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SPATIAL DISTRIBUTION OF CARABIDS ALONG GRASS-FOREST TRANSECTS

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Spatial distribution of ground-beetles and associations between carabids and environmental variables were studied in grass-forest transects in the Aggtelek National Park in Hungary. The carabid assemblages of the grass, the forest edge and the forest interior can be separated from each other by principal coordinates analysis, suggesting that all habitats have a characteristic and distinct species composition. The collected carabid species can be divided into five groups by indicator species analysis: (1) habitat generalists, (2) forest generalists, (3) species of the grass, (4) forest edge species, and (5) forest specialists. Distributions of the eighteen most frequent carabids were generally aggregated. There were significant correlations between the carabid abundance and the following abiotic factors: relative cover of the leaf litter, the herbs, the shrubs, and the canopy layer. Biotic factors, like the abundance of the carabids' prey, and the occurrence of other carabids were also correlated significantly with the distribution of particular species at the studied spatial scale. For the eighteen most frequent species we found 7 significant positive and 4 significant negative correlations of the abundance patterns. For two species (*Molops piceus* (PANZER, 1793) and *Pterostichus burmeisteri* HEER, 1841), which are of similar size, spatial pattern and seasonal activity, we found significant negative interaction suggesting interspecific competition between them. The results stress the importance of an integration of biotic and abiotic factors in carabid ecology, and also provide an empirical approach for understanding spatial distribution of carabids.

Key words: forest edge, aggregation indices, indicator species, community organisation

INTRODUCTION

There is a current debate whether the spatial distribution of a species in a community is determined by their autecological characteristics or by community organisation (NIEMELÄ & SPENCE 1994, LÖVEI & SUNDERLAND 1996).

Quantitative knowledge about habitat associations and spatial pattern of carabids in Hungary is relatively poor. Further studies, based on comparisons among habitat types are necessary to demonstrate more precisely the habitat requirements of carabid species. This knowledge is essential to assess the relative importance of environmental factors and species interactions in structuring communities in different habitats. Knowledge of exact habitat requirements is also needed for the purposes of nature conservation and conservation biology, in order to identify potentially rare habitats and species, and to assess their vulnerability and needs of protection (NIEMELÄ & HALME 1992).

Carabid beetles, like most organisms, are generally non-randomly distributed on several spatial scales (LUFF 1986, BÁLDI & ÁDÁM 1991, NIEMELÄ & SPENCE 1994, NIEMELÄ *et al.* 1990). This non-random carabid occurrence is determined by the heterogeneous distribution of abiotic conditions and resources (NIEMELÄ *et al.* 1992*a*). However, there are several scales of environmental heterogeneity, and species responses may be determined by different factors at various levels of environmental pattern (NIEMELÄ *et al.* 1992*b*). For example, on the regional scale the distribution of a particular carabid species may be determined mainly by geographic, climatic and historical factors (HENGEVELD 1987, PENEV & TURIN 1994, PENEV 1996). But on a local scale, that is, in an area which is well within the dispersal radius of the species, variation in distribution across habitat types may be determined by environmental conditions and interspecific interactions (NIEMELÄ *et al.* 1985, 1996, LUFF *et al.* 1992, HALME & NIEMELÄ 1993, EYRE 1994, EYRE & LUFF 1994).

In this paper we present an analysis of ground-beetle distribution on a local scale, in grass-forest transects at the ecological scale of interacting populations (NIEMELÄ & SPENCE 1994). Our objectives were to assess the extent of variation in the distribution of carabid species, and to relate this to habitat characteristics and to spatial distribution of co-occurring carabid species.

MATERIAL AND METHODS

Study area and sampling

Sampling area was located at the Northern Mountains in the Aggtelek National Park, near the Mogyorós Peak (Haragistya). In this region oak-hornbeam forests (*Querco-Carpinetum*) and a grass association (*Polygalo majori-Brachypodietum pinnati*) are the most extensive. There are three habitat types on the research area:

(1) Grass (*Polygalo majori-Brachypodietum pinnati*), with dense herbaceous vegetation dominated by *Polygala major, Brachypodietum pinnatum, Filipendula vulgaris, Salvia pratensis, Inula hirta, Geranium sanguineum.* The litter layer, the shrubs and the canopy layer are missing in this habitat. Its area was approx. 40 ha.

