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Effects of newly planted hedges on ground-beetle diversity (Coleoptera, Carabidae) in an agricultural landscape

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The diversity of ground-beetle communities (Coleoptera, Carabidae) was studied to assess the short-term impact of new hedges planted in an intensive agro-ecosystem. Hedges represent a new and undisturbed habitat for those polyphagous predators and may provide increased prey availability. Carabids were sampled with pitfall traps in a hedge and an adjacent cultivated field during the whole activity period of these insects to assess the effect of distance from the hedge on species diversity. Fenced pitfall traps were also used to estimate absolute population densities.
Several diversity indices were calculated at various sampling levels (total area, distance treatment, trap). Kendall's coefficient of rank correlation between communities at adjacent distances showed that the greatest changes in species relative abundances occurred close to the hedge. Indices of species richness, dominance concentration, equitability and Fisher's α all indicated a significant decrease in species diversity with increasing distance from the hedge. These trends are explained by two complementary factors. First, the number of species decreased significantly with distance from the centre of the hedge. Second, the various species had different spatial patterns of total capture and absolute density. Four groups of species can thus be distinguished: species restricted to the hedge, species preferring the hedge, species preferring the crop, and species unaffected by the hedge. The respective roles of small-scale abiotic changes in habitat structure and differences in prey availability are discussed.

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The intensification of agriculture has been a general trend in Europe since the end of the second world war, generating a homogenisation of the landscape. The French region of Beauce is a typical example of this phenomenon: very large plots (mean 25 ha) dominate in open field landscapes, and less perturbed habitats (such as hedges, groves or woods) are very rare. These intensive agro-ecosystems show a high spatial homogeneity, a low species richness, a reduction of genetic diversity and a simplification of food webs, all features that contribute to a decrease in biodiversity (Barbault 1992). These trends demand new management options consistent with developments in sustainable agriculture.

Two new practices have been used since 1995 on a farm situated in Beauce. First, hedges were planted during the winter 1994–1995. Second, ploughing was replaced by a system of superficial soil management, which disturbs only the top 10 cm and thus preserves soil structure and fauna.

To follow the impact of those changes on the ecosystem, we chose to study the diversity of ground beetles (Coleoptera, Carabidae). Ground beetles live on the soil surface and feed on other ground-dwelling invertebrates. They are abundant, diversified, their biology is now well known and they can be studied with a standardised methodology (pitfall trapping), which makes them suitable for monitoring landscape changes. They

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have been intensively studied in agricultural ecosystems (Sanderson 1994, Alderweireldt and Desender 1994). The influence of various agricultural factors (e.g., crop type, management practices, use of pesticides) on carabid biology (phenology, density, activity, spatial distribution, survival, dispersal) has been investigated, with a particular attention given to their predation impact on agricultural pests (Thiele 1977, Sunderland and Vickerman 1980, Pollet and Desender 1985, 1986, Carcamo and Spence 1994).

In our case, carabids are likely to be influenced by the two new practices (presence of hedge and soil management). The use of a simplified soil practice has a direct impact on carabid survival (Stassart and Gregoire-Wibo 1983) and may benefit their potential prey. The hedge represents a new, undisturbed and permanent habitat for the beetles. Several studies have shown the importance, for several predatory arthropod groups, of undisturbed habitats such as hedges (Pollard 1968a, b, Lewis 1969, Sotherton et al. 1981), field margins (Sotherton 1984, Desender et al. 1989), island habitats (Thomas et al. 1992) or herbaceous strips in the middle of agricultural crops (Lys 1992, 1994, Zangger 1994). These habitats allow a diversification of potential prey and provide suitable available overwintering sites. Numerous studies addressed the question of habitat choice and spatial distribution of species, but changes in species diversity have rarely been measured quantitatively although they provide a useful way to assess changes in the community as a whole.

Our first aim here was to understand how the diversity, composition and structure of carabid communities change in the presence of hedges, using various diversity indices. A second objective was to assess absolute population densities in this managed agro-ecosystem. In 1996 we sampled a part of the experimental farmland comprising one hedge and transects through the adjacent cultivated field. We thus studied the short-term effect (during an activity season one year after hedge plantation) of distance from the hedge on carabid diversity.

Materials and methods

Study site

The experimental farm is situated in Ouarville, near Chartres (100 km south of Paris). The mean annual rainfall was 580 mm for the period 1961–1990, and 680 mm in 1994; the minimum and maximum temperatures were, respectively, 0.5 and 6°C in January 1994, and 12 and 22°C in July 1994 (meteorological station of Chartres). Soils are silts, with mean pH 6.25 (SD 0.67).

Hedges were planted on the farmland as shown in Fig. 1. They represented 1% of the useful agricultural surface of the farmland. They were composed of two elements: 1) two rows of shrubs 200 m long and 6 m-wide ("hedges" sensu stricto), and 2) a mixed fodder crop (oats and cabbages) 100 m-long and inserted between the two rows of shrubs. This composite line (total length 500 m) is separated from the adjacent crop by a 9 m-wide zone planted with oat and sorghum (Fig. 1). The physical structure of the vegetation is more complex in the hedges (sensu stricto and mixed crops) than in the adjacent barley crop. However, maximum height did not exceed 2 m; therefore this composite line cannot be considered a closed habitat. The main difference with the adjacent crop is the lack of disturbance.

