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Effects of changes in plant species richness and community traits on carabid assemblages and feeding guilds

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ABSTRACT

Experiments were conducted between 2001 and 2003 in constructed plant communities that were set up in 1996 on abandoned agricultural land. The primary aim of the experiment was to study how different secondary vegetation succession scenarios influence community development of invertebrates in different trophic levels. The succession scenarios were obtained by sowing high diversity or low diversity seed mixtures of mid-successional plant species in 1996 in comparison with unsown plots where agriculture ceased in 1996 or 1999. Carnivorous carabid species generally preferred plots characterized by open vegetation, whereas herbivorous carabids generally favored plots associated with high plant diversity. However, carabid community composition was affected most by sampling year and there was also a dramatic shift over the three years in the relative proportion of the different trophic groups. Irrespective of treatment, the proportion of carnivores in the community declined with time, whereas phytophages increased over the course of the three years. By contrast, the proportion of omnivores peaked during the second year. These long-term changes were, at least to some extent, related to short-term changes in the structure and composition of the plant communities. The importance of local variation and temporal changes in plant species richness on carabids and other insect fauna are discussed.

1. Introduction

Structural and chemical aspects of habitats at small scales, which are often correlated with plant species richness, are known to strongly influence the abundance and diversity of invertebrate consumers (Schmitz et al., 2004). At larger scales, however, other characteristics of the plant community may play a more important role in shaping the community of higher trophic levels. Several studies have argued that a diverse resource base is capable of supporting more species of herbivores than a simple resource base because more species of herbivores are able to exploit diverse plant communities than simple communities (the 'taxonomic diversity hypothesis', sensu Siemann et al., 1998; Bröse, 2003a,b). By association, these effects may also affect organisms, such as predators and parasitoids, in the third trophic level (Hunter and Price, 1992).

Other characteristics of the plant community, such as plant architecture and structural heterogeneity, may also affect the distribution and abundance of higher trophic levels (the 'structural heterogeneity hypothesis', sensu Murdoch et al., 1972; Dennis et al., 1997; Bröse, 2003a,b). Increased structural heterogeneity in the vegetation may increase the number of niches available for consumers and thus enhance local species richness (Root, 1973). Studies examining the relationship between plant species diversity and/or vegetation structure on invertebrate diversity have used spiders (Jeanneret et al., 2003) parasitoid wasps (Koricheva et al., 2000) and butterflies (Collinge et al., 2003), with some examining the effects of plant diversity on total arthropod abundance (Siemann et al., 1998; Longcore, 2003). However, amongst all groups of terrestrial arthropods, by far the most attention has been paid to ground beetles (Carabidae) in studies exploring factors determining species richness in communities. For example, carabid assemblages have been found to be correlated with a range of parameters, including differences in plant species richness (Ter Braak and Schaffers, 2004), vegetation complexity and microhabitat (Bröse, 2003a,b; Irmler, 2003; Pearce et al., 2003), canopy cover (Varchola and Dunn, 1999) and changes in habitat quality along spatial gradients (Magura et al., 2000; Ishitani et al., 2003).

Thus far, few studies have investigated if habitat preference is correlated with selected carabid life-history traits (but see Ribera et al., 2001; Weller and Ganzhorn, 2004). In particular, little is

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known about the effects of plant diversity on the various feeding guilds (carnivores, phytophages and omnivores) that are found in the Carabidae. Most studies instead assume that carabids occupy a single trophic level (the third, as carnivores) or else carabids are not assigned to any trophic level (e.g. Varchola and Dunn, 1999; Magura et al., 2000; Ishitani et al., 2003).

This study examines the temporal relationship between plant species diversity, structural vegetation complexity and the diversity and abundance of carabid beetles in plant communities that represent different trajectories of secondary (old field) succession on former production land. The primary objectives were to: (1) ascertain the species composition of carabid beetles in the different treatments over three years, (2) determine if carabid assemblages and different feeding guilds are correlated with (i) plant species richness, or (ii) spatial/structural aspects of the different plots, thus testing the 'structural complexity' and 'taxonomic diversity' hypotheses, and (3) determine temporal patterns in carabid community composition and relative abundance of carnivores, phytophages and omnivores.