(2) Forest edge, with dense herbaceous vegetation originating from the adjacent grass. The shrub layer is also dense in this habitat, consisting mainly of shrubs and saplings of the canopy trees (*Carpinus betulus, Corylus avellana* and *Prunus spinosa*). The litter layer is thick and the canopy layer is less closed than in the forest interior.

(3) Forest interior: oak-hornbeam forest, with thick litter layer, moderate herbaceous and shrub layer and with 85–95 % canopy cover. The size of the forest stand was greater than 100 ha.

Beetles were collected using unbaited pitfall traps, consisting of plastic cups (diameter 100 mm, volume 500 ml) containing ethylene-glycol as a killing-preserving solution (SPENCE & NIEMELÄ 1994). Three replicated parallel transects of pitfall traps were set across the three studied habitats, about 50–70 meters from each other. The transects were perpendicular to the forest edge.

There were 42 traps placed every 1.25 meter along each transect (14 traps per habitat). Altogether there were 3×3×14=126 traps. Trapped individuals were collected monthly (NIEMELÄ *et al.* 1990) from March to November. All carabid beetles taken in pitfall traps were identified to species using standard keys (FREUDE *et al.* 1976).

To study associations between the distribution of carabids and the environmental variables, we studied five environmental factors. We estimated the percentage cover of the leaf litter layer, the herbs, the shrubs and the canopy layer within a radius of 0.5 meter around each trap. We also studied the abundance of the potential food resources of the carabids (abundance of other animals that fell in the traps). These invertebrates (e.g. Lumbricidae, Mollusca, Isopoda, Chilopoda, Aranea, and Coleoptera larvae) are surface dwellings, therefore they can be regarded as food source for the carabids. It was proved by serological method (SERGEEVA 1994) that these invertebrates are prey for carabids.

Data analyses

Principal coordinates analysis (PCoA) using the Bray-Curtis index of similarity was used for carabid abundances to asses similarities in carabid assemblages of the traps (GAUCH 1986). We used the NuCoSA package (TÓTHMÉRÉSZ 1993).

The IndVal (Indicator Value) approach was applied to find indicator species and species assemblages characterising the grass, the forest edge and the forest interior (DUFRÊNE & LEGENDRE 1997). Its goal is to find indicator species and/or species assemblages characterising groups of samples. The novelty of this approach lies in the way that this method combines a species' relative abundance to its relative frequency of occurrence in the various groups of samples. Statistical significance of the species indicator values is evaluated using a randomisation procedure. The start of this approach consists of obtaining a classification of sample units using one of the classical methods of data analysis. We obtained a typology from the principal coordinates analysis using Bray-Curtis index of percentage similarity for carabid abundances. Based on this site typology IndVal identifies the indicator species corresponding to the various groups. Indicator species are defined as the most characteristic species of each group, found mostly in a single group of the typology and present in the majority of the sites belonging to that group. This duality, which is of ecological interest, is rarely exploited completely in such analyses; often only the distribution of abundances in the various groups is used. In these cases, species occupying only one or two sites in one habitat group and present only in that group (rare species) receive the same indicator value as species occupying all sites of that habitat group and found only in that group. There is an important difference between these two species. The first one is an asymmetrical indicator, according to the IndVal terminology, which means that its presence cannot be predicted in all sites of one habitat, but contributes to the habitat specificity. The second type of species, on the contrary, is a true symmetrical indicator: its presence contributes to the habitat specificity and one can predict its presence in all sites of the group. With the IndVal it is possible to distinguish the two types of indicator species; the species that have an indicator value greater than 55% are regarded as symmetrical indicator species (DUFRÊNE & LEGENDRE 1997).

To characterise the spatial distribution of carabids, we calculated the index of dispersion, I_δ, which is defined as the variance-to-mean ratio (DIGGLE 1983): $I_\delta = s^2/\bar{x}$, where s^2 the variance, and $\bar{x}$ the average number of individuals. An I_δ value close to one indicates a random distribution. $I_\delta > 1$ indicates aggregated, while $I_\delta < 1$ indicates regular distribution. The departure from randomness can be tested by the test statistic $ID = (n\text{-}1)s^2/\bar{x}$. It has approximately χ^2 distribution with (n-1) degrees of freedom. This approximation is reasonable provided $n > 6$ and $\bar{x} > 1$.