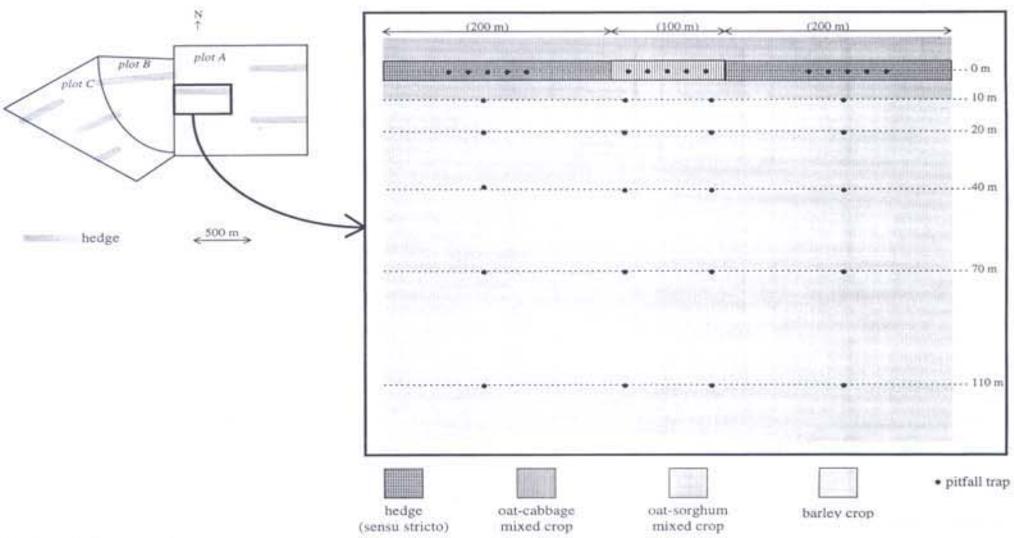

Fig. 1. Limits of the experimental farm and part of the sampling design in plot A relevant to the present study. The experimental farmland (total area 200 ha) is divided in three plots: plots A and B are separated by a trail, plots B and C by a road. In this study sampling of carabid beetles was limited to plot A.

'able Captures and related measures at various sampling levels.

	Trap level (k)	Distance level (d)	Total area level
Number of species	S_k	S_d	
Total catch of species i over the whole period	$N_{i,k}$	$N_{i,d} = \left(\frac{1}{t_d}\right) * \sum_{k=1}^{t_d} N_{i,k}$ $i \in \{1, \ldots, S_d\}$ t_d: number of traps at distance d ($t_0 = 15$, $t_d = 4$ for $d \neq 0$)	$N_i = \sum_k N$ $i \in \{1, \ldots, S$
Total capture of all species over the whole period	$N_k = \sum_{i=1}^{S_k} N_{i,k}$	$N_d = \sum_{i=1} N$	$N = \sum_i N_i$
Relative abundance of species I	$p_{i,k} = \frac{N_{i,k}}{N_\cdot}$	$p_{i,d} = \frac{N_{i,d}}{N_\cdot}$	$p_i = \frac{N_i}{N}$

Sampling methods and design

We sampled carabid beetles in one of the three plots (plot A) of the farm (Fig. 1). We used pitfall traps made of plastic bottles to collect beetles (Greenslade 1964, Baars 1979b, Desender and Pollet 1988). They were filled with a 4% formalin solution with detergent, and emptied every two to four weeks during a period of 5 months (from the beginning of April to mid October 1996, except 5 weeks in August). They were installed in the hedges and at various distances along transects in the adjacent crops. The results presented here concern the central hedge and the adjacent transects through spring barley (Fig. 1).

We also estimated absolute densities using fenced pitfall traps (Desender and Maelfait 1986). Each fence was of 1 m^2 and contained two traps. These were emptied every day during 8 days in June 1996. Twelve enclosures were installed in the hedge (8 in the hedge sensu stricto, 4 in the oat-cabbage mixed crop) and 3 at 110 m in the crop.

Activity density at different levels

Communities were described at three levels (Table 1): a) trap: for each trap, catches were summed over the 5-month study period. b) Distance from the centre of the hedge ($d \in \{0, 10, 20, 40, 70, 110$ m$\}$): at each distance, the catches from traps situated at the same distance (see Fig. 1) were summed. As there were 15 traps in the centre of the hedge, and 4 traps at other distances, these totals were divided by the number of traps to express the results per trap at each distance. c) Total area (hedge and crop): catches from all traps were summed.

The total capture of a species over the whole period measures the species' "activity density", which is a function of both absolute density and activity. Several authors (Thiele 1977, Baars 1979a, Loreau 1992) showed that it gives an estimate of the ecological importance of each species in a biotope, when the period is long enough to cover the most part of the beetles' activity period. Relative abundances were also used to describe ecological dominance and make comparisons between species.

Community characteristics over the whole area

For the species sampled, several ecological characteristics were checked in the literature (den Boer 1977, Thiele 1977, Lindroth 1992): habitat preference, reproductive period, size, and dispersal power.

Species were ranked by order of decreasing total capture. Species that were captured in small numbers (arbitrary limit: <25 individuals captured during the whole activity season, i.e., a percentage of the total capture lower than 0.1%), were classified as "rare species", the other were classified as "common species".

Comparisons of communities at different distances

At each distance d, the S_d species sampled were ordered by decreasing abundance $N_{i,d}$. We defined $R_{i,d}$ as the rank of species i at distance d. Dominance-diversity curves were drawn by plotting the relative abundance of species i at distance d, $p_{i,d}$, on a logarithmic scale against $R_{i,d}$. These curves are useful to describe community structure.

For each pair of adjacent distances (0/10, 10/20, 20/40, 40/70, 70/110 m), we compared the distributions of species ranks by calculating Kendall's coefficient of rank correlation. For this comparison species that were not captured at any of the two distances considered were not taken into account in the calculations.

Measurement of diversity in each trap

Several diversity indices were calculated at the trap level (Hill 1972, Whittaker 1972, Southwood 1978, Loreau 1984):

number of species censused, or species richness: S_k.
dominance concentration: $C_k = \sum_i p_{i,k}^2$.

Defined by Simpson (1949), this index accounts for the distribution of relative abundances between the dominant species.

$$\text{equitability:} \quad E_k = \frac{S_k - 1}{\log_{10}(p_{1,k} - p_{S,k})}.$$

This index is a modification of Whittaker's (1972) equitability index; it takes all species into account equally.
Parameter α_k of the logarithmic series (Fisher et al. 1943), defined by:

$$S_k = \alpha_k \times \ln(1 + N_k/\alpha_k).$$

Linear regressions as a function of the distance from the centre of the hedge were calculated for these various indices. As will be discussed further, all these indices are complementary, because they give different weights to different aspects of species diversity. This makes their joint use more informative than the use of only one of them.

Species distribution patterns

Common species
For each common species (defined as in Community characteristics over the whole area), the total capture over the whole period was analysed with a linear regression model as a function of the distance from the centre of the hedge (0–110 m), or with an ANOVA model as a function of the site (hedge or crop). We thus defined 4 distribution types according to the kind of relationship found: 1) "hedge-restricted species": species found only in the hedge or very close to it. For these species, the mean total capture was significantly higher in the hedge than in the crop (ANOVA with factor = site), and the mean total capture in the crop was not significantly different from zero. 2) "Hedge-preferring species": for these species, there was either a significant difference in the total capture between the two sites (mean total capture higher in the hedge than in the crop, and mean total capture in the crop differing significantly from zero), or a significant negative linear regression with the distance from the centre of the hedge. 3) "Crop-preferring species": the mean total captures of those species were significantly higher in the crop than in the hedge, or showed a significant positive linear regression with the distance from the centre of the hedge. 4) "Hedge-indifferent species": species showing no significant relationship with site or distance.

