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Diversity of carabids (Coleoptera: Carabidae) within two Dutch cereal fields and their boundaries

Pavel Saska

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In this paper, the diversity and species richness of carabid beetles (Coleoptera: Carabidae) is reported for the two fields of winter wheat and their boundaries. Active carabid beetles were recorded in Wageningen, the Netherlands, using pitfall traps during the spring and early summer, and overwintering carabids were sampled by the soil cores in winter of 2004. 75 carabid species in adult stage and 12 carabid taxa as larvae were found in the pitfall traps. In addition, 11 taxa were found in the soil cores. Rarefaction curves indicated that species richness was identical in both fields and that observed differences were due to higher activity-density of carabids in field 1. Both fields hosted identical assemblages, although species in field 2 were more evenly distributed among ranks. The pre-requisites for high diversity of carabids in the study fields are discussed and the causes for the differences in overwintering densities and activity-densities between fields are hypothesized.

Key words: ground beetles, diversity estimators, rarefaction, overwintering

Pavel Saska. Crop Research Institute, Drnovska 507, Prague 6 – Ruzyne, 161 06, Czech Republic, saska@vurv.cz.

Introduction

Ground beetles (Coleoptera: Carabidae) are the key group in natural pest and weed control in agro-ecosystems (for recent reviews, see Kromp 1999; Tooley & Brust 2002; Sunderland, 2002). Their impact depends on abundance, composition and diversity of their assemblage, which, however, vary between as well as within fields.

The variability in abundance and diversity of carabid assemblages is driven by many environmental factors beyond one˙s control (reviewed by Thiele 1977; Holland 2002), but carabids are also sensitive to man-made modifications of the landscape such as field sizes or complexity of landscape structures (Holland 2002; Purtauf et al. 2005a). For example, reduction of non-crop habitats resulted in species decline during past decades in Europe (Desender & Turin 1989; Niemelä 2001; Kotze & O´Hara 2003), because many species use these sites for overwintering (Thomas 1990; Pfiffner & Luka 2000), from where they re-colonize fields in early spring (Coombes & Sotherton 1986; Kromp & Steinberger 1992).

In 2004, we conducted a large field trial, in which the density and distribution of overwintering carabids, their subsequent spatial and temporal distribution, and its consequences for predation of weed seeds, was studied. The experiment was conducted within two fields of winter wheat and adjacent field boundaries. In this paper we report on the diversity and structure of the sampled assemblages.

Materials and methods

Experimental fields were located at farm "Droevendaal", near Wageningen, province of Gelderland, the Netherlands (51°58'N, 05°40'E, 20 m of altitude), on sandy soil. This farm had been converted to organic farming in 2003. The sampled fields of winter wheat (*Triticum aestivum* L.; sown late October, 2003, and harvested 4 August, 2004) were about 500 m apart. Field 1 was 100 x 160 m and was surrounded by 2-3 m wide boundary strips sown by rye-grass (*Lolium perenne* L.) on all sides (Fig. 1A). Field 2 was 100 x 180 m and was surrounded by sown rye-grass boundary strips on three sides (Fig. 1B). The remaining side was bordered by a set-aside strip that grew with weedy vegetation later in the season (Fig. 1B). In field 1, a narrow (0.5 m) strip of weedy vegetation naturally regenerated by the edge of crop and grassy boundary as a result of improper cultivation previous autumn (Fig. 1A).

Carabid beetles that overwintered in the soil were sampled using soil cores at four consecutive weeks between 22 January and 24 February, 2004. Five soil cores (volume 1l) were taken from the upper soil level within each field interior and grassy boundary each week (i.e. 20 samples per site in total). The samples were transferred to laboratory and processed as follows: first soil and plant roots were separated by hand and moving carabids were collected. Then soil was placed into the bucket (5 l) with tap water, stirred and floating carabids were collected. The solute was finally washed through a metal sieve (1 mm mesh size), from which carabids and their larvae were picked up. Carabid adults were identified to species (Hurka 1996; Boeken et al. 2002) and larvae to species or (in most cases) genus (Luff 1993).