Multiple regression was used to study whether any of the environmental measurements and of abundance of the other carabids could be used to predict distribution of a particular carabid species. Catches of the common carabid species were compared among fourteen traps in habitats with Kruskal-Wallis nonparametric ANOVA. A Tukey-type multiple comparison was then used to compare catches from the habitat types (SOKAL & ROHLF 1981). For the eighteen most frequent species the correlation between the number of trapped individuals and the degree of their aggregation was calculated by the Pearson's product-moment correlation. Before the calculations the number of individuals was transformed by a logarithmic transformation to provide normality. The correlation between the abundance of a species and number of traps from which it was recorded was calculated by the Spearman rank correlation. The analyses were done by the SPSS-PC program.

RESULTS

A total of 40 carabid species (4339 individuals) were recorded in the pitfall traps (Table 1). The ground-beetle catch was dominated by *Abax parallelepipedus* (PILLER et MITTERPACHER, 1783). This species accounted for 35.05 % of the individuals caught.

Table 1. Two-way indicator table showing the species indicator power for the habitats. In the columns for each species the first number indicates the number of specimens, the second the number of traps wherein the species was captured, in this sample group. The IndVal(%) column indicates the species indicator value for the corresponding clustering level. ** indicates a significant ($p<0.01$), while *ns* means a not significant IndVal value.

	IndVal (%)		Grass	Forest edge	Forest interior
GRASS					
Pterostichus melanarius	79.69	**	158/34	3/3	2/2
Synuchus vivalis	70.54	**	79/30	2/2	0/0
Carabus violaceus	67.36	**	134/36	59/27	14/13
Harpalus rufipes	51.54	**	61/22	1/1	1/1
Carabus arcensis	34.29	**	48/18	21/15	3/3
Carabus montivagus	34.01	**	25/16	2/2	4/4
Pterostichus ovoideus	26.19	**	16/11	0/0	0/0
Amara convexior	8.47	**	4/4	1/1	0/0
Amara communis	7.14	**	3/3	0/0	0/0
Calathus fuscipes	7.14	**	3/3	0/0	0/0
Poecilus cupreus	7.14	**	3/3	0/0	0/0
Cicindela campestris	4.76	ns	2/2	0/0	0/0
Platynus dorsalis	2.38	ns	1/1	0/0	0/0
Agonum viridicupreum	2.38	ns	1/1	0/0	0/0
Amara aenea	2.38	ns	1/1	0/0	0/0
Amara apricaria	2.38	ns	1/1	0/0	0/0
Amara familiaris	2.38	ns	1/1	0/0	0/0
Amara lucida	2.38	ns	1/1	0/0	0/0
Anisodactylus signatus	2.38	ns	1/1	0/0	0/0

	IndVal (%)		Grass	Forest edge	Forest interior
Badister meridionalis	2.38	ns	1/1	0/0	0/0
Bembidion lampros	2.38	ns	1/1	0/0	0/0
Harpalus latus	2.38	ns	1/1	0/0	0/0
Harpalus rubripes	2.38	ns	1/1	0/0	0/0
Platyderus rufus	2.38	ns	1/1	0/0	0/0
ALL HABITATS					
Abax parallelepipedus	96.03	ns	143/37	591/42	787/42
Molops piceus	84.13	ns	94/33	126/34	169/39
Carabus convexus	31.75	ns	15/13	17/10	26/17
Carabus nemoralis	27.78	ns	15/12	14/11	19/12
Carabus intricatus	15.87	ns	8/8	9/8	4/4
Panagaeus bipustulatus	4.76	ns	3/3	3/3	0/0
FOREST EDGE					
Carabus coriaceus	28.57	**	4/4	28/18	10/8
Amara ovata	4.76	ns	0/0	2/2	0/0
Pterostichus niger	2.38	ns	0/0	1/1	0/0
FOREST EDGE AND FOREST INTERIOR					
Pterostichus oblongopunctatus	91.67	**	0/0	178/35	620/42
Pterostichus burmeisteri	86.48	**	3/3	74/33	248/41
Carabus hortensis	59.88	**	5/5	101/34	35/20
FOREST INTERIOR					
Aptinus bombarda	69.71	**	1/1	3/3	68/31
Abax ovalis	68.77	**	10/7	26/16	170/35
Abax parallelus	25.56	**	11/8	3/3	24/17
Abax carinatus	8.57	ns	2/2	2/2	6/6