Estimation of absolute density

We recorded the total captures for each species in each fenced area (described in Sampling methods and design) at the end of the 8 days. The mean total capture was taken as an estimate of a species' absolute density in the site.

Results

Species composition in the whole area

In total, 30 species were collected (Table 2). Except *Notiophilus biguttatus*, the species censused prefer open habitats (21) or are eurytopic (8) (den Boer 1977, Thiele 1977, Lindroth 1992). Eighteen species were classified as "common", twelve as "rare". *Pterostichus melanarius* and *Pterostichus cupreus* were strongly dominant (Table 2).

Comparisons of communities at different distances

The general shape of dominance-diversity curves did not change with distance: the curves were slightly concave-up, almost straight (Fig. 2), thus approaching Fisher et al.'s logarithmic series (Whittaker 1972, Southwood 1978), which justifies the use of α as a measure of diversity. At distance 0 m (centre of composite line), there was no difference in community composition and structure between the hedge sensu stricto and the oat-cabbage mixed crop line. The physical structure of these two elements was quite similar, so that the composite line can be considered a unique entity; this composite line will be called "hedge" in the rest of the paper.

Irrespective of the distance from the centre of the hedge, the two dominant species remained the same. However, there was a marked change in the dominance relationship between them: *Pterostichus melanarius* was more dominant away from hedge (Table 3 and Fig. 3). The ranks of other species also changed with distance. The rank correlation between communities at adjacent distances tended to increase with distance from the hedge (Table 4). Thus, the greatest changes in relative abundances occurred close to the hedge.

Changes in diversity with distance from the centre of the hedge

The mean number of species per trap decreased significantly with distance ($F_{33} = 24054$, $r^2 = 0.43$, $p < 0.0001$) (Fig. 4). The other diversity measures also changed significantly with distance (Fig. 4); dominance concentration increased significantly ($F_{33} = 66.09$, $r^2 = 0.67$,

$p < 0.0001$), and equitability and Fisher's α decreased significantly (for E_k: $F_{33} = 24.89$, $r^2 = 0.39$, $p < 0.0001$; for α_k: $F_{33} = 21.06$, $r^2 = 0.39$, $p < 0.0001$).

Thus all indices indicated a decrease of species diversity when moving away from the hedge: the farther from the hedge, the lower the number of species present in the community, and the stronger the dominance of the most abundant species *Pterostichus melanarius*.

Species distribution patterns as a function of the distance from the centre of the hedge

The total capture of each species was analysed as a function of the distance from the centre of the hedge, which allowed classification of species in four groups according to its spatial distribution pattern (Table 5). Differences in distribution patterns among species generate changes in species relative abundances as a function of distance, which explain the previously observed significant changes in diversity with distance.

We found a significant relationship between habitat preferences found in the literature (den Boer 1977, Thiele 1977, Lindroth 1992) (Table 2) and our classification in distribution groups (G-test: $G = 6.38$, 2 DF, $p < 0.05$). Surprisingly enough, species preferring open habitats were mainly classified as "hedge-restricted" or "hedge-preferring", whereas ubiquitous species were rather indifferent to the presence of the hedge. As noticed in Study site, the hedge cannot be considered as a closed habitat; the major differences between this habitat and the adjacent cultivated crop are the lack of disturbance and the more complex physical structure of vegetation. For ubiquitous species these differences do not seem to be sufficient to induce any habitat preference, whereas species preferring open habitats are likely to be influenced by those micro-scale modifications. Species spatial distribution patterns did not depend on other ecological characteristics like reproductive period, size and dispersion power (G-tests not significant).

Absolute densities estimated within enclosures generally confirmed the results previously found on species distribution patterns (Table 6). However, these results were variable, with high standard deviations. Hence we performed non-parametric tests only for the two dominant species.

Table 2. Ecological characteristics, total captures, and relative abundances of species encountered in the whole area (den Boer 1977, Thiele 1977, Lindroth 1992). Reproductive period: A = autumn breeders (hibernating as larvae); S = spring breeders (hibernating as adults); ? = unknown.

Species name	Code	Habitat preference	Reproductive period	Size (mm)	Dispersion power	Total capture N_i	Relative abundance $100{*}p_i$
Common species							
Pterostichus melanarius	pternel	open	A	12–18	uncertain	14 305	51.944
Pterostichus cupreus	ptecup	open	S	11–13.4	high	6 583	23.905
Harpalus rufipes	harruf	open	A	10–16.7	high	1 613	5.857
Harpalus aeneus	haraen	open	S	8.5–12	high	1 561	5.667
Trechus obtusus	treobt	eurytopic	A	3.6–4.1	uncertain	668	2.426
Bembidion obtusum	bemobt	open	S	2.8–3.5	uncertain	487	1.767
Agonum dorsale	agodor	open	S	6–8.2	uncertain	438	1.590
Notiophilus biguttatus	notbig	closed	S	5–6	high	363	1.319
Amara similata	amasim	open	S	7.8–10	uncertain	318	1.155
Bembidion lampros	bemlam	eurytopic	S	3.4–4.4	high	301	1.092
Scybalicus oblongiusculus	scyobl	open	?	11–13	?	286	1.040
Harpalus dimidiatus	hardim	open	?	12–14	?	153	0.556
Nebria brevicollis	nebbre	eurytopic	A	10–14	uncertain	113	0.410
Diachromus germanus	diager	open	?	7.5–10	?	77	0.279
Microlestes maurus	micmau	open	S	2.5–2.8	uncertain	47	0.169
Badister sodalis	badsod	eurytopic	S	3.9–4.8	low	44	0.158
Notiophilus aquaticus	notaqu	eurytopic	?	4.5–6	uncertain	32	0.115
Amara apricaria	amaapr	open	A	6.5–9	high	30	0.110
Rare species							
Trechus quadristriatus	trequa	open	A	3.6–4	high	23	0.085
Agonum muelleri	agomue	open	S	7.2–9.5	uncertain	21	0.075
Amara consularis	amacon	open	A	8–9.4	uncertain	20	0.073
Calathus melanocephalus	calmel	eurytopic	A	6–8.8	low	15	0.055
Amara aulica	amaaul	open	A	11–14.3	uncertain	14	0.051
Loricera pilicornis	lorpil	eurytopic	A	6–8.5	high	10	0.034
Leistus ferrugineus	leifer	open	A	6.5–8	low	9	0.034
Asaphidion flavipes	asafla	eurytopic	S	3.9–4.7	high	4	0.015
Notiophilus germinyi	notger	open	A	4.5–5.5	uncertain		0.007
Amara aenea	amaaen	open	S	6.2–8.8	high	1	0.005
Amara plebeja	amaple	open	S	6.3–7.8	high	1	0.004
Bembidion aeneum	bemaen	open	S	3.4–4.5	uncertain	1	0.004
Total						27 539	100