Active carabid beetles were sampled using pitfall traps. They consisted of plastic cups (diameter 10.5 cm, volume 0.5 l), half-filled with a saturated saline solution as fixative, placed with the rims at ground level, and covered with a metal roof to avoid flooding by rainfall. Pitfall traps were arranged in seven transects perpendicular to the field edge and extending 50 m into the crop and 1 m into the boundary strip (Fig. 1). Transects were 3 to 6 m apart each consisting of six sampling stations: one in the boundary strip, one immediately or 50 cm from the field edge, and four within the field at 4, 11, 24 and 49 m distance from the field edge (Fig. 1). Each sampling station consisted of two pitfall traps, placed 1 m apart at the same distance from the edge. The sampling continued between 4 March and 28 July, 2004 (crop harvest). Pitfall traps were emptied weekly and fixative was supplied if needed. Collected individuals were transferred to 75% ethanol, where they were stored until identification (see above). Species were assigned granivorous if seeds constitute at least part of the diet of particular species (Goldschmid & Toft 1997; Honek et al. 2003; 2007). For each sampling station (both traps pooled) and week, activity-density (number of individuals caught; Thiele 1977) per taxon formed the basic data set.

Due to small number of individuals in the soil samples, only data from the pitfall traps were statistically analyzed. Observed species richness (S_{obs}) was calculated for each sampling site and date. Species accumulation curves and sample-based rarefaction curves were plotted for each field separately using data for each sampling week (all sampling stations pooled). The rarefaction curves were produced by repeatedly re-sampling the pool of N individuals and Q samples at random for 50 times (Colwell 2005). Since rarefaction curves did not reach asymptotes, total species richness (S_{max}) was estimated using Chao 1, Chao 2, ACE, ICE, Jacknife 1, Jacknife 2 and bootstrap species richness estimators (Colwell 2005). These estimators use information on the presence of rare species in the assemblage, assuming that the greater the number of rare species was recorded, the more likely it is that other