2. Materials and methods

In the spring of 1996, an experimental field was set-up on abandoned arable land near Ede, The Netherlands (Van der Putten et al., 2000). Until then, the area (0.5 ha) had been cultivated with maize (*Zea mais*) in rotation with sugar beet (*Beta vulgaris*), potatoes (*Solanum tuberosum*), barley (*Hordeum vulgare*) and occasionally, ryegrass (*Lolium perenne*). The surrounding area was 50 ha comprised of heathland, mixed forest, and abandoned land. The soil consisted of sandy loam with the following particle size distribution: <2 μm 3.4%; 2–63 μm 17.3%; $>$ 63 μm 79.4%. At the time in which ground beetles were first collected (May, 2000), the soil contained 4.5% organic matter, with pH(H_2O) of 6.4.

Four treatments were set up in plots from which all of the vegetation was removed and where the soil was then plowed. The plots were then sown with different mixtures of forbs, legumes and grasses. Sowing consisted of (i) low diversity (four species, LDS) and (ii) high (15 species, HDS) diversity seed mixtures of grasses, leguminous species and other forbs, (iii) plant colonization in unsown plots after land abandonment in 1996 (UNS96) and (iv) continued agriculture until 1998 followed by plant colonization in unsown plots (UNS99). The plots were not weeded, so that in all plots the communities were the result of self-assemblage following initial sowing or abandonment of agriculture. The experimental treatments were installed using a randomized block design with five blocks. Each replicate plot measured 10 m × 10 m and each block contained one replicate of each treatment. Within each block the four plots were regularly spaced forming a square and plots were separated by lanes that were 2 m wide, and which were mown regularly. Distance between the blocks was at least 2 m. Every September all plots were mown and the aboveground biomass was removed. All HDS replicates were sown with the same combination of 15 species (Table 1). To prevent confusion between effects of the LDS treatment and effects of plant specific traits (Huston, 1997), each of the low diversity replicates contained a different subset of the high diversity mixture (Table 1). The high and low diversity mixtures consisted of the same number of seeds (grasses 2500 seeds m^{-2}; legumes 500 seeds m^{-2}; other forbs 500 seeds m^{-2}).

2.1. Assessments

Annually, at peak standing biomass (end July), plant species cover and percentage of bare ground in every experimental plot of 10 m × 10 m were recorded in 12 permanent quadrats of 1 m × 1 m each. Number of plant species per m^2, grass cover and the Shannon-Wiener index (H′) were calculated. For each plot the data from the 12 quadrats was averaged to obtain for each species the average cover per m^2. Because cover was assessed for each species individually, total cover within a quadrat can exceed 100% reflecting overlapping of the plant species. Every year, in late August aboveground biomass was clipped at 2 cm above the soil surface in twelve 0.25 m × 0.25 m subplots adjacent to the permanent quadrats. Plant material was oven-dried at 70 °C and weighed to calculate the mean aboveground biomass per m^2 for each 10 m × 10 m plot.

Over three successive years, beginning in 2000, carabid beetles were collected in all plots. Four pitfall traps (9 cm diameter, 11 cm deep) filled with 100 ml 3% formaldehyde were placed at the four angles of an imaginary 2.5 m × 2.5 m^2 situated at the middle of each plot for 14 days during spring (April–May) and 14 days during autumn (August–September). Each trap was sheltered 2 cm above the soil surface by a transparent plastic cover to protect the trap from damage inflicted by animals and from precipitation. Once a week beetles were collected and pitfall traps refilled. For each plot, individuals collected from different traps and sampling dates within one year were pooled. Beetles were identified to species in the laboratory, and assigned to one of three feeding guilds: (1) carnivores, (2) phytophages, (3) omnivores.

Table 1
Plant species sown in the different high diversity (HDS) and low diversity (LDS) plots

HDS plots	LDS plots				
	1	2	3	4	5
Grasses					
Festuca rubra	X	X			
Phleum pratense	X				X
Poa pratensis		X	X		
Anthoxanthum odoratum			X	X	
Agrostis capillaris				X	X
Legumes					
Lotus corniculatus	X				
Vicia cracca		X			
Trifolium pratense			X		
Trifolium dubium				X	
Trifolium arvense					X
Other forbs					
Plantago lanceolata	X				
Tanacetum vulgare			X		
Hypericum perforatum				X	
Hypochaeris radicata		X			
Linaria vulgaris					X

All five HDS replicate plots were sown with the same mixture of 15 plants while each LD plot was sown with a different subsample of the HDS mixture, consisting of two grass species, one legume and one other forb. UNS96 and UNS99 plots were not sown.