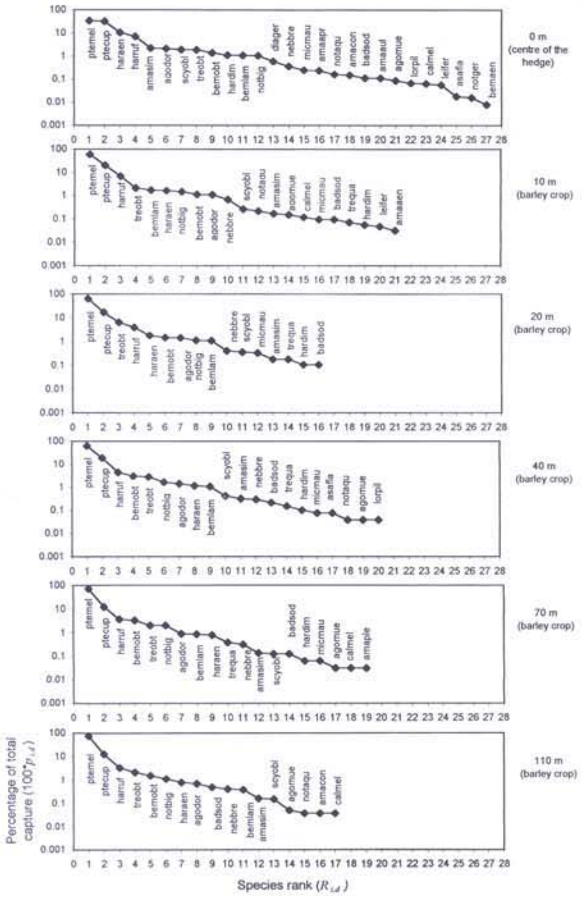

Fig. 2. Dominance–diversity curves at each distance. (Species code: see Table 2).

Pterostichus melanarius was classified as one of the four (rare species included) "crop-preferring species" (Table 5: ANOVA with factor = site significant, $F_{33} = 15.9$, $p = 0.0003$, $r^2 = 0.325$). However, the increase of its total capture with distance was weak (Table 5: linear regression significant with slope $b = 0.005$, $F_{33} = 5.7$, $p = 0.02$, $r^2 = 0.148$). For this species, absolute densities measured in fenced traps (Table 6) tended to decrease between the centre of the hedge (0 m) and the middle of the crop (110 m), but the difference in density between the two extreme distances was not significant (Kruskall-Wallis test: $H/D = 1.025$, 1 DF, $p > 0.05$). Thus we concluded that this species exhibited a weak preference for cultivated areas.

On the contrary, *Pterostichus cupreus* belonged to a wider group of 17 (rare species included) "hedge-preferring species" whose total capture decreased significantly with distance (Table 5). For this species, the decrease of absolute densities between 0 and 110 m was significant (Kruskall-Wallis test: $H/D = 4.797$, 1 DF, $p < 0.05$).

Finally, when taking into account rare species, there were as many species restricted in the hedge or preferring it, as species preferring the crop or indifferent to the presence of the hedge (number of "hedge-preferring" + "hedge-restricted" species = 19, number of "hedge-indifferent" + "crop-preferring" species = 11, $\chi^2 = 2.13$, 1 DF, $p > 0.05$).

Discussion

The main objective of this study was to assess the influence of hedges on the diversity of ground-beetle communities one year after planting the hedges in an intensive agricultural landscape. Several diversity indices were used, and all of them showed that diversity decreased with increasing distance from the centre of the hedge because of the habitat preferences of a large group of species for the hedges.

Kendall's coefficient of rank correlation was used to compare carabid communities at different distances; this coefficient measures β-diversity (Whittaker 1972, Southwood 1978), that is to say, the level of similarity between communities. It clearly appeared that the difference between species ranks in communities decreased with distance from the centre of the hedge. Duelli (1990) found similar results using Sørensen's index of similarity in a study on movements of arthropods between semi-natural habitats and cultivated fields; dissimilarity was greatest close to the wheat field grassy edge. The modification of the level of dissimilarity in our case was gradual, indicating that there was a mutual influence between hedge and crop.

We used the indices S, C, E and α to describe α-diversity, that is to say, the local diversity within a community (Whittaker 1972, Southwood 1978). S, C and E are part of "Hill's family" of diversity indices. They essentially differ in the way they take rare species into account (Hill 1972). S, which measures species richness within a sample of the community, is strongly affected by the presence of rare species. C expresses the distribution of relative abundances between the dominant species, whereas E takes into account the whole community. The fact that they are related allows focusing on different aspects of species abundance distributions. In our case, the joint use of S, C and E was very informative: we learnt 1) that rare species were lost when moving away from the hedge (significant decrease of S), but also 2) that distance affects the relative abundances of dominant species, with *Pterostichus melanarius* dominating more and more far from the hedge (significant increase of C), and finally 3) that the relative abundances in the community as a whole become less evenly distributed as one moves away from the hedge (significant decrease of E).

The index α is part of another group of indices that describe theoretical species abundance distributions underlying dominance-diversity curves. Here these curves approached the logarithmic series, so that α was an adequate measure of diversity.

Table 3. Mean catch number per trap and relative abundance of common species at each distance from the centre of the hedge. (Species codes: see Table 2).