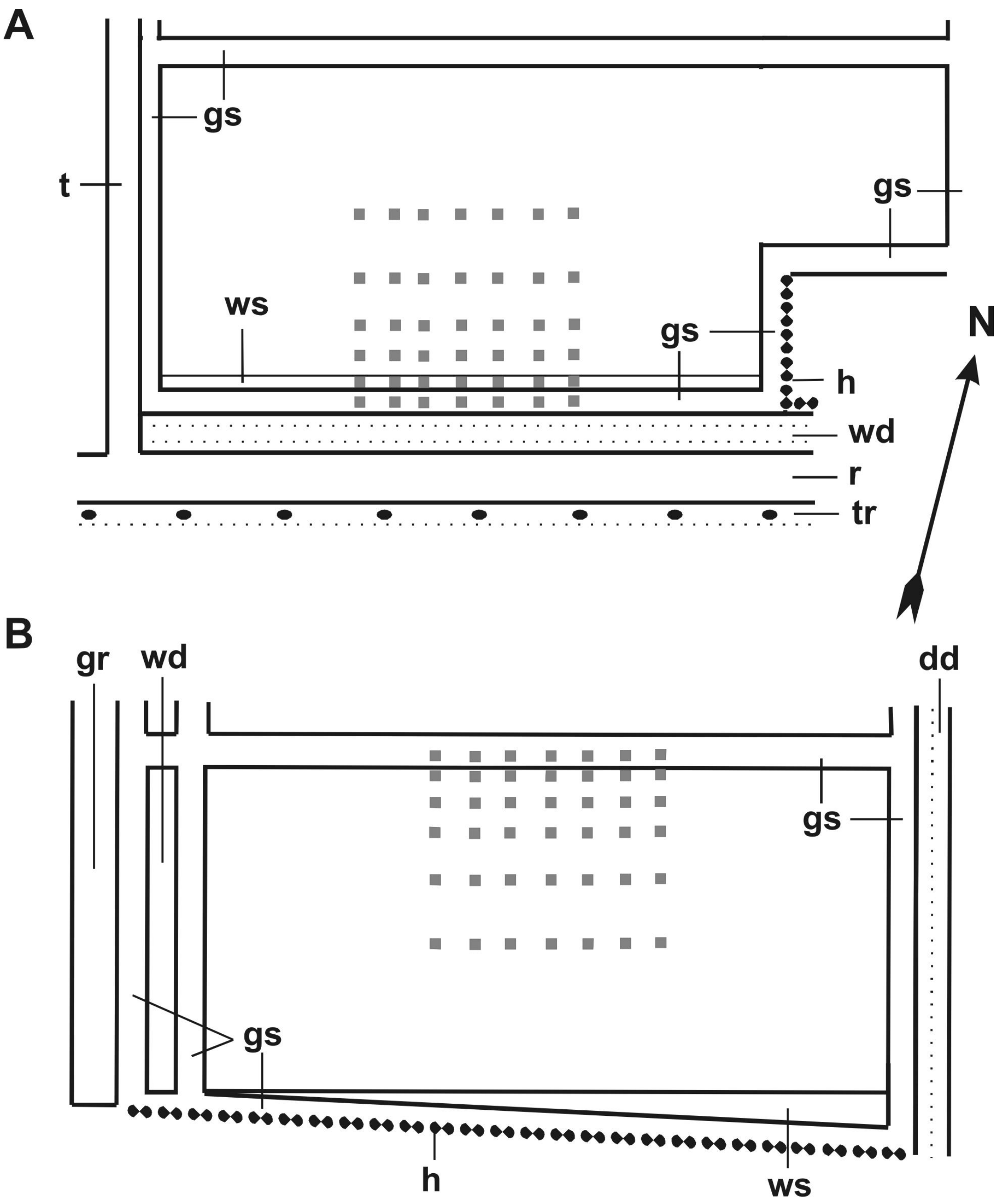

Fig. 1. Positions of sampling locations (squares) within two fields of winter wheat, Droevendaal farm, Wageningen. A – field 1; B – field 2. dd – dry ditch; gr – 2 m high grassy ridge; gs – grassy strip; h – hedge; r – tarred road; t – paved track; tr – tree row; wd – water ditch; ws – weedy strip.

Table 1. Carabid species and their larvae collected by soil sampling within two winter wheat fields and their boundaries in Wageningen, the Netherlands, between January 22 and February 24 2004.

Carabid species	Number of individuals Field 1	 Field 2
Adults		
Amara aenea	9	3
Amara familiaris	1	0
Amara spreta	2	0
Amara similata	1	0
Amara plebeja	1	0
Bembidion lampros	2	2
Harpalus affinis	0	2
Anisodactylus binotatus	1	0
Total adults	17	7
Larvae		
Amara spp.	1	1
Nebria brevicollis	1	0
Carabidae gen. sp.	0	3
Total larvae	2	4
Total	19	11

rare species are present although not recorded (Gotelli & Colwell 1999). More different indexes were used because there is no method generally preferred (Southwood & Henderson 2000). For the formulas of computation, see Colwell (2005). Additionally, classical diversity indexes (Shannon-Weaver and Simpson) were computed (Southwood & Henderson 2000). To be able to compare the species richness between fields a correction must be made for number of specimens collected (see Gotelli & Colwell 2001, for further discussion). Therefore, rarefied species richness was plotted ("re-scaled") against rarefied number of collected specimens; this standardization eliminates the effect of sample sizes on observed species richness.

The evenness of the assemblages was visually tested on log-abundance plots with species ranked according to their activity-density for both fields (Southwood & Henderson 2000). In order to assess the dominance of the assemblages, relative activity-density, i.e. proportion of total individuals accounted, was determined for each species. The species that together constitute 95% of relative activity-density were considered dominant (Luff 2002). Relative activity-densities of 5 most common species were also compared (Luff 2002).

The composition of carabid assemblages was compared between fields using the classical Jaccard similarity index and the estimated abundance-based Chao-Jaccard similarity index (Chao et al. 2005). The latter index is based on the probability that two randomly chosen individuals both belong to species shared by both samples, and the contribution made per species estimated to be present at both sites (but not detected) is also taken into account (Colwell 2005). This approach substantially reduces the negative bias that weakens the usefulness of traditional similarity indices when rich assemblages are incompletely sampled (Colwell 2005). All rarefaction curves, species richness estimators and indexes were computed using the free software program EstimateS 7.50 (Colwell 2005); http://viceroy.eeb.uconn.edu/EstimateS).

Results

Carabid assemblage

Thirty individuals (24 adults and 6 larvae) of 11 taxa were found in the upper soil level in the field boundaries, while no specimens were found within the field (Table 1). The abundance was higher in boundary of field 1 (19 individuals) compared to that of field 2 (11 individuals; Table 1). The same species found in the soil samples were collected in the pitfall traps later in the season (Tables 1 and 2).