2.2. Data analyses

Species composition of the plant community in each plot was analyzed with principal component analyses (PCA) using Canoco 4.2 (Ter Braak and Šmilauer, 2003). This was done for the three years together (four sowing treatments × five blocks × three years = 60 samples). Species abundances were log-transformed, centered by species, and species with less than three occurrences in the database were excluded from the analyses. Data indicated that PCA was more suitable than detrended correspondence analyses (DCA) according to Lepš and Šmilauer (2003; longest gradient length was 2.4). The effects of plot treatment on vegetation characteristics (% bare ground, species richness, % grass cover, Shannon-Wiener index, aboveground biomass) were analyzed using ANOVA. Mean values over the sampling period (2000–2002) were analyzed. To achieve normality and homogeneity of variance, percentage data (bare ground and grass cover) were arc-sine transformed, and biomass data log-transformed prior to analyses. Data on Shannon diversity and species richness did not require transformation. For characteristics with a significant plot treatment effect, individual treatments were compared using a Tukey HSD test ($P < 0.05$).

To determine whether sowing treatment, year, or vegetation characteristics significantly explained variation in carabid community composition a constrained ordination analysis was carried out using using Canoco 4.2 (Ter Braak and Šmilauer, 2003). This was done for the three groups of explaining variables separately. RDA was carried out with log-transformed species abundances. Data were centered by species, and species with less than three occurrences in the database were excluded from the analyses. Blocks were included as covariables and significance was tested using a Monte-Carlo permutation test restricted for block design with 999 permutations. Treatments and years were entered as dummy variables (Lepš and Šmilauer, 2003). The importance of sowing vs. not sowing, high or low seed diversity, and, for unsown plots, time since abandonment were also tested. To determine whether the temporal trends in species composition depended on treatment or vegetation characteristics, repeated measures analyses RDA was carried out (Lepš and Šmilauer, 2003). For this analysis interactions with sampling year were entered as explanatory variables, and year, plot identity, and block as covariables. This was also done for individual explanatory variables and for the importance of sowing, sowing diversity, and time since abandonment for unsown plots. Percentage explained variation of all canonical axes was determined and F-ratio and P-value estimated based on a permutation test, with block defined as a covariable and restricted for split-plot design.

To determine whether temporal patterns of abundance in carnivores, phytophages and omnivores were influenced by sowing treatments, data were analyzed using repeated measures analyses of variance (RANOVA) in Statistica Version 7. For each year relative abundance of each feeding guild was calculated. To fulfill requirements of normal distribution of errors, data were arc-sine transformed prior to analyses. To determine whether there was a relationship between vegetation characteristics and relative abundance within feeding guilds backward stepwise multiple regression was performed.

3. Results

The first two axes of the PCA explained more than 40% of variation in plant community composition (Fig. 1a). Plots sown in 1996 with high diversity seed mixtures grouped together in the PCA analysis, while both unsown treatments were also rather similar. Community composition of unsown plots changed more during the three years than HDS plots (larger distance between circles, triangles and squares in Fig. 1a). Plots sown individually in 1996 with different low diversity seed mixtures also distinctly differed from each other. LDS1 and LDS2, where *Festuca rubra* was one of the sown species, were most similar to HDS plots, while LDS4 and LDS5 were most similar to unsown plots. In 2000, one year after cessation of agriculture, plant communities in UNS99 plots were still different from UNS96 communities (black vs. white circles in Fig. 1a) but in 2001 and 2002 this difference had largely disappeared, indicating that UNS99 plots were converging to UNS96 plots. Most of the variance in community composition of HDS plots was explained by some of the sown species, in particular *Festuca rubra*, *Lotus corniculatus*, and *Linaria vulgaris*, and to a lesser extend by *Plantago lanceolata* and *Tanacetum vulgare* (Fig. 1b). Other sown species, the grass *Phleum pratense*, and the legumes *Trifolium arvense* and *Vicia cracca*, were associated with plots that were not sown, while some early successional species such as *Elymus repens*, *Senecio jacobaea* and *Taraxacum officinale* were also important in unsown plots (Fig. 1b).