Species	Distance from the centre of the hedge (m)											
	0 m		10 m		20 m		40 m		70 m		110 m	
	$N_{i,0}$	$100*p_{i,0}$	$N_{i,10}$	$100*p_{i,10}$	$N_{i,20}$	$100*p_{i,20}$	$N_{i,40}$	$100*p_{i,40}$	$N_{i,70}$	$100*p_{i,70}$	$N_{i,110}$	$100*p_{i,110}$
ptemel	289.89	34.31	169.64	60.88	92.5	63.60	111.62	64.07	154.47	72.51	135.51	75.41
ptecup	273.47	32.37	57.84	20.76	24.89	17.11	32.40	18.60	26.82	12.59	23.47	13.06
harruf	60.41	7.15	19.56	7.02	5.87	4.03	7.78	4.46	7.82	3.67	6.09	3.39
haraen	91.71	10.85	4.58	1.64	2.64	1.82	2.02	1.16	1.67	0.78	1.42	0.79
treobt	15.96	1.89	5.98	2.15	9.51	6.54	4.87	2.79	4.33	2.03	3.89	2.16
bemobt	11.86	1.40	3.20	1.15	2.18	1.50	5.27	3.02	7.11	3.34	2.82	1.57
agodor	18.31	2.17	3.13	1.12	2.13	1.47	2.47	1.42	1.89	0.89	1.27	0.70
notbig	9.10	1.08	4.22	1.52	1.67	1.15	2.84	1.63	4.33	2.03	2.04	1.14
amasim	19.34	2.29	0.47	0.17	0.27	0.18	0.56	0.32	0.29	0.14	0.29	0.16
bemlam	9.20	1.09	4.89	1.75	1.60	1.10	1.87	1.07	1.80	0.84	0.69	0.38
scyobl	16.56	1.96	0.73	0.26	0.53	0.37	0.73	0.42	0.27	0.13	0.27	0.15
hardim	9.58	1.13	0.16	0.06	0.16	0.11	0.18	0.10	0.13	0.06	0	0
nebbre	3.06	0.36	1.93	0.69	0.60	0.41	0.51	0.29	0.67	0.31	0.76	0.42
diager	5.12	0.61	0	0	0	0	0	0	0	0	0	0
micmau	2.08	0.25	0.27	0.10	0.49	0.34	0.13	0.08	0.13	0.06	0	0
badsod	0.95	0.11	0.27	0.10	0.16	0.11	0.38	0.22	0.27	0.13	0.89	0.42
notaqu	1.38	0.16	0.60	0.22	0	0	0.07	0.04	0	0	0.07	0.04
amaapr	2.02	0.24	0	0	0	0	0	0	0	0	0	0

Each of these indices possesses advantages and weaknesses in describing the structure and diversity of a community, depending on the properties considered (theoretical, statistical, mathematical, or biological properties) (Whittaker 1972, Southwood 1978, Taylor 1978, Kvalseth 1991). Consequently, it is more interesting to use several of them together because of their complementarity.

In our case the four indices provided concordant results, indicating a decrease in diversity with increasing distance from the hedge; a smaller number of species dominated the communities more and more when moving away from the hedge. Lewis (1969) also reported a decrease in the diversity of the arthropod communities as a function of the distance from a hedge using the single index α.

These changes in species diversity could be due to two kinds of factors. First, there could be an arrival of new species from the surroundings, adding new species in some places and thus modifying relative abundances from place to place. Second, without immigration, species already present in the area could reorganise spatially, some being attracted in a particular place, thus generating corresponding changes in community diversity.

The first hypothesis is unlikely to be verified in our case. Twenty-nine of the 30 species censused in the area (hedge and crop) were species of open habitats or very eurytopic species (Jeannel 1941, 1942, Lindroth 1974, 1992). The hedges were young (planted only one year before the study) and composed of shrubs that were not higher than 2 m. Therefore they cannot be regarded as closed habitats like forests, as already noticed earlier. Moreover they do not form corridors between the cultivated area and surrounding woodland; there is thus a weak probability of recolonisation by species of closed habitats from those surrounding forest areas (Burel 1989). However, *Notiophilus biguttatus*, a species known to prefer closed habitats, is present in the hedge and in the crop. According to den Boer (1977), this species has a high dispersal power.

Although hedges are not closed habitats, they have a different vegetation structure and are not exposed to disturbances. These small-scale features are likely to have a profound short-term effect on species that were already present in the cultivated area before their plantation; some species colonised the hedges, others avoided them depending on their micro-habitat preferences. As noticed in Species distribution patterns as a function of the distance from the centre of the hedge, species preferring open habitats seemed to be more sensitive to these small-scale modifications. We do not have data on the temporal changes in community structure over several years. But Thomas (1990) described such a change in the composition of predatory species in new "island" habitats installed in the middle of agricultural plots; the proportion of species using such island habitats as overwintering sites increased from the

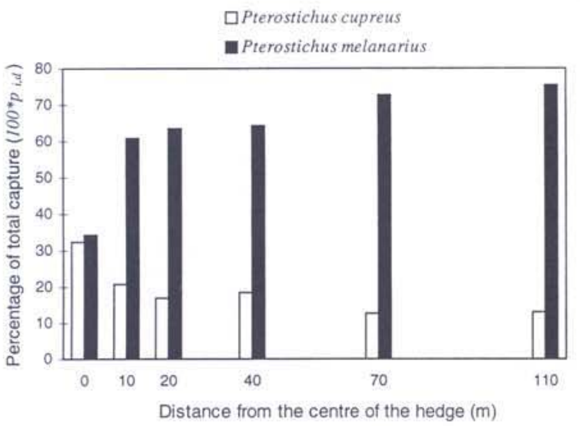

Fig. 3. Dominance, as measured by the percentage in the total capture at each distance ($100^*p_{i,d}$), of *Pterostichus melanarius* and *Pterostichus cupreus* as a function of distance from the centre of the hedge.

first to the third winter. Studying grassy strips planted in a cereal crop, Nentwig (1988) similarly found that the number of arthropod species increased from year to year, generating an increase in the ratio of the number of predatory and parasitic arthropod species to the number of phytophagous arthropod species.

We found that the various species had different spatial distribution patterns as a function of the site or the distance from the centre of the hedge. Our classification of species in four "distribution groups" is consistent with general knowledge of the biology of those species (Thiele 1977, Lindroth 1992), as well as with other studies on their behaviour in cultivated areas and field margins. In particular, our results concerning the high abundances of the two dominant species *Pterostichus melanarius* and *Pterostichus cupreus* and their different spatial distributions in the presence of undisturbed field margins are in agreement with several publications (Coombes and Sotherton 1986, Wallin 1987, Thomas 1990, Lys 1992), which also reported that *Pterostichus melanarius* was slightly favoured by the crop or at least indifferent to the presence of the hedge, and that *Pterostichus cupreus* preferred the hedge.