In total, 75 carabid species were recorded as adults in the two fields of winter wheat that were sampled using pitfall traps (Table 2). Altogether more than 11,000 adult carabids were collected (Table 2). Both granivorous and carnivorous species were found, and their contribution to observed species richness, S_{obs}, was identical (38 granivorous vs. 37 carnivorous species). However, the total relative activity-density was higher for granivorous (63.4%) than for carnivorous species (Table 2). The proportion of granivorous

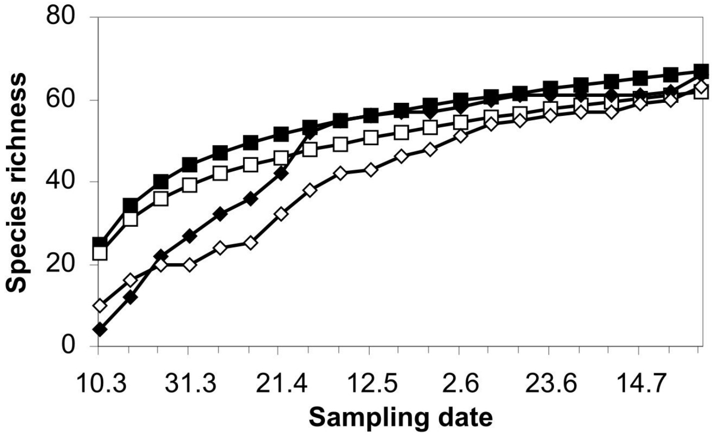

Fig. 2. Increase in observed (species accumulation curves) and predicted (rarefaction curves) species richness in course of time. Closed diamond – species accumulation curve, field 1; open diamond – species accumulation, curve field 2; closed square – rarefaction curve, field 1; open square – rarefaction curve, field 2.

carabids was higher in field 1 (70.3%) than in field 2 (53.0%), mostly as a result of a high abundance of *Amara spreta* in field 1. Weekly observations on activity-density on the two fields were highly correlated (Pearson's $R^2 = 0.87$, $p << 0.001$), suggesting similarity in phenological processes and effects of environmental conditions in the two fields.

Beside adult carabids, 1,600 individuals of carabid larvae belonging to 12 taxa were recorded by pitfalls (Table 2). However, they could be identified to species level in four cases only. The remaining taxa were identified to genus or (sub-)tribus. Larvae of the genus *Amara* constituted at least half of the total amount of larvae in both fields (Table 2).

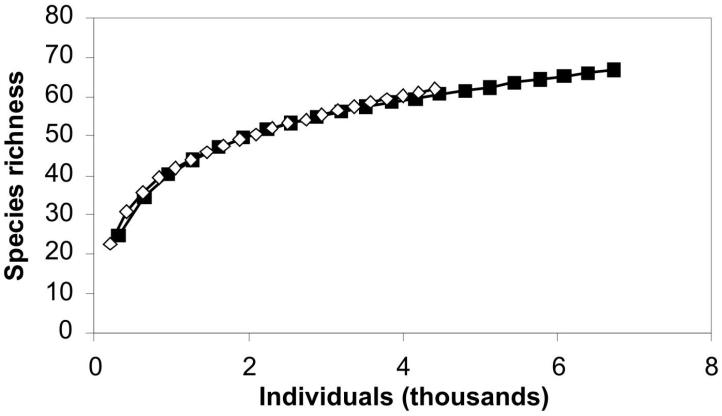

Fig. 3. Sample-based rarefaction curves of increase of species richness re-scaled to number of individuals. Closed square – field 1; open diamond – field 2.

Table 2. Carabid species and their larvae collected by pitfall traps in two winter wheat fields in Wageningen, the Netherlands, between 4 March and 28 July 2004.
DT – development type (s – species that overwinter as adults and reproduction and larval development takes place in spring and early summer, a – species that overwinter mostly as larvae, new generation emerges in early summer and reproduction takes place in late summer and autumn; Turin 2000); O – species response to organic farming ("+" – species promoted by organic farming; "–" – species suppressed by organic farming; Hokkanen & Holopainen 1986; Kromp 1999; Döring & Kromp 2003; Pfiffner & Luka 2003; Purtauf et al. 2005b); AD – Activity-density, number of individuals collected; RAD – Relative activity-density, proportion of total activity-density taken by individual species [%].