Plots exposed to different treatments differed in percentage bare ground ($F_{3,12} = 35.09$; $P < 0.001$), grass cover ($F_{3,12} = 4.18$; $P = 0.03$), aboveground biomass ($F_{3,12} = 8.71$; $P = 0.002$) and Shannon diversity ($F_{3,12} = 9.23$; $P = 0.002$). Unsown plots had, on average, more bare ground, less grass cover, lower biomass production and higher Shannon diversity than sown plots (Fig. 2).

3.1. Carabid community composition

Carabid community composition varied greatly between years (Table 2), and year explained by far the highest amount of variation

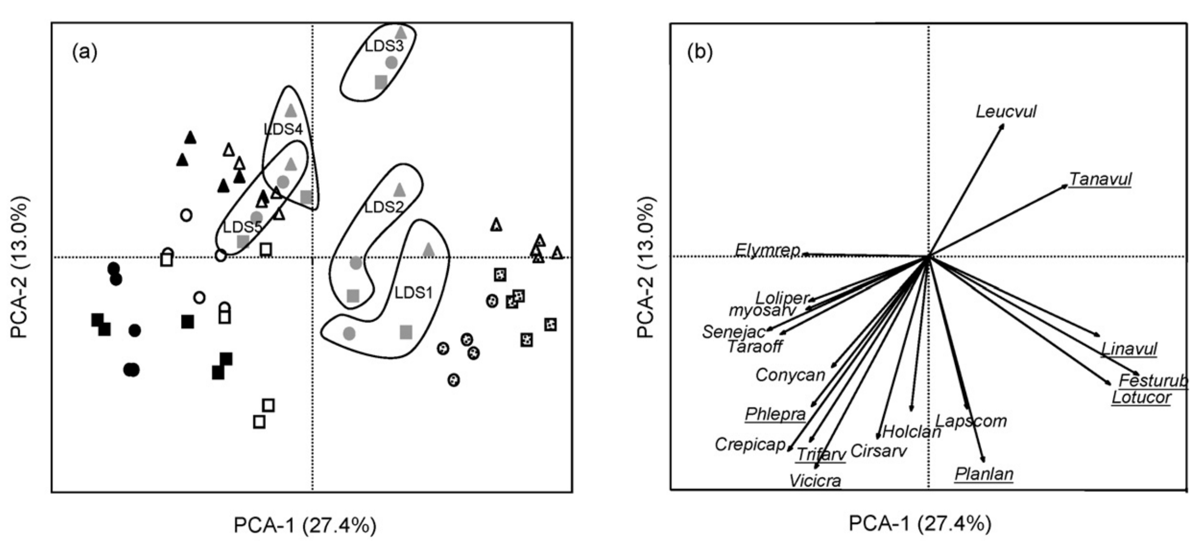

Fig. 1. PCA of plant community composition during 2000 (circles), 2001 (triangles) and 2002 (squares). Shown are biplots of (a) samples, and (b) species and eigenvalues of the first and second PCA axis. Plot treatments are indicated by different symbols: HDS (stippled), LDS (grey), UNS96 (white), UNS99 (black). Individual LDS replicates were sown with different species combinations and are encircled. In (b) only species that explain more than 20% of variation were selected. Sown species are underlined. *Species abbreviations*: Cirsarv: *Cirsium arvense*, Conycan: *Conyza canadensis*, Crepicap: *Crepis capillaris*, Elymrep: *Elymus repens*, Festrub: *Festuca rubra*, Holclan: *Holcus lanatus*, Lapscom: *Lapsana communis*, Leucvul: *Leucanthemum vulgare*, Linavul: *Linaria vulgaris*, Loliper: *Lolium perenne*, Lotucor: *Lotus corniculatus*, Myosarv: *Myosotis arvensis*, Planlan: *Plantago lanceolata*, Pleupra: *Phleum pratense*, Senejac: *Senecio jacobaea*, Tanavul: *Tanacetum vulgare*, Taraoff: *Taraxacum officinale*, Trifarv: *Trifolium arvense*, Vicicra: *Vicia cracca*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of the article.)

