, 1994 for a study on the first 5 years of carabid succession in uncultivated fields and meadows). We addressed the following questions: (i) Does species richness of carabids increase during grassland succession? (ii) Does community composition change with grassland age? and (iii) Is species richness of carabids at the larger spatial scale increased by the simultaneous availability of grassland sites of different age?

## 2. Site and methods

### 2.1. Study area and landscape structure analysis

The study was carried out in the rural district of Steinbrücken (320–420 m a.s.l., mean annual temperature 6.6 °C, mean annual precipitation 1100–1200 mm). Most of the study area consists of

moderately managed grassland, but a small fraction is still under agricultural use. GIS-supported stereoscopic analysis of black and white aerial photographs (scale: approximately 1:10,000) from the years 1953, 1961, 1972, 1989 and 1997 showed that apparently homogeneous grassland areas are composed of a mosaic of different age classes (Fuhr-Boßdorf et al., 1999).

### 2.2. Study sites

Sites belonging to five classes of grassland age were selected based on the GIS-supported analysis mentioned above (the term ‘age’ refers to time since last ploughing): age class 1 (1–2 years), age class 2 (3–10 years), age class 3 (21–27 years), age class 4 (28–38 years) and age class 5 (39–46 years). The interval between the age classes was determined by the availability of aerial photographs. In addition to the grassland sites, arable sites (age class 0) were included as a reference to identify initial situations as starting points for system dynamics (Pickett, 1989). Three replicate sites were selected for each age class.

Eleven of the sites were situated in an 18 ha area on the south facing slope of the Sasenberg (Fig. 1), while seven sites were situated on neighbouring slopes of the same aspect. The soils vary between acidic shallow rankers and moderately shallow cambisols that have developed on slopes (>20°) over Devonian clay slates, gravel slates, and greywacke. The arable sites were cultivated with winter wheat, barley or potatoes. Grassland sites have been moderately grazed since 1973 by about 20 sheep ha<sup>-1</sup> for a period of maximum 2 weeks per year. The grassland sites were mulched once a year in early August. Plant species richness increased from 12 (age class 1) to 24 species (age class 5). No plant communities typical for mature grassland had developed on the young sites converted after 1979. The sites of age class 1 had a total vegetation cover of 65% with high relative abundance of the sown species *Lolium perenne* and *Trifolium repens* (Waldhardt et al., 2000). *Festuca rubra*–*Agrostis tenuis* communities dominated at the older sites converted before 1979, with vegetation cover reaching about 80%. The growth height of the vegetation increased from age classes 1 to 2, but slightly decreased again in later age classes. For a further description of the vegetation at the study sites, see Waldhardt et al. (2000). The chance of ground beetles to reach

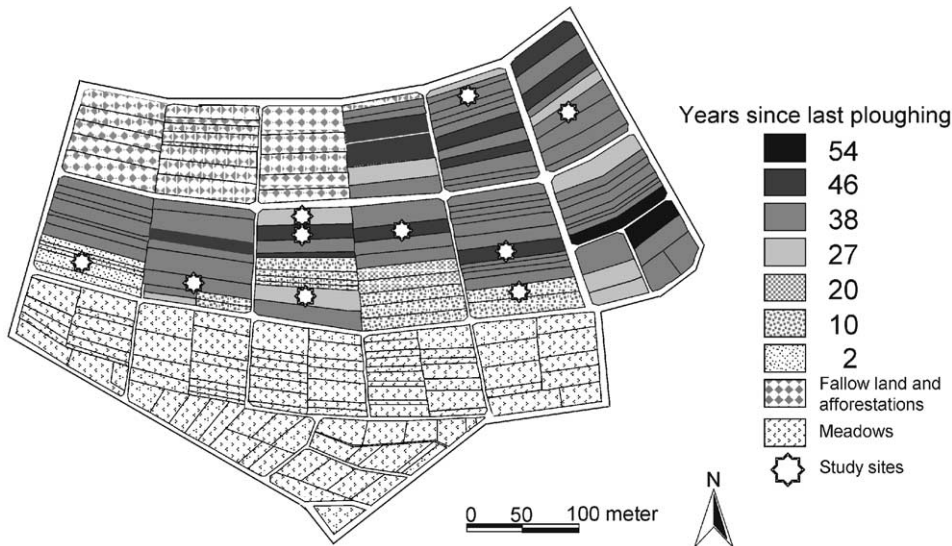


Fig. 1. Spatio-temporal mosaic of the study sites at the 'Sasenberg' (Lahn-Dill-Bergland, Central Hesse, Germany).

a newly created grassland patch was almost identical for each age class, because the maximum distance between a newly created grassland patch and grassland patches that were already established never exceeded 80 m.