Thus, the hypothesis of a spatial redistribution of species already present in the area due to micro-habitat preferences seems most likely.

Table 4. Kendall's coefficient of rank correlation (τ) between communities at adjacent distances.

Site	All species τ	Without rare species τ
0m/10m	0.059	0.55
10m/20m	0.75	0.80
20m/40m	0.86	0.79
40m/70m	0.85	0.92
70m/110m	0.74	0.84

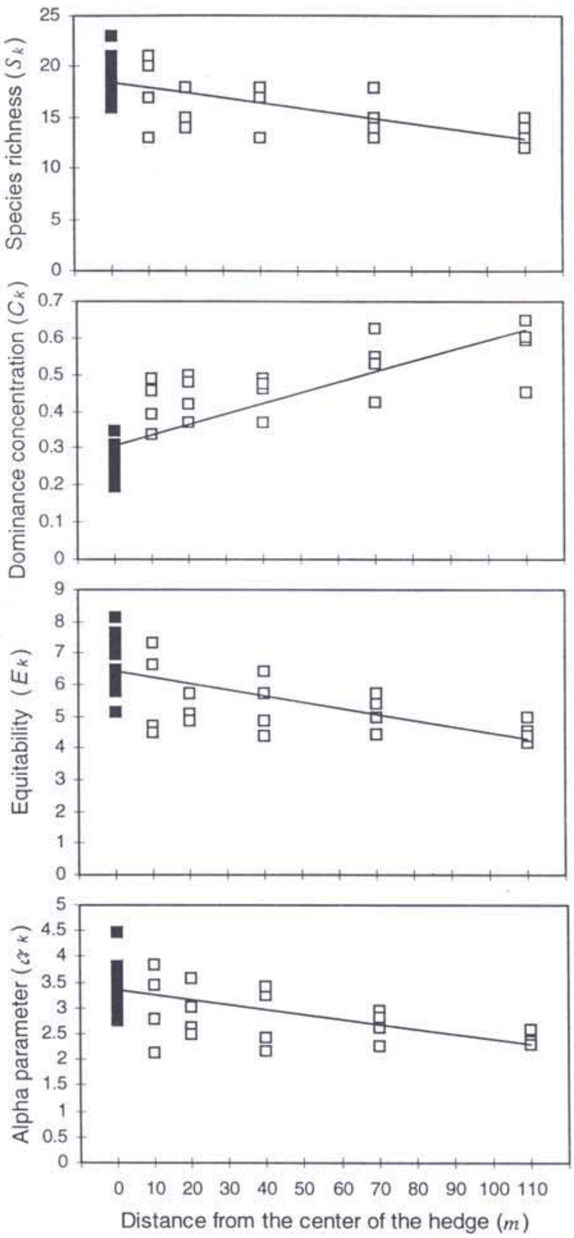

Fig. 4. Changes in diversity as a function of distance from the centre of the hedge (traps situated in the hedge: ■; traps situated in the adjacent crop: □). Linear regressions as a function of distance, *d*: species richness $S_k = -0.05^*d + 18.44$ ($F = 24.54$, $DF = 33$, $p = 0.0001$, $r^2 = 0.43$); dominance concentration $C_k = 0.003^*d + 0.305$ ($F = 66.09$, $DF = 33$, $p = 0.0001$, $r^2 = 0.67$); equitability $E_k = -0.019^*d + 6.448$ ($F = 24.89$, $DF = 33$, $p = 0.0001$, $r^2 = 0.43$); Fisher et al.'s alpha $\alpha_k = -0.009^*d + 3.364$ ($F = 21.06$, $DF = 33$, $p = 0.0001$, $r^2 = 0.39$).

What are the factors responsible for the habitat preferences of the various species? This question raises the controversial issue of habitat choice. One factor that is often mentioned to explain habitat choice is preference for an overwintering site (Sotherton 1984, 1985, Desender et al. 1989). Sotherton classified cara bids in a cultivated area into "boundary species" and "open-field species" according to their overwintering preferences. These preferences for overwintering sites seems to be mostly determined by abiotic factors such as temperature, humidity or sod layer (Desender et al. 1981, 1989). Our own classification is consistent with differences in overwintering; for example, most of Sotherton's "boundary species" were classified as "hedge-restricted" or "hedge-preferring" species, whereas Sotherton's "open-field species" were included in the other groups of our classification. Thus the choice of overwintering sites may be related to the spatial distribution of species during the rest of the season.

However, several authors demonstrated the existence of movements from one site to another during the activity period (Coombes and Sotherton 1986, Duelli 1990, Lys and Nentwig 1991, Lys 1992). The quality of overwintering sites should not be responsible for those exchanges from spring to autumn. Several other factors could have an influence: field margins could play the role of refuge in case of intense disturbances in the crop (Sotherton et al. 1981, Desender et al. 1989, Chiverton and Sotherton 1991, Hassal et al. 1992) or could offer reproduction sites (Zangger 1994). Abiotic factors, however, do not seem to play an important role. Duelli (1990) found that vegetation structure had a weak influence on the spatial distribution of species, except for some species with a particular biology (like the plant climber *Demetrias atricapillus*, or some *Amara* species that eat crucifers). Hawthorne and Hassal (1995) also showed that temperature, humidity and vertical diversity of plant cover are not important factors for the distribution of species, and that the most important factor was food availability. Loreau (1986) and Guillemain et al. (1997) suggested the same conclusion in forest ecosystems.

Conclusion

This study illustrates the importance, for ground beetles, of undisturbed habitats such as hedges in the middle of large and open cultivated areas. On a relatively short time scale regular changes in the diversity and structure of communities were observed as a function of the distance from the centre of the hedge. These changes appeared to be strong even though the hedge was only one year old.

Changes in community structure appeared to be due to differences in micro-habitat preferences of the various species during the period considered (from spring to autumn). The underlying mechanism seems to be dynamic exchanges of individuals between habitats, with direction and intensity differing among species.

Table 5. Distribution patterns of common species as a function of distance from the centre of the hedge. We performed linear regressions as a function of distance from the hedge, or one-way analysis of variance with 1 factor (site: hedge/crop). Only significant results are shown here. Bold results outlined the best model according to the r^2 value. According to the results species were classified in four spatial distribution groups: HR = "hedge-restricted species", HP = "hedge-preferring species", HI = "hedge-indifferent species", CP = "crop-preferring species". (Species codes: see Table 2).