Carabid species	DT	O	Total		Field 1		Field 2	
			AD	RAD	AD	RAD	AD	RAD
Adults								
Amara spreta	s		3 298	29.58	2 604	38.68	694	15.72
Harpalus affinis	s	+	1 214	10.89	596	8.85	618	14.00
Bembidion femoratum	s		924	8.29	744	11.05	180	4.08
Clivina fossor	s	+/–	816	7.32	202	3.00	614	13.91
Pseudoophonus rufipes	a	+	803	7.20	485	7.20	318	7.20
Demetrias atricapillus	s		590	5.29	306	4.55	284	6.43
Poecilus versicolor	s	+	360	3.23	102	1.52	258	5.84
Bembidion lampros	s	+	357	3.20	155	2.30	202	4.56
Agonum muelleri	s	+	326	2.92	95	1.41	231	5.23
Amara aenea	s	+	256	2.30	138	2.05	118	2.67
Harpalus distinguendus	s	+	240	2.15	187	2.78	53	1.20
Amara plebeja	s	+	167	1.50	135	2.01	32	0.73
Bembidion tetracolum	s	–	136	1.22	70	1.04	66	1.50
Loricera pilicornis	a	+/–	136	1.22	67	1.00	69	1.56
Bembidion properans	s	+	132	1.18	42	0.62	90	2.04
Pterostichus melanarius	a	+/–	132	1.18	55	0.82	77	1.74
Amara similata	s	+	118	1.06	26	0.39	92	2.08
Anchomenus dorsalis	s	+	111	1.00	85	1.26	26	0.59
Amara familiaris	s	+	103	0.92	83	1.23	20	0.45
Harpalus tardus	s		101	0.91	79	1.17	22	0.50
Calathus erratus	a		73	0.66	46	0.68	27	0.61
Amara lunicollis	s		70	0.63	67	1.00	3	0.07
Anisodactylus binotatus	s	+	67	0.60	39	0.58	28	0.63
Amara anthobia	s		65	0.58	64	0.96	1	0.02
Amara fulva	a		63	0.57	35	0.52	28	0.63
Clivina collaris	s		60	0.54	8	0.12	52	1.18
Bembidion quadrimaculatum	s	+	56	0.50	11	0.16	45	1.02
Poecilus cupreus	s	+	45	0.40	13	0.19	32	0.73
Amara bifrons	a		32	0.29	17	0.25	15	0.34
Nebria brevicollis	a	+	29	0.26	26	0.37	3	0.07
Stenolophus teutonus	s		24	0.22	9	0.13	15	0.34
Notiophilus substriatus	s?		20	0.18	10	0.15	10	0.23
Trechus obtusus	a		19	0.17	5	0.07	14	0.32
Amara communis	s		17	0.15	14	0.21	3	0.07
Harpalus latus	s		16	0.14	15	0.22	1	0.02
Amara apricaria	a		15	0.14	3	0.05	12	0.27

(Table 2. Continued.)

Pterostichus vernalis	s		15	0.14	10	0.15	5	0.11
Badister lacertosus	s		14	0.13	13	0.19	1	0.02
Calathus melanocephalus	a		14	0.13	4	0.06	10	0.23
Amara consularis	a		10	0.09	9	0.13	1	0.02
Amara ovata	s		10	0.09	1	0.02	9	0.20
Harpalus rubripes	s/a		10	0.09	7	0.10	3	0.07
Bembidion guttula	s		8	0.07	1	0.02	7	0.16
Notiophilus biguttatus	s	–	8	0.07	7	0.10	1	0.02
Notiophilus palustris	s		6	0.05	5	0.07	1	0.02
Syntomus foveatus	s		6	0.05	5	0.07	1	0.02
Acupalpus meridianus	s		5	0.05	5	0.07	0	0
Amara convexior	s		4	0.04	4	0.06	0	0
Bembidion lunulatum	s		4	0.04	1	0.02	3	0.07
Trechus quadristriatus	a		4	0.04	2	0.03	2	0.05
Agonum afrum	s		3	0.03	3	0.05	0	0
Dyschirius thoracicus	s		3	0.03	1	0.02	2	0.05
Pterostichus strenuus	s	–	3	0.03	2	0.03	1	0.02
Acupalpus parvulus	s		2	0.02	0	0	2	0.05
Amara aulica	a		2	0.02	0	0	2	0.05
Badister sodalis	s		2	0.02	2	0.03	0	0
Bembidion aeneum	s		2	0.02	1	0.02	1	0.02
Broscus cephalotes	a		2	0.02	1	0.02	1	0.02
Harpalus signaticornis	s		2	0.02	1	0.02	1	0.02
Microlestes minutulus	s		2	0.02	0	0	2	0.05
Synuchus vivalis	a	–	2	0.02	1	0.02	1	0.02
Acupalpus brunnipes	s?		1	0.01	0	0	1	0.02
Agonum marginatum	s		1	0.01	0	0	1	0.02
Amara curta	s		1	0.01	1	0.02	0	0
Amara eurynota	a/s	–	1	0.01	1	0.02	0	0
Amara famelica	s		1	0.01	1	0.02	0	0
Amara lucida	s		1	0.01	1	0.02	0	0
Harpalus anxius	s/a		1	0.01	1	0.02	0	0
Harpalus smaragdinus	s/a		1	0.01	1	0.02	0	0
Microlestes maurus	s		1	0.01	0	0	1	0.02
Olistophus rotundatus	a		1	0.01	1	0.02	0	0
Ophonus rufibarbis	a		1	0.01	1	0.02	0	0
Platynus assimilis	s		1	0.01	0	0	1	0.02
Syntomus truncatellus	s		1	0.01	1	0.02	0	0
Trechoblemus micros	s		1	0.01	0	0	1	0.02
Total adults			11 148	100	6 733	100	4 415	100
Total adults granivorous			7 071	63.43	4 732	70.28	2 339	52.98
Larvae								
Amara spp.			913	56.36	775	57.88	138	49.11
Demetrias atricapillus			184	11.36	143	10.68	41	14.59
Bembidion spp.			161	9.94	144	10.75	17	6.05
Nebria brevicollis			94	5.80	90	6.72	4	1.42
Loricera pilicornis			90	5.56	73	5.45	17	6.05
Agonum muelleri			70	4.32	49	3.66	21	7.47
Harpalina genn. spp.			42	2.59	33	2.47	9	3.20
Notiophilus spp.			36	2.22	23	1.72	13	4.63