### 2.3. Sampling

Carabids were sampled with pitfall traps consisting of 500 ml polyethylene beakers (diameter 85 mm) filled with approximately 170 ml of an ethanol:glycerine solution (2:1). A detergent was added to reduce surface tension. Acrylic glass covers (250 mm × 250 mm) were positioned approximately 10 cm above each trap to prevent flooding by rain. Five pitfall traps were placed in the centre of each site forming a line with about 10 m distance between neighbouring traps. Sampling took place in 1999 in weekly periods between 18 May and 15 June, 12 and 26 August, and two additional periods between 30 September and 13 October. All individuals were determined to the species level and assorted to functional groups according to their dispersal ability (brachypterous, macropterous, dimorphic) and to their feeding mode (carnivorous, phytophagous, mixophagous) (Lindroth, 1945; Barndt et al., 1991; Frisch, personal communication).

### 2.4. Data analysis

The following parameters were derived from the data: (i) two different parameters of species richness ( $S_T$ , the total number of species found on the replicate sites of each age class, and  $S_M$ , the mean number of species found per age class), (ii) mean total abundance, (iii) the number of species not present in any of the previous age classes ('immigrating species'), and (iv) the number of species that are lost from an age class and do not occur in any of the subsequent age classes ('lost species'). The effect of grassland age (age classes 0–5) on mean species richness, mean abundance as well as on the species richness and abundance of the two functional groups was tested by means of one-way ANOVA's. Homogeneity of variances was tested with the Sen and Puri-test.  $S_M$  and the abundance per functional group had to be ln-transformed prior to analyses. Means were compared using the Tukey HSD-test ( $P < 0.05$ ).

Since the age of adjacent fields varied between replicate sites, the potential influence of the age of neighbouring patches on the carabid community of the study sites was tested by calculating a regression between the parameter 'external age' (Gomá et al., 1988) and carabid species richness. No significant relationship was found and the geometry of the sites is

therefore not considered further below. The correlation between parameters of vegetation structure (plant species richness, total ground cover, growth height) and parameters of carabid community structure (abundance per site, species number per site, abundance and species number per feeding mode) was analysed by means of the Spearman rank correlation. All statistical treatments were performed using the STATISTICA for Windows Package (StatSoft Inc., Tulsa, USA). In addition, a detrended correspondence analysis (DCA) was carried out (Canoco 4 software package; ter Braak and Smilauer, 1998). The downweighting of rare species reduced a potential bias caused by accessory species.

### 3. Results

A total of 4107 carabids belonging to 52 species were trapped at the 18 study sites (Appendix A). Total species richness ( $S_T$ ) and mean species richness ( $S_M$ ) closely paralleled each other (Fig. 2). A significant effect of the factor ‘age class’ on  $S_M$  ( $F = 6.4$ ,  $P < 0.001$ ) reflects the significantly higher values of  $S_M$  in the age classes 0 and 1 than in all subsequent age classes. A significant difference could not be established between  $S_M$  in age classes 0 and 1 or between age classes 2 and 5. The mean carabid abundance varied between 102 and 363 individuals trapped per age class and was not significantly different between the age classes.

A high number of immigrating carabid species points to particularly strong changes in community composition during the early stages of grassland succession, with immigration being especially high in age class 1 (16 species; Fig. 3). The majority of grassland species was already present after 10 years (age class 1), but a few species still immigrated into the subsequent age classes 2 and 3. No further immigration was found for age classes 4 and 5. Species loss, in contrast, continued until age class 5, though a large proportion of species preferring arable land had already vanished from age classes 1 and 2 (Fig. 3).