Species	Model (dependant variable: $\ln(N_{i,k}+1)$) ANOVA 1 factor: site (hedge/crop)					Linear regression $\ln(N_{i,k}+1) = b + a^*distance$					Distribution group
	mean value of $\ln(N_{i,k}+1)$		F_{33}	p	r^2	b	a	F_{33}	p	r^2	
	in hedge	in crop									
diager	**1.5**	**0**	**55.2**	**0.0001**	**0.626**	−0.013	1.01	12.9	0.0011	0.28	HR
amaarp	**0.6**	**0**	**9.1**	**0.0048**	**0.217:**						HR
ptecup	**5.6**	**4.7**	**36.8**	**0.0001**	**0.527**	−0.012	5.412	34	0.0001	0.507	HP
harruf	4.1	3.3	10.5	0.0027	*0.242*	**−0.011**	**3.964**	**16**	**0.0003**	**0.326**	HP
haraen	**4.5**	**2.1**	**202.7**	**0.0001**	**0.860**						HP
agodor	2.8	2	11.2	0.002	0.254	**−0.01**	**2.633**	**11.9**	**0.0016**	**0.264**	HP
amasim	**2.2**	**0.7**	**21.8**	**0.0001**	**0.397**	−0.014	1.783	8.2	0.0074	0.198	HP
bemlam						**−0.008**	**2.265**	**7**	**0.0126**	**0.174**	HP
scyobl	**2.7**	**0.8**	**73.1**	**0.0001**	**0.689**	−0.021	2.250	31.3	0.0001	0.487	HP
hardim	**2.3**	**0.3**	**213.8**	**0.0001**	**0.866**	−0.02	1.725	32.6	0.0001	0.497	HP
micmau	0.9	0.4	7.88	0.008	0.193	**−0.009**	**0.88**	**12.2**	**0.0014**	**0.27**	HP
notaqu	0.7	0.3	44	0044	0.117	**−0.007**	**0.65**	**7.3**	**0.0109**	**0.18**	HP
bemobt											HI
notbig											HI
nebbre											HI
badsod											HI
ptemel	**5.6**	**6.1**	**15.9**	**0.0003**	**0.325**	0.005	5.78	5.7	0.0226	0.148	CP
treobt	**2.6**	**3**	**4.2**	**0.047**	**0.114**						CP

Table 6. Absolute population densities of ground beetles estimated by fenced pitfall traps in the hedge and in the centre of barley crop in June 1996. Kruskall-Wallis non-parametric tests were performed only for *Pterostichus melanarius* and *Pterostichus cupreus*. (Species code: see Table 2).

Species	Site (distance from the hedge) Hedge (0 m)		Crop (110 m)		Kruskall-Wallis test		
	mean	SD	mean	SD	H/D	DF	p
ptemel	17.42	13.85	9	9.64	1.025	1	>0.05
ptecup	12.92	14.70	1.33	2.31	4.797**	1	<0.05
haraen	11.83	7.52	0	0			
amasim	3.17	7.16	0	0			
harruf	2.00	2.04	0.33	0.58			
agodor	1.58	2.50	0	0			
bemlam	1.50	1.62	1	1			
diager	1.25	1.36	0	0			
micmau	0.58	1.00	0	0			
hardim	0.50	1.00	0	0			
badsod	0.42	0.90	0	0			
treobt	0.33	0.65	0.33	0.58			
notbig	0.25	0.45	0	0			
agomue	0.08	0.29	0	0			
notger	0.08	0.29	0	0			
scyobl	0.08	0.29	0	0			

One hypothesis to explain this differential habitat preferences could be the distribution of food resources among habitats and the different reactions of species to food availability.

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References

Alderweireldt, M. and Desender, K. 1994. Belgian carabidological research on high-input agricultural fields and pastures: a review. – In: Desender, K. et al. (eds), Carabid beetles: Ecology and evolution. Kluwer Academic Publ., pp. 409–415.

Baars, M. A. 1979a. Catches in pitfall traps in relation to mean densities of Carabid beetles. – Oecologia 41: 25–46.

Baars, M. A. 1979b. Patterns of movements of radioactive Carabid beetles. – Oecologia 44: 125–140.

Barbault, R. 1992. Des baleines, des bactéries et des hommes.– Odile Jacob, Paris.

Burel, F. 1989. Landscape structure effects on Carabid beetle spatial patterns in western France. – Landscape Ecol. 2: 215–226.

Carcamo, H. A. and Spence, J. R. 1994. Crop types effects on the activity of ground beetles (Coleoptera, Carabidae). – Environ. Entomol. 23: 684–692.

Chiverton, P. A. and Sotherton, N. W. 1991. The effects on beneficial arthropods of the exclusion of herbicides from cereal crop edges. – J. Appl. Ecol. 28: 1027–1039.

Coombes, D. S. and Sotherton, N. W. 1986. The dispersal and distribution of polyphagous predatory Coleoptera in cereals. – Ann. Appl. Biol. 108: 461–474.

den Boer, P. J. 1977. Dispersal power and survival: Carabid beetles in a cultivated countryside. – Misc. Pap. L. H. Wageningen 14: 1–190.

Desender, K. and Maelfait, J. P. 1986. Pitfall trapping within enclosures: a method for estimating relationship between the abundances of coexisting carabid species (Col, Carabidae). – Holarct. Ecol. 9: 245–250.

Desender., K. and Pollet, M. 1988. Sampling pasture carabids with pitfalls: evaluation of species richness and precision. – Med. Fac. Landbouww. Rijksuniv. Gent 53: 1109–1117.

Desender, K. et al. 1981. Ecological and faunal studies on *Coleoptera* in agricultural land. 1: Seasonal occurrence of *Carabidae* in the grassy edge of a pasture. – Pedobiologia 22: 379–384.

Desender, K., Alderweireldt, M. and Pollet, M. 1989. Field edges and their importance for polyphagous predatory arthropods. – Med. Fac. Landbouww. Rijksuniv. Gent 54: 823–833.

Duelli, P. 1990. Population movements of Arthropods between natural and cultivated areas. – Biol. Conserv. 54: 193–207.

Fisher, R. A., Corbet, A. S. and Williams, C. B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. – J. Anim. Ecol. 12: 42–58.

Greenslade, P. J. M. 1964. Pitfall trapping as a method for studying populations of Carabidae (Coleoptera). – J. Anim. Ecol. 33: 301–310.