(Table 2. Continued.)

Pterostichus spp.	22	1.36	5	0.37	17	6.05
Platynini genn. sp.	6	0.37	3	0.22	3	1.07
Dyschirius spp.	1	0.062	0	0	1	0.36
Leistus spp.	1	0.062	1	0.08	0	0
Total larvae	1 620	100	1 339	100	281	100
Total individuals	12 767		8 072		4 695	

[a] species of the genera *Amara*, *Acupalpus*, *Harpalus*, *Anisodactylus*, *Pseudoophonus*, *Ophonus*, *Stenolophus*, *Calathus*, *Trechus* and *Agonum muelleri*.

Diversity

In field 1, S_{obs} slightly exceeded that of field 2 (65 in field 1 compared to 61 in field 2, respectively). The shape of rarefaction curves indicated that S_{obs} underestimated S_{max} in both fields since curves did not reach asymptotes (Fig. 2). All of the estimators confirmed this suggestion providing much higher values of S_{max} than S_{obs} (Table 3). After re-scaling for individuals, rarefaction curves for both fields had nearly identical slope (Fig. 3). This revealed that difference in S_{obs} between the two fields may be ascribed to the greater number of individuals caught in the field 1.

Amongst the species recorded, 13 occurred only in field 1 and 8 were unique for field 2, resulting in value of the classical Jaccard index = 0.74. However, these 21 unique species altogether made up only 34 individuals in total, therefore the value of estimated abundance-based Chao-Jaccard similarity index = 1 indicated that despite these differences the composition of assemblages in both fields was identical.

Evenness of the assemblages as compared on log-abundance rank plots showed that the values of activity-density of carabids in field 2 were more evenly distributed across species than in field 1 (Fig. 4). The differences in values of the

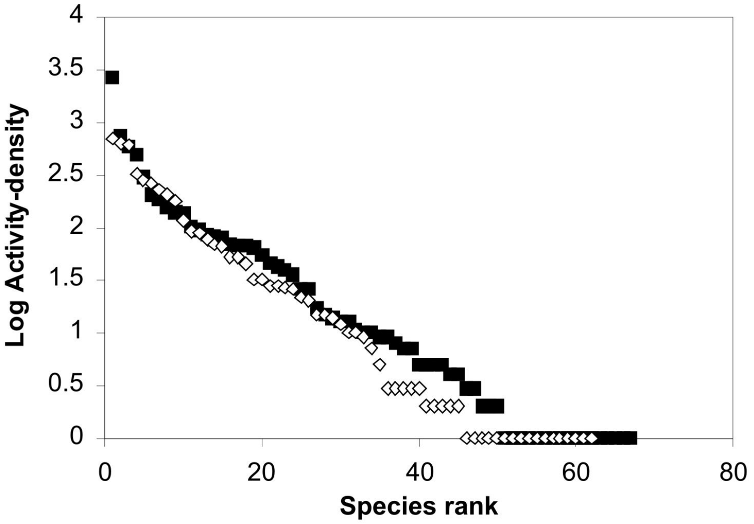

Fig. 4. Activity-density of carabid beetles (log) plotted along species ranked from the most to least abundant. Closed square – field 1; open diamond – field 2.

classical diversity indexes paralleled this result (Table 3). That was because in field 1 the most common species *Amara spreta* dominated by approximately 4-fold over the second most common species, *Bembidion femoratum* (Table 1). In field 1, the five most common species together constituted 70.3% of total adult activity-density. In field 2, the five most common species constituted 57.3% of the catch (Table 1), demonstrating greater evenness in the second field. The number of species forming 95% of relative abundance was similar in both fields: 22 in field 1, and 23 species in field 2. Thus the number of dominant species was practically the same in the two fields.