Significant results of the ANOVAs on the effect of the factor ‘age class’ on feeding groups reflect a shift from the higher richness of carnivorous and mixophagous species in arable land ( $F = 10.6$ ,  $P < 0.001$ ;  $F = 10.5$ ,  $P < 0.001$ ) to a higher richness of phytophagous species in grassland ( $F = 8.7$ ,  $P < 0.001$ ). While the abundance of carnivorous species was not significantly different between age classes, that of mixophagous carabids was higher in age classes 0 and 1 than in later age classes (Tukey test,  $P < 0.05$ ). The significant effect of the factor ‘age class’ on the abundance of phytophagous species ( $F = 6.2$ ,  $P < 0.005$ ) is largely due to the higher abundance of these species in grassland than in arable land. Neither the density nor the species number of phytophagous species was significantly different between grassland sites of different age according to the comparison of means, while several positive correlations to parameters of the vegetation structure were found: (i) plant

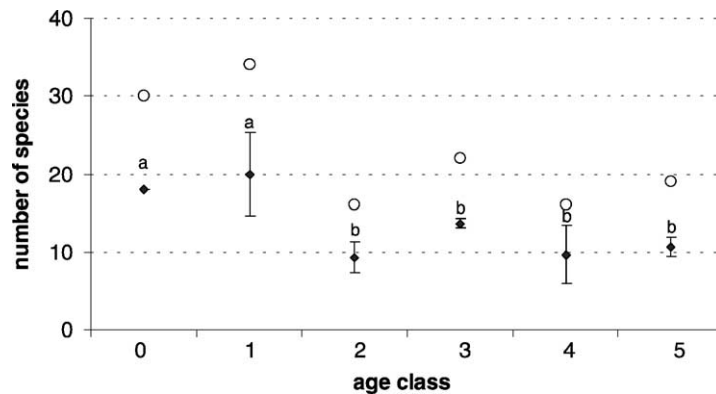


Fig. 2. Mean species richness ( $S_M$ , diamonds) and total species richness ( $S_T$ , open circles) of carabids at different stages of grassland succession. Bars represent standard deviations. Values with identical letter are not significantly different at the  $P < 0.05$  level (Tukey HSD-test).

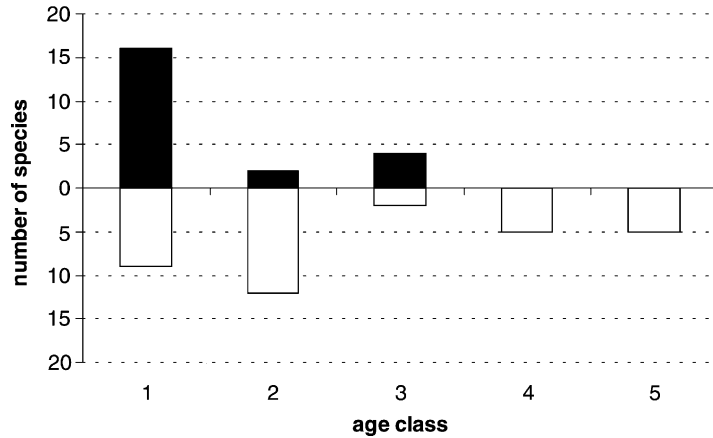


Fig. 3. ‘Immigrating species’ (number of species not present in any of the previous age classes; black columns) and ‘lost species’ (number of species that are lost from an age class and do not occur in any of the subsequent age classes; white columns) at different successional age classes.

species richness and both abundance ( $r = 0.45$ ,  $P < 0.001$ ) and species richness of phytophagous species ( $r = 0.26$ ,  $P < 0.05$ ), and (ii) vegetation ground cover and abundance of phytophagous species ( $r = 0.36$ ,  $P < 0.01$ ). This points to a stimulation of phytophagous species by dense and rich grassland veg-

etation that is only loosely related to grassland age. No significant correlation between parameters of vegetation structure and the total abundance or the total number of carabid species could be established.

The ANOVAs revealed a significant effect of age classes on the abundance and species richness of