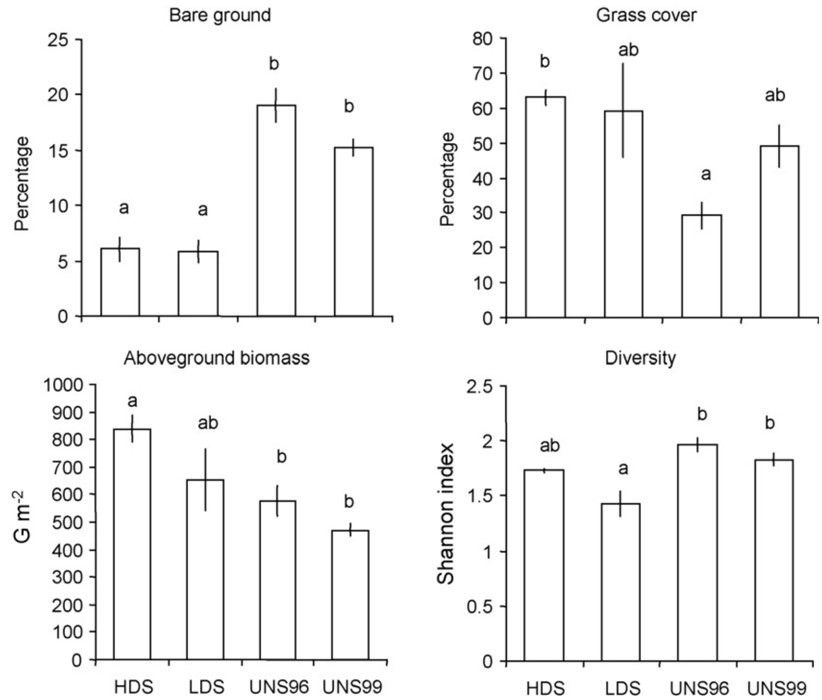

Fig. 2. Vegetation characteristics of plant communities in different plots with different treatments. Means for 2000–2002 (±S.E., $n = 5$) are shown for percentage bare ground, grass cover, aboveground biomass and Shannon diversity. Bars with identical letters are not significantly different based on a Tukey HSD test ($P < 0.05$).

in community composition (48.4%; *F*-ratio = 28.24; *P* = 0.001). Independent of year, vegetation characteristics also explained a large part of the variation (33.4%; *F*-ratio = 7.03; *P* = 0.001), while sowing treatment independently explained 9.1% (*F*-ratio = 1.85; *P* = 0.035). Variation in carabid community composition could be significantly explained by whether plots were sown or not (*F*-ratio = 3.15; *P* = 0.013), but not by sowing diversity level (*F*-ratio = 0.571; *P* = 0.71) or by time since abandonment for unsown plots (*F*-ratio = 1.68; *P* = 0.12).

A few carabid species stood out in the RDA analyses (Fig. 3a and b). *Amara lunicollis* is a phytophage which responded quite differently from other species and was more closely associated with HDS plots (Fig. 3a). In terms of abundance over the three years, the predator, *Poecilus versicolor*, was by far the most common species, representing almost half of the total number of beetles captured. Temporal patterns of species captures were also highly variable. Whereas no *Pterostichus melanarius* was captured in 2000, 206 were caught in 2001, but only another 9 in 2002. *Nebria brevicollis* is a ruderal predatory species that was particularly abundant in the first year of the study (2000) but was almost absent from samples collected in the following two years (Fig. 3b). By contrast, many other species were most abundant in the 2001 samples.

Multivariate repeated measures analyses showed that both plot treatments and vegetation characteristics had an effect on the temporal changes in carabid species composition (Table 3). Of the individual treatments, UNS99 explained most variation, but HDS and UNS96 also had a significant effect. Sowing diversity did not significantly explain variation in carabid species composition, but sowing, and time since abandonment of unsown plots did (Table 3). The percentage of bare ground, aboveground biomass, and grass cover also significantly influenced species composition. The effect of plant diversity was not significant (Table 3).

The relative abundance of carabids in different feeding guilds changed greatly during the three sampling years, indicated by the highly significant time effects in the repeated measures analyses