Discussion

Diversity of carabid assemblage

The assemblages of carabid beetles sampled in the two study fields of winter wheat were highly species-rich and diverse. Although the observed species richness is very high for a cereal field, maximum species richness was predicted to be even higher. This is not surprising, as only half of the season was sampled and many autumn-breeding species could not be recorded due to disparity of the sampling season and their phenology (den Boer & den Boer-Daanje 1990). Nevertheless, the highest predicted values of S_{max} given by, for example, Chao 2 estimator (121±40 species), do not seem realistic, as they predicted S_{max} of the two 250 m^2 large plots to be as high as one third of the carabid fauna of the whole Netherlands (Turin 2000). We suppose that this overestimation resulted from a number of autumn-breeding species that started to emerge at the end of the sampling and therefore collected only once or twice. Since singletons and doubletons have large impact on the estimated number of other rare species that were not recorded but probably live in the sampled area (Colwell 2005), S_{max} is largely overestimated by some indexes. Thus, these estimators should be used with caution in studies when season was only partly sampled. In spite of high similarity in assemblage composition between the two fields, classical diversity indexes suggest higher diversity in field 2. This was probably caused by the high activity-density of *A. spreta*, which dominated in field 1, as shown by the ranked plots.

Although comparisons between studies are intricate due to differences in sampling methods (number of traps, trapping period etc.) the evidence for comparatively high diversity in the current study is compelling as there is only one study from cereal fields (Kromp and Steinberger, 1992) that recorded a comparably high number

Table 3. Species richness (mean ± S.D.) observed and estimated for assemblages of carabid beetles in two winter wheat fields in Wageningen, the Netherlands, sampled between 3 March and 28 July 2004.

Index	Field 1	Field 2
Species richness estimator		
S_{obs}	66 ± 5.61	61 ± 4.51
S_{max} Chao 1	114.17 ± 36.98	89.90 ± 19.81
S_{max} Chao 2	121 ± 40.91	80.06 ± 11.65
S_{max} ACE	88.23 ± 0.0	93.61 ± 0.0
S_{max} ICE	83.42 ± 0.04	82.21 ± 0.0
S_{max} Jacknife 1	84.14 ± 5.22	78.19 ± 3.55
S_{max} Jacknife 2	97.85 ± 0.0	86.7 ± 0.0
S_{max} Bootstrap	73.97 ± 0.0	69.19 ± 0.0
Diversity index		
Shannon-Weaver	2.48	5.51
Simpson	2.86	11.66

of species and similarly low value of relative activity-density for the five common species (Luff 2002). Literature data combined with this study indicate three possible pre-requisites of high diversity and richness in arable fields. (i) *Sandy soils* host more diverse assemblages compared to other soil types according to Thiele (1977). Also experiment of Kromp and Steinberger (1992), the only comparable data available, was located on sandy soil. Thus, presented data support suitability of sandy soils for development of diverse carabid assemblages in arable land. (ii) *Organic farming* promotes arthropod species richness and diversity in cereal fields (Döring & Kromp 2003). Of the 22 dominant species recorded in this study, 16 have been reported to benefit considerably from organic farming before (Hokkanen & Holopainen 1986; Kromp 1999; Döring & Kromp 2003; Pfiffner & Luka 2003; Purtauf et al. 2005b) (Table 1). Since "Droevendaal" experimental farm, where the experimental fields were located, was converted to organic farming one year before the experimental season, the effect of reduced input of chemicals may have not appeared yet. However, data on how fast the enhancing effect appears after the conversion from conventional to organic farming are not available. (iii) *High diversity of habitats*. Recent studies show that high diversity of habitats at farm and landscape scale may have bigger effect on local diversity and species richness of carabids than field management (Purtauf et al. 2005b; but see Pfiffner & Luka 2003). Since the "Droevendaal" farm consists of a mosaic of small (1-3 ha) fields or grasslands, surrounded by various pre-existing landscape features such as hedges, tree rows, grassy boundaries, ditches or canals with grassy banks, it is very likely that the high diversity of habitats in the surroundings of experimental fields contributed significantly to the enormous diversity of carabid beetles recorded.