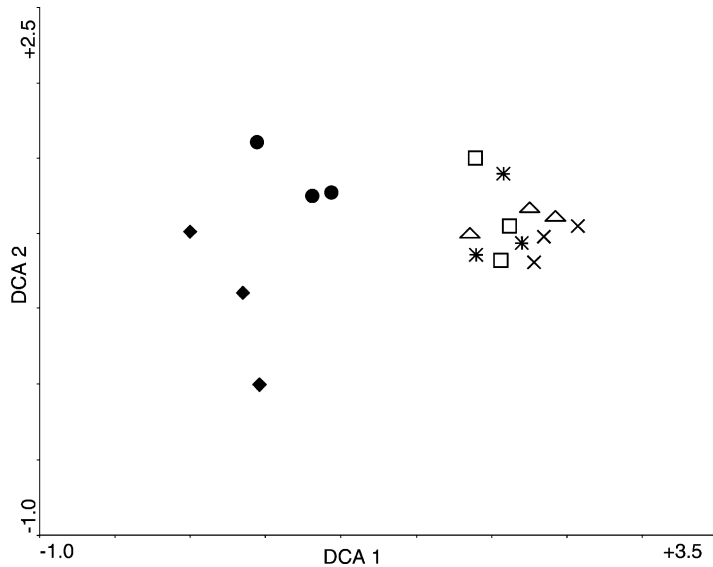


Fig. 4. DCA ordination diagram of replicate sites of grassland succession: age class 0, diamonds; age class 1, filled circle; age class 2, star; age class 3, square; age class 4, triangle and age class 5, x. (DCA 1) variance explanation: 34%, eigenvalue 0.51; (DCA 2) variance explanation: 9%, eigenvalue 0.13.

dimorphic species ( $F = 5.3$ ,  $P < 0.01$ ;  $F = 7.4$ ,  $P < 0.01$ ) and on the abundance of brachypterous species ( $F = 5.1$ ,  $P < 0.01$ ). However, the fact that no effect on macropterous species was found and that even the significant effects on dimorphic and brachypterous species were not accompanied by any consistent pattern of differences between means suggests that dispersal ability is not an important factor for the colonisation of the sites included in our study.

The two factors extracted by the DCA together explain about 43% of the total variance (Fig. 4). The first axis (DCA 1; variance explanation: 34%, eigenvalue 0.51) represents the shift in community structure with increasing grassland age. Younger sites (incl. arable land) are plotted on the left of the DCA diagram and older sites are plotted on the right. Three stages in the development of the carabid community can be distinguished: (i) an arable land community (age class 0), (ii) an intermediate stage between the arable land and the grassland communities (age class 1), and (iii) a grassland community (age classes 2–5). The second axis (DCA 2; variance explanation: 9%, eigenvalue 0.13) reflects the degree of spatial heterogeneity in species composition and abundance. Younger sites show a very scattered ordination along the axis, while the replicate sites of later successional age classes are much less separated by this factor. The strong variability of the carabid communities during the initial stage of grassland establishment points to strong site-specific differences in carabid species richness at this stage of the chronosequence.

#### 4. Discussion

The main objective of this study was to quantify the effect of grassland age on carabid community composition in successional grassland at the landscape level. The particularly high species richness immediately after the conversion of arable land to grassland was due to a temporary mix of species belonging to communities of both arable land and grassland. The high number of species immigrating during this stage of carabid succession confirms that early successional stages are dominated by colonisation processes (Walker and Chapin, 1987). Our analyses indicate that colonisation was largely independent of the dispersal abilities of the carabid species involved.

Ground beetles are known to be capable of moving several hundred metres, or even kilometres, in their lifetime (Kinnunen and Tiainen, 1999). Considering the high spatial connectivity of suitable habitats in the small-scale landscape mosaic of the Lahn-Dill-Bergland, early stages of grassland succession could thus easily be reached by both good dispersers (macropterous species) and bad dispersers (brachypterous species) within a single year.

A complete change of an arable land to a grassland carabid community took place within 10 years after the conversion. The accompanying shift in the species richness of feeding modes (i.e. decrease of carnivorous and mixophagous species, increase of phytophagous species) confirms that habitat preferences of carabids are affected by the distribution of food resources and different reactions of species to food availability (Fournier and Loreau, 1999). Though the species richness of the carabid community remained fairly constant during subsequent stages of grassland succession, our data show a significant response of phytophagous species to site-specific differences in the richness and the density of the grassland vegetation. The fact that no clear-cut relationship to grassland age could be established may partly be explained by the site-specific variability of the vegetation. It also suggests that the carabid communities remained in an early state of maturation due to continuous grassland management (cf. Walker and Chapin, 1987). This is consistent with the conclusion that grasslands are in a state of dynamic equilibrium between succession and opposing forces, of which management is the most important (Morris, 2000).

Marginal regions host more than 50% of Europe's most highly valued biotopes (Bignal and McCracken, 1996). The threat of land-use change on to species richness in these regions might be reduced by new management practices that increase the heterogeneity of the landscape by superimposing temporal patterns on the landscape's habitat mosaic (cf. Burel and Baudry, 1995). In our case, however, temporal patterns contributed only little to total carabid richness due to the high similarity of the carabid communities of later stages of grassland succession. The strong differences between carabid communities inhabiting arable land and those inhabiting grassland suggest that a mosaic of various biotope patches provided by a high degree of habitat heterogeneity (Duelli et al., 1990) contributes

considerably more to total species richness of carabids than the temporal pattern of differently aged grasslands.

## 5. Conclusions

Species richness as one aspect of biodiversity is a major target of conservation ecology. Our study proves the need for sustaining arable farming in marginal landscapes to preserve the particularly species-rich carabid communities of arable land. Moreover, the rapid establishment of grassland communities indicates that 10–15-year cycles of low-intensive farming and grassland cultivation might be sufficient to maintain carabid communities of both arable land and grassland. It has to be tested in the future whether the low impact of grassland age also applies to landscapes with a higher degree of grassland fragmentation, where the colonisation of newly created grassland

patches is more restricted by isolation or dispersal barriers than in the landscape investigated in our study.

## Acknowledgements

We are indebted to Katja Fuhr-Boßdorf for data on landscape history. We are grateful to Rainer Waldhardt for providing vegetation data and to Johannes Frisch for support on functional classification of carabids. We thank Klemens Ekschmitt for assistance in statistical analyses. R.A. O'Neill and Carsten Thies commented on an early version of this manuscript. We thank two anonymous referees for critical comments. This study was funded by the German Research Foundation (DFG) in the context of the SFB 299 and by the Federal Ministry of Education and Research of Germany (BMBF) in the context of BIOPLEX.

## Appendix A

Carabids captured at the 18 study sites: species list, abundance (total capture per age class), and functional classification (feeding mode, dispersal ability). The species are ordered according to occurrence in the chronosequence.

Species name	Feeding mode <sup>a</sup>	Dispersal ability <sup>b</sup>	Abundance					
			0	1	2	3	4	5
<i>Poecilus versicolor</i> (Sturm, 1824)	ca	ma	135	387	460	370	178	256
<i>Calathus fuscipes</i> (Gz., 1777)	ca	di	37		1	4	10	5
<i>Harpalus rubripes</i> (Dft., 1812)	ph	ma	10	1		3	4	2
<i>Calathus melanocephalus</i> (L., 1758)	ca	di	1	2		3	5	3
<i>Harpalus rufipes</i> (Deg., 1774)	mi	ma	4			4	6	5
<i>Pterostichus vernalis</i> (Pz., 1796)	ca	di	3	4				2
<i>Synuchus vivalis</i> (Ill., 1798)	ph	di	2	1				1
<i>Abax parallelepipedus</i> (Pill. & Mitt., 1783)	ca	br	7	2	2			1
<i>Badister bullatus</i> (Schränk, 1798)	ca	ma	1			3		1
<i>Carabus nemoralis</i> (Müll., 1764)	mi	br	5	3	2	2		1
<i>Carabus auratus</i> (L., 1761)	ca	br	39	22	4	3		1
<i>Bembidion lampros</i> (Hbst., 1784)	ca	di	74	35	1	5		1
<i>Harpalus affinis</i> (Schränk, 1781)	mi	ma	15	10	5	2	3	
<i>Trechus quadristriatus</i> (Schränk, 1781)	ca	ma	17	3			1	
<i>Carabus granulatus</i> (L., 1758)	ca	di	15	13	2	1		
<i>Nebria salina</i> (Fairm. & Lab., 1854)	ca	?	21	6	1			
<i>Bembidion obtusum</i> (Aud.-Ser., 1821)	ca	di	23					