There was a strong, positive correlation between the abundance of a species and the number of traps from which it was recorded (Spearman r_S=0.9923, p<0.0001, n=40). The collected 40 species can be partitioned into four distinct groups according to their frequency of occurrence among the 126 traps. Two species (*Abax parallelepipedus* (PILLER et MITTERPACHER, 1783) and *Molops piceus* (PANZER, 1793)), which were found in more than 100 traps and represented by a mean of more than 3 individuals per trap, were designated as habitat generalists and eudominant species. Five other species (*Pterostichus oblongopunctatus* (FABRICIUS, 1787), *Pterostichus burmeisteri* HEER, 1841, *Carabus violaceus* LINNAEUS, 1758, *Abax ovalis* (DUFTSCHMID, 1812) and *Carabus hortensis* LINNAEUS, 1758) that were captured in more than 55 traps with more than 1 individuals per trap, can be referred to as dominant species. Eleven other species, which were found in 20–40 traps and were represented by a mean catch of more than 0.15 individuals per trap, can be designated as subdominant species. The other 22 species that were captured in less than 20 traps with less than 0.15 individuals per trap, are rare species.

The result of the ordination (PCoA) shows that there was an arch effect suggesting a gradient in the data (GAUCH 1986), namely, the carabid assemblages change gradually from the grass towards the forest interior along the transects (Fig. 1). Carabid samples of traps from the grass, the forest edge, and the forest interior were separated from each other. The composition of the carabid samples of the forest edge was more similar to the forest interior than to the grass. It is also evident, that there is a gradient in the species composition, because the traps are arranged along an arch.

The collected carabid species can be divided into five groups by characterising the habitats by indicator species (IndVal approach; Table 1):

(1) habitat generalists that occurred numerously in all habitat types (e.g. *Abax parallelepipedus* (PILLER et MITTERPACHER, 1783), *Molops piceus* (PANZER, 1793), *Carabus convexus* FABRICIUS, 1775, *Carabus nemoralis* O. F. MÜLLER, 1764 and *Carabus intricatus* LINNAEUS, 1761);

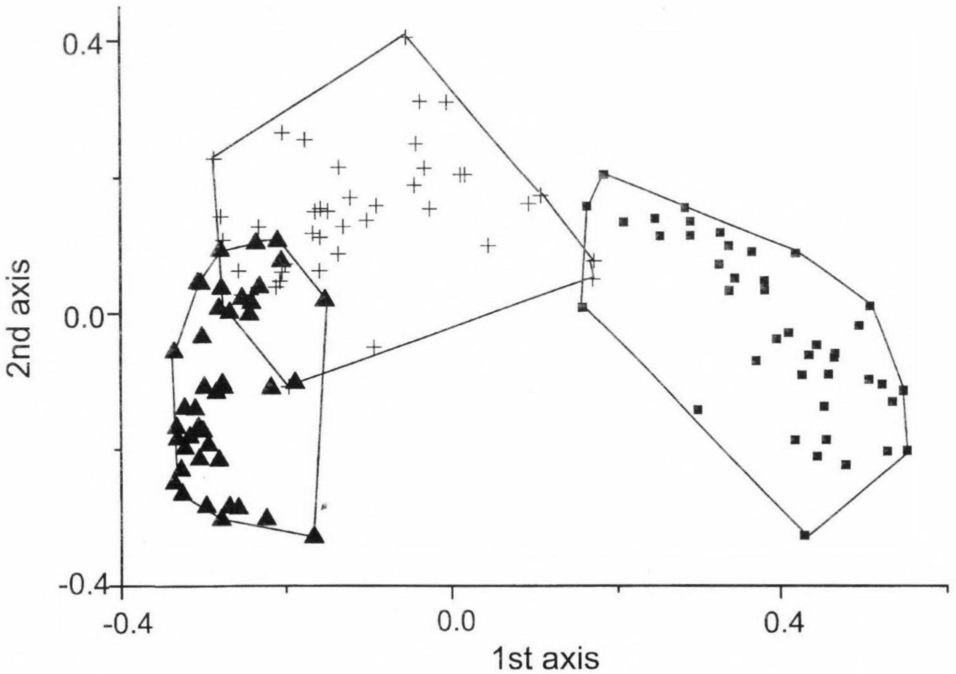

Fig. 1. Ordination of pitfall catches by principal coordinates analysis using the Bray-Curtis index of dissimilarity. ■: grass, +: forest edge, ▲: forest interior