Although not shown by the similarity index values, the relative abundance of particular species differs between fields, probably due to interaction of environmental factors with their requirements. For example, soil moisture is responsible for differences in relative activity-density between fields: higher activity-density of hygrophilous species such as *Clivina* species, *Agonum muelleri* or *Bembidion quadrimaculatum* in field 2, and higher catches of xerophilous *Amara spreta*, *A. anthobia* or *Harpalus tardus* in field 1 can be ascribed to virtually higher soil humidity in field 2 compared to field 1. Indeed, the massive occurrence of *A. spreta* in field 1, where this species dominated 4-fold over the second most numerous *B. femoratum*, support the conclusion of Döring and Kromp (2003) that xerophilus and typical field-inhabiting species benefit from organic farming the most. Small sizes of experimental fields may also explain low numbers of *Trechus quadristriatus*, which is generally one of the most abundant species in cereals (Luff 2002), but negatively responds to decrease in field size (Irmler 2003). Hence using species richness for comparison of effect of landscape structure or farming systems on carabid diversity without looking at response of individual species may be misleading.

Among the species recorded, *H. signaticornis* was found. In the Netherlands, this species was known from old records in the southern Limburg (Turin 2000). Recently it has been reported from the Veluwe, ca. 20 km apart (H. Turin, pers. comm.). The present record thus confirms the occurrence of this species in the Netherlands.

Overwintering density

Soil sampling of overwintering carabids within the fields gained no carabids, compared to nearly 30 specimens found in the boundaries. The species recorded included *B. lampros*, *H. affinis*, *Anisodactylus binotatus* and five species of the genus *Amara*. This supports the earlier results of Sotherton (1984) and Dennis et al. (1994), who determined field boundaries as crucial overwintering habitats for carabids.

Differences were found between fields: in field 1 comparatively more specimens were found than in field 2. High catches in pitfall traps in field 1 suggest that overwintering densities may be important for determination of carabid densities in the fields subsequently. For example, Coombes and Sotherton (1986) found a correlation between numbers of overwintering individuals of *Demetrias atricapillus* at grassy boundaries and amounts of individuals, collected at 5 m apart the boundary. Since only little attention has been paid to factors that determine the overwintering densities, selection of overwintering sites and survival during hibernation, possible mechanisms that are involved are discussed below.

Boundary type affects attractiveness or suitability as hibernation sites for carabids (Dennis et al. 1994; Asteraki et al. 1995; Pywell et al. 2005), but those examined in this study were both formed by the sown rye-grass (*Lolium perenne*) strips. Factors other than vegetation structure important for selection of overwintering sites and carabid winter survival are less clear. It is assumed that higher density in the boundary of the field 1 could be a combined result of the character of pre-existing boundary in field 1 and higher soil moisture level in field 2. The pre-existing boundary features behind the sown strip in field 1 (a ditch which sides were grown by well established *Dactylis glomerata* L., and a row of *Quercus robur* L.) might have increased attractiveness of the non-crop habitat and subsequently overwintering densities of carabids compared to field 2 (here the non-crop habitat consisted of the sown grassy strip only). *D. glomerata* was found to be the most suitable plant for hibernating carabids (Dennis et al. 1994), as their tussocks buffer the temperature fluctuation during the winter (Luff 1965). Carabids may have been attracted to the tree silhouettes when searching for hibernation sites, since directed movement towards vertical objects in autumn was observed both for walking and flying carabids (Lauterbach, 1964; Neumann 1971; Van Huizen 1977), which may explain why hedgerows often host more hibernating carabids than non-crop habitats free of vertical objects (Asteraki et al. 1995; Pywell et al. 2005). Moreover, leaf litter may provide suitable substrate for overwintering carabids (Maudsley et al. 2002). Several carabid species (e.g. *A. spreta*) were found hidden in the leaf litter in winter (P. Saska, pers. obs.).

In general, lower winter survival rate in moist environments (e.g. due to higher probability of being attacked by pathogens) is thought to be the reason why terrestrial arthropods favour dry habitats for hibernation (Leather et al. 1993). However, positive, neutral and negative response to soil moisture at overwintering sites within hedgerows was found in carabids. Negative response was exhibited by xerophilous species such as *Anchomenus dorsalis* or *Pseudoophonus rufipes*, positive response by several species of the genus *Bembidion* (Maudsley et al. 2002). Thus, there is a high need for better understanding of factors and mechanisms affecting selection of hibernation sites. The role of tree-rows, leaf-litter and soil humidity seem to be promising topics on which manipulative field studies may focus.

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