## Appendix A. (Continued)

Species name	Feeding mode <sup>a</sup>	Dispersal ability <sup>b</sup>	Abundance						
			0	1	2	3	4	5	
<i>Pterostichus melanarius</i> (Ill., 1798)	ca	di	10						
<i>Pterostichus niger</i> (Schall., 1783)	ca	di	1						
<i>Amara similata</i> (Gyll., 1810)	mi	ma	1						
<i>Harpalus rufibarbis</i> (F., 1792)	ph	ma	1						
<i>Harpalus honestus</i> (Dft., 1812)	ph	ma	2						
<i>Harpalus latus</i> (L., 1758)	ph	ma	1						
<i>Notiophilus palustris</i> (Dft., 1812)	ca	di	2						
<i>Notiophilus aquaticus</i> (L., 1758)	ca	di	1						
<i>Poecilus cupreus</i> (L., 1758)	mi	ma	286	100					
<i>Nebria brevicollis</i> (F., 1792)	ca	ma	83	135					
<i>Platynus dorsalis</i> (Pont., 1763)	ca	ma	54	66					
<i>Anisodactylus binotatus</i> (F., 1787)	?	ma	25	1					
<i>Loricera pilicornis</i> (F., 1775)	ca	ma	1	15					
<i>Trechus obtusus</i> (Erichs., 1837)	?	di		1					
<i>Acupalpus meridianus</i> (L., 1761)	ca	ma		1					
<i>Harpalus distinguendus</i> (Dft., 1812)	ph	ma		1					
<i>Cicindela campestris</i> (L., 1758)	ca	ma		1					
<i>Agonum sexpunctatum</i> (L., 1758)	ca	ma		1					
<i>Agonum muelleri</i> (Hbst., 1785)	ca	ma		6					
<i>Amara plebeja</i> (Gyll., 1810)	ph	ma		48					
<i>Amara aenea</i> (Deg., 1774)	ph	ma		200	7	117	4	2	
<i>Amara communis</i> (Pz., 1797)	ph	ma		4	135	36	26	80	
<i>Amara lunicollis</i> (Schiödte, 1837)	ph	ma		7	32	21	38	113	
<i>Amara convexior</i> (Stph., 1828)	ph	ma		4	16	26	22	38	
<i>Amara familiaris</i> (Dft., 1812)	ph	ma		2	8	26	2	1	
<i>Syntomus truncatellus</i> (L., 1761)	ca	di		1		10	2	3	
<i>Bembidion properans</i> (Stph., 1828)	ca	di		3			1		
<i>Bembidion lunulatum</i> (Fourcr., 1785)	ca	ma		1			1		
<i>Brachinus explodens</i> (Dft., 1812)	ca	?		1		1			
<i>Panagaeus bipustulatus</i> (F., 1775)	ca	ma			1		1		
<i>Amara montivaga</i> (Sturm, 1825)	ph	ma			3				
<i>Harpalus dimidiatus</i> (Rossi, 1790)	ph	?				1			
<i>Harpalus smaragdinus</i> (Dft., 1812)	mi	ma				1			
<i>Amara tibialis</i> (Payk., 1798)	ph	ma				1			
<i>Amara equestris</i> (Dft., 1812)	ph	ma				1		1	

<sup>a</sup> ca: carnivorous, ph: phytophagous, mi: mixophagous, ?: no classification possible.

<sup>b</sup> ma: macropterous, br: brachypterous, di: dimorphic, ?: no classification possible.

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**Tobias Purtauf** is a PhD student at the Department of Animal Ecology of Giessen University. He focuses on the effects of spatio-temporal landscape mosaics on ground beetle communities. In addition, he co-ordinates the animal ecology project funded by the German Research Foundation in the context of a Collaborative Research Center (SFB 299). He is also involved in teaching landscape and animal ecology to undergraduate students.

**Jens Dauber** received his PhD with a landscape-oriented study on ants. He leads the landscape ecology group at the Department of Animal Ecology, University of Giessen and co-ordinates the project ‘Biodiversity and Spatial Complexity in Agricultural Landscapes under Global Change’ funded by the Federal Ministry of Education and Research of Germany. His fields of research are (i) biodiversity in agricultural landscapes, (ii) assessment of landscape complexity using remote sensing data and GIS and (iii) functioning of ants as ecosystem engineers in the soil system. He is teaching landscape and animal ecology.

**Volkmar Wolters** is the head of the Animal Ecology Group at University of Giessen and is the director of the Department of Zoology. He has long-term expertise in invertebrate diversity, soil biology, landscape ecology, and ecosystem research. Currently, he runs several projects funded by the EU, by the Federal Ministry of Education and by the Research of Germany, and German Research Foundation. In addition, he received several grants from the EU, from the NATO and from the German Government. He is a member of the Scientific Steering Committee of IGBP-GCTE and has recently been appointed as a coordinator of a large German biodiversity program (BIOLOG).