Guillemain, M., Loreau, M. and Daufresne, T. 1997. Relationships between the regional distribution of carabid beetles (Coleoptera, Carabidae) and their abundance of their potential prey. – Acta Oecol. 18: 465–483.

Hassal, M. et al. 1992. Effects of headland management on invertebrates communities in cereal fields. – Agric. Ecosyst. Environ. 40: 155–178.

Hawthorne, A. and Hassal, M. 1995. The effect of cereal headland treatments on carabid communities. – In: Toft, S. and Riedel, W. (eds), Arthropod natural enemies in arable land I. Density, spatial heterogeneity and dispersal. – Acta Jutlandica, pp. 185–198

Hill, M. O. 1972. Diversity and evenness: a unifying notation and its consequences. – Ecology 54: 427–432.

Jeannel, R. 1941. Faune de France No. 39: Coléoptères carabiques (I). – Lib. Fac. Sci., Paris.

Jeannel, R. 1942. Faune de France No. 40: Coléoptères carabiques (II). – Lib. Fac. Sci., Paris.

Kvalseth, T. O. 1991. Note on biological diversity, evenness, and homogeneity measures. – Oikos 62: 123–127.

Lewis, T. 1969. The diversity of the insect fauna in a hedgerow and neighbouring fields. – J. Appl. Ecol. 6: 453–458.

Lindroth, C. H. 1974. Handbooks for the identification of British insects. IV, part 2: Coleoptera, Carabidae. – Royal Entomol. Soc. London.

Lindroth, C. H. 1992. Ground beetles (Carabidae) of Fennoscandia, a zoogeographic study. Part 1: Specific

knowledge regarding the species. – Smithsonian Lib. Nat. Sci. Found.
Loreau, M. 1984. Composition et structure de trois peuplements forestiers de Carabides. – Acad. Roy. Belg., Bull. Cla. Sciences: 125–160.
Loreau, M. 1986. Niche differentiation and community organization in forest carabid beetles. – In: den Boer, P. J. et al. (eds), Carabid beetles: Their adaptations and dynamics. Gustav Fisher, pp. 465–487.
Loreau, M. 1992. Species abundance patterns and the structure of ground-beetle communities. – Ann. Zool. Fennici 28: 49–56.
Lys, J. A. 1992. Augmentation of beneficial arthropods by strip-management. 4: Surface activity, movements and activity density of abundant Carabid beetles in a cereal field. – Oecologia 92: 373–382.
Lys, J. A. 1994. The positive influence of strip-management on ground beetles: increase, migration and overwintering. – In: Desender, K. et al. (eds), Carabid beetles: Ecology and evolution. Kluwer Academic Publ., pp. 451–455.
Lys, J. A. and Nentwig, W. 1991. Surface activity of Carabid beetles inhabiting cereal fields: seasonal activity and the influence of farming operations on five abundant species. – Pedobiologia 35: 129–138.
Nentwig, W. 1988. Augmentation of beneficial arthropods by strip management. 1: Succession of predacious arthropods and long-term change in the ratio of phytophagous and predacious arthropods in a meadow. – Oecologia 7: 597–606.
Pollard, E. 1968a. Hedges 2. The effect of the removal of the bottom flora of a hawthorn hedgerow on the fauna of the hawthorn. – J. Appl. Ecol. 5: 109–123.
Pollard, E. 1968b. Hedges 3. The effect of removal of the bottom flora of a hawthorn hedgerow on the Carabidae of the hedge bottom. – J. Appl. Ecol. 5: 125–139.
Pollet, M. and Desender, K. 1985. Adult and larval feeding ecology in *Pterostichus melanarius* Ill. (Coleoptera, Carabidae). – Med. Fac. Landbouw. Rijksuniv. Gent 50: 581–594.
Pollet, M. and Desender, K. 1986. Prey selection in Carabid beetles (Coleoptera, Carabidae): Are diel activity patterns of predator and prey synchronized? – Med. Fac. Landbouw. Rijksuniv. Gent 51: 957–971.
Sanderson, R. A. 1994. Carabidae and cereals: a multivariate approach. – In: Desender, K. et al. (eds), Carabid beetles: Ecology and evolution. Kluwer Academic Publ., pp. 457–463.
Simpson, E. H. 1949. Measurement of diversity. – Nature 163: 688.
Sotherton, N. W. 1984. The distribution and abundance of predatory arthropods overwintering on farmland. – Ann. Appl. Biol. 105: 423–429.
Sotherton, N. W. 1985. The distribution and abundance of predatory Coleoptera overwintering in field boundaries. – Ann. Appl. Biol. 106: 17–21.
Sotherton, N. W. et al. 1981. Aspects of hedge management and their effects on hedgerow fauna. – Sonderdruck aus Bd 92: 425–432.
Southwood, T. R. E. 1978. Ecological methods. – Chapman and Hall.
Stassart, P. and Gregoire-Wibo, C. 1983. Influence du travail du sol sur les populations de Carabides en grandes cultures, résultats préliminaires. – Med. Fac. Landbouw. Rijksuniv. Gent 48: 465–474.
Sunderland, K. D. and Vickerman, G. P. 1980. Aphid feeding by some polyphagous predators in relation to aphid density in cereal fields. – J. Appl. Ecol. 17: 389–396.
Taylor, L. R. 1978. Bates, Williams, Hutchinson: a variety of diversities. – In: Morand, L. A. and Waloff, N. (eds), Symp. Roy. Entomol. Soc. No. 9. Blackwell, pp. 1–18.
Thiele, H. U. 1977. Carabid beetles in their environments. – Springer.
Thomas, M. B. 1990. The role of man-made grassy habitats in enhancing Carabid populations in arable land. – In: Stork, N. E. (ed.), The role of ground beetles in ecological and environmental studies. Intercept, pp. 77–85.
Thomas, M. B., Wratten, S. D. and Sotherton, N. W. 1992. Creation of 'island' habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. – J. Appl. Ecol. 29: 524–531.
Wallin, H. 1987. Dispersal and migration of carabid beetles inhabiting cereal fields. – Acta Phytopath. Entomol. Hung. 22: 449–453.
Whittaker, R. H. 1972. Evolution and measurement of species diversity. – Taxon 21: 213–251.
Zangger, A. 1994. The positive influence of strip-management on carabid beetles in a cereal field: accessibility of food and reproduction in *Poecilus cupreus*. – In: Desender, K. et al. (eds), Carabid beetles: Ecology and evolution. Kluwer Academic Publ., pp. 469–472.