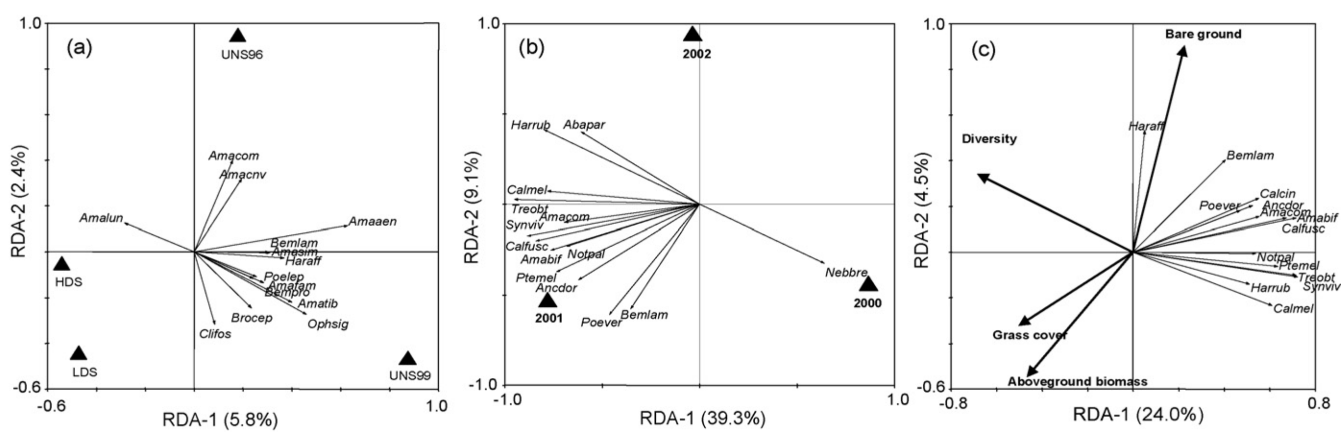

Fig. 3. RDA showing the effect of plot treatment (a), sampling year (b) or vegetation characteristics (c) on carabid community composition. Eigen values of first and second canonical axis are also shown. For each graph the 14 species that explain most variance are presented. Abbreviations of species are as in Table 2.

Table 2
Abundance of carabid beetles trapped during the spring and autumn in the years 2000, 2001 and 2002

Species	Abbrev.	Feeding guild	2000	2001	2002	Total
Poecilus versicolor	Poever	C	2568	5163	1646	9377
Harpalus tardus	Hartar	P	712	1478	1300	3490
Trechus obtusus	Treobt	O	3	766	178	947
Harpalus rubripes	Harrub	P	55	418	437	910
Amara aenea	Amaaen	P	89	361	421	871
Amara lunicollis	Amalun	P	3	418	384	805
Calathus fuscipes	Calfus	O	8	480	72	560
Bembidion lampros	Bemlam	O	137	322	76	535
Calathus melanocephalus	Calmel	O	18	316	117	451
Amara communis	Amacom	P	17	286	98	401
Synuchus vivalis	Synviv	O	0	251	40	291
Pterostichus vernalis	Ptever	O	23	163	96	282
Amara similata	Amasim	P	25	168	55	248
Pterostichus melanarius	Ptemel	O	0	206	9	215
Amara bifrons	Amabif	P	1	172	25	198
Amara convexior	Amacon	P	1	76	110	187
Broscus cephalotes	Brocep	C	119	16	0	135
Notiophilus palustris	Notpal	C	4	102	22	128
Abax parallelepipedus	Abapar	C	3	53	61	117
Pseudoophonus rufipes	Pseruf	P	60	49	8	117
Clivina fossor	Clifos	O	39	40	36	115
Nebria brevicollis	Nebbre	C	104	3	3	110
Calathus cinctus	Calcin	O	9	73	27	109
Harpalus affinis	Haraff	P	55	48	6	109
Ophonus signaticornis	Ophsig	P	27	20	58	105
Bembidion properans	Bempro	C	3	13	66	82
Amara tibilalis	Amatib	P	9	12	50	71
Bradycellus harpalinus	Brahar	P	0	41	26	67
Amara familiaris	Amafam	P	44	11	10	65
Syntomus foveatus	Synfov	U	1	32	22	55
Carabus nemoralis	Carnem	C	13	21	20	54
Anchomenus dorsalis	Ancdor	C	0	43	0	43
Poecilus lepidus	Poelep	C	29	8	4	41
Carabus violaceus ssp. purp.	Carvio	C	1	26	9	36
Notiophilus aquaticus	Notaqu	C	7	20	4	31
Syntomus truncatellus	Syntru	U	0	23	5	28
Amara consularis	Amacon	P	1	22	0	23
Amara ovata	Amaova	P	0	1	19	20
Calathus rotundicollis	Calrot	O	1	18	1	20
Amara aulica	Amaaul	P	1	14	1	16
Pterostichus strenuus	Ptestr	O	0	7	1	8
Lebia chlorocephala	Lebchl	C	0	6	0	6
Loricera pilicornis	Lorpil	C	1	5	0	6
Panagaeus bipustulatus	Panbip	O	0	0	6	6
Pterostichus niger	Ptenig	O	0	4	1	5
Anisodactylus binotatus	Anibin	O	1	1	2	4
Laemostenus terricola	Laeter	O	3	1	0	4
Agonum muelleri	Agomue	C	1	2	0	3
Stomis pumicatus	Stopum	C	0	3	0	3
Cychrus caraboides	Cyccar	C	0	1	1	2
Harpalus distinguendus	Hardis	P	1	1	0	2
Stenolophus teutonus	Steteu	O	0	1	1	2
Amara apricaria	Amaapr	P	1	0	0	1
Amara lucida	Amaluc	P	1	0	0	1
Amara majuscula	Amamaj	P	0	1	0	1
Calathus ambiguus	Calamb	O	1	0	0	1
Carabus problematicus	Carpro	C	0	1	0	1
Cicindela campestris	Ciccam	C	1	0	0	1
Notiophilus germinyi	Notger	C	0	1	0	1
Notiophilus substriatus	Notsub	C	0	0	1	1
Ophonus rufibarbis	Ophruf	P	0	1	0	1
Total			4201	11789	5535	21525