(2) forest generalists that were recorded exclusively in the forest habitats or were the most abundant in the forest habitats (forest edge and forest interior) (e.g. *Pterostichus oblongopunctatus* (FABRICIUS, 1787), *Pterostichus burmeisteri* HEER, 1841 and *Carabus hortensis* LINNAEUS, 1758);

(3) species of open habitat that were captured exclusively in the grass or were the most abundant in the grass (e.g. *Pterostichus melanarius* (ILLIGER, 1798), *Synuchus vivalis* (PANZER, 1797), *Carabus violaceus* LINNAEUS, 1758, *Harpalus rufipes* (DE GEER, 1774), *Carabus arcensis* HERBST, 1784, *Carabus montivagus* PALLIARDI, 1825 and *Pterostichus ovoideus* (STURM, 1824));

(4) forest edge species that occurred exclusively or were the most abundant in the forest edge (e.g. *Carabus coriaceus* LINNAEUS, 1758, *Amara ovata* (FABRICIUS, 1792) and *Pterostichus niger* (SCHALLER, 1783)); and

(5) forest specialists that were recorded exclusively or numerously in the forest interior (e.g. *Aptinus bombarda* (ILLIGER, 1800), *Abax ovalis* (DUFT-

Table 2. The index of dispersion to characterise the spatial distribution of frequent carabid species in the habitats. A value close to one indicates a random distribution. A significantly greater value than one indicates aggregated spatial distribution, while a value smaller than one indicates a regular dispersion. The "-" sign shows that the statistical test is not applicable. *, ** and *** indicate significant ($p<0.05$, $p<0.01$ and $p<0.001$, respectively), while *ns* not significant departure from the randomness.

	Grass	Forest edge	Forest interior
Carabus arcensis	3.2683 ***	–	–
Carabus convexus	–	–	–
Carabus coriaceus	–	–	–
Carabus hortensis	–	1.8674 ***	–
Carabus intricatus	–	–	–
Carabus montivagus	–	–	–
Carabus nemoralis	–	–	–
Carabus violaceus	4.1624 ***	1.7383 **	–
Harpalus rufipes	2.7609 ***	–	–
Pterostichus burmeisteri	–	1.4067 *	2.0390 ***
Pterostichus melanarius	2.9799 ***	–	–
Pterostichus oblongopunctatus	–	2.7717 ***	6.9289 ***
Molops piceus	1.2600 ns	1.5285 *	1.7031 **
Abax parallelepipedus	2.7517 ***	4.4699 ***	3.7124 ***
Abax parallelus	–	–	–
Abax ovalis	–	–	2.8798 ***
Synuchus vivalis	2.6505 ***	–	–
Aptinus bombarda	–	–	1.6858 **

SCHMID, 1812), *Abax parallelus* (DUFTSCHMID, 1812) and *Abax carinatus* (DUFTSCHMID, 1812)).

The dominant and subdominant species generally showed aggregated distribution (Table 2). There was significant positive correlation between the number of individuals and the degree of aggregation for a species (r=0.6375, p=0.0033, n=19) indicating that more abundant species were more aggregated.

Sometimes, variation in carabid catches among the fourteen traps in the same habitat was greater than the variation among habitats (Table 3) indicating the importance of strong microhabitat variations controlling carabid distribution. Differences among the habitats in the number caught individuals, on the other hand, were significant for all the dominant and subdominant species, except *Carabus convexus* FABRICIUS, 1775, *Carabus nemoralis* O. F. MÜLLER, 1764 and *Carabus intricatus* LINNAEUS, 1761. This result suggests the clear habitat preference of carabid species.

Multiple regression analyses between the distribution of carabids and the environmental variables and occurrence of other carabids were significant (p<0.05) for all the dominant and subdominant species, except *Carabus intricatus* LINNAEUS, 1761 and *Carabus nemoralis* O. F. MÜLLER, 1764, while the multiple regression was marginally significant for *Abax parallelus* (DUFTSCHMID, 1812) (Table 4). Relative cover of the leaf litter was a significant negative predictor for two carabid species (*Abax parallelepipedus* (PILLER et MITTERPACHER, 1783) and *Aptinus bombarda* (ILLIGER, 1800). Cover of the herbs was a significant positive predictor for *Carabus coriaceus* LINNAEUS, 1758. Relation-