Species are classified into three feeding guilds: carnivores (C), phytophages (P) and omnivores (O). Feeding habit of *Syntomus* is unknown (U).

(Table 4). In all plots, carnivores were very abundant in 2000, but their abundance declined sharply over time. An opposite response was found for phytophages, whose abundance increased during the three years. Omnivores were the least abundant group and were most abundant in the second sampling year (Fig. 4). For all three feeding guilds, the temporal pattern also significantly differed between plot treatments (Table 4). Relative abundance of phytophages, which directly depend on plants for their food, was most strongly influenced by plot treatment. Sown plots did not differ significantly from unsown plots, and HDS plots did not differ from LDS plots for any of the three feeding guilds. However, relative abundance of phytophages (within effect, time interaction: $F_{2,8} = 5.78$; $P = 0.028$) and omnivores (between effect, independent of time: $F_{1,4} = 11.83$; $P = 0.026$) differed significantly between plots abandoned in 1996 and 1999. Multiple regression analyses showed that relative abundance of all three feeding guilds was related to vegetation characteristics (data not shown).

Table 3
Results of multivariate repeated measures analyses using RDA to determine power of plot treatments and vegetation characteristics in explaining carabid community composition

Explanatory variables	Explained variance (%)	*F*-ratio	*P*-value
Plot treatment × year	6.8	1.760	0.001
HDS × year	2.2	1.536	0.015
LDS × year	1.6	1.120	0.14
UNS96 × year	2.4	1.740	0.004
UNS99 × year	2.9	2.125	0.003
(Sown vs. unsown) × year	2.5	1.767	0.006
(HDS vs. LDS) × year	3.5	1.195	0.207
(UNS96 vs. UNS99) × year	5.7	2.224	0.001
Vegetation characteristics × year	10.9	1.422	0.002
Bare ground × year	3.2	1.520	0.002
Aboveground biomass × year	3.4	1.633	0.03
Diversity × year	2.3	1.085	0.44
Grass cover × year	3.2	1.530	0.002

4. Discussion

Irrespective of sowing treatment, the relative proportion of carnivores decreased with time, whereas phytophages became more predominant. By contrast, the relative abundance of omnivorous carabids peaked in the second year of the study. Although plant species composition of the plots changed little over the course of three years, this result may be partially attributable to the effects of temporal changes in the size or density of the vegetation that occurred both within and between years. This means that the plants did not grow in uniform stands during the sampling period but that the amount of plant biomass and thus the structure of the micro-habitats within the plots changed with time. Consequently, our results provide support for the 'structural diversity hypothesis' but not the 'taxonomic diversity' hypothesis.

Irrespective of the short-term changes in feeding guilds, certain patterns emerged from the longer term analyses of the data. For

Table 4
Results of repeated measures analysis of variance for the effect of plot treatment on relative abundance of carabid feeding guilds

Effect	Carnivores		Phytophages		Omnivores	
	F	*P*	*F*	*P*	*F*	*P*
Between subjects						
Treatment	1.42	0.28	1.54	0.25	0.93	0.46
Block	0.73	0.59	0.66	0.63	0.38	0.81
Within subjects						
Year	137.54	<0.0001	187.16	<0.0001	106.38	<0.0001
Year × treatment	2.82	0.03	5.37	0.001	2.65	0.04
Year × block	3.14	0.02	3.31	0.01	1.03	0.44

F- and *P*-values are shown for the overall effects independent of time, (between subjects analysis), and for the interaction with time (within subjects).

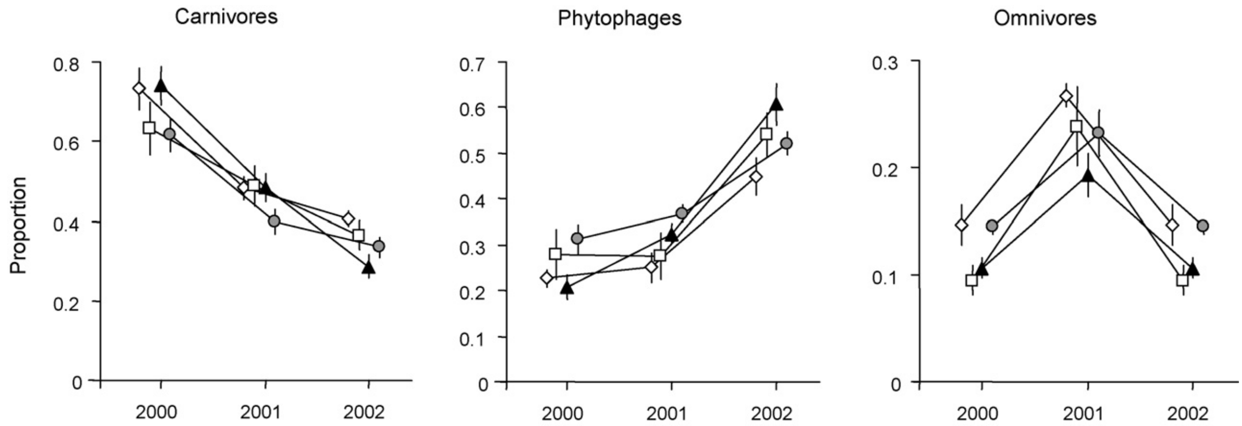

Fig. 4. Temporal changes in relative abundance of carnivores, phytophages and omnivores in HDS (white diamonds), LDS (white squares), UNS 96 (black triangles) and UNS99 (grey circles) plots. Means are shown (±S.E.).

instance, carnivorous species were well represented in sites with a combination of high amounts of canopy (above-ground biomass) and openness at ground level, whereas the abundance of phytophages was positively correlated with plant species richness. Unlike predators, which actively forage on the ground, phytophagous carabids, such as species in the tribe *Harpalini*, are less active and are often found on or near their food plants, where they often exhibit preference for flowers or seeds (Lovei and Sunderland, 1996). For these herbivores, plant diversity may give a greater range of potential food sources (Haddad et al., 2001), which may account for the difference in plant traits associated with assemblages of herbivorous and predatory guilds.

In our study fewer carabids were captured in pitfall traps in plots dominated by grasses that grew in thick swards than in more open plots, which were frequently characterized by bare expanses of ground amongst the interstitial vegetation. This was especially true of plots that were dominated by *S. jacobeae*, which was not sown in the original treatment but invaded from adjacent fields and soon dominated in unsown plots (Bezemer et al., 2006). The spatial structure of plots dominated by forbs, like *S. jacobeae*, is likely to be more variable than plots dominated by grasses, because plant species in the former group are more architecturally complex than species in the latter group. As a result, the movement of cursorial insects is impeded by tightly assembled stands of vegetation at the soil surface (Thomas et al., 2006). It is important, however, to recognize that there are limitations in the accuracy of results obtained solely from pitfall trapping, at least with respect to interguild variation.

In understanding temporal changes in the abundance of carabids and other insects, most work has thus shown that plant species richness and habitat structural heterogeneity are the most important underlying factors (Bröse, 2003a,b; Collinge et al., 2003; Ter Braak and Schaffers, 2004). Future research should therefore consider the importance of plant species diversity structural variation as this affects populations of insect predators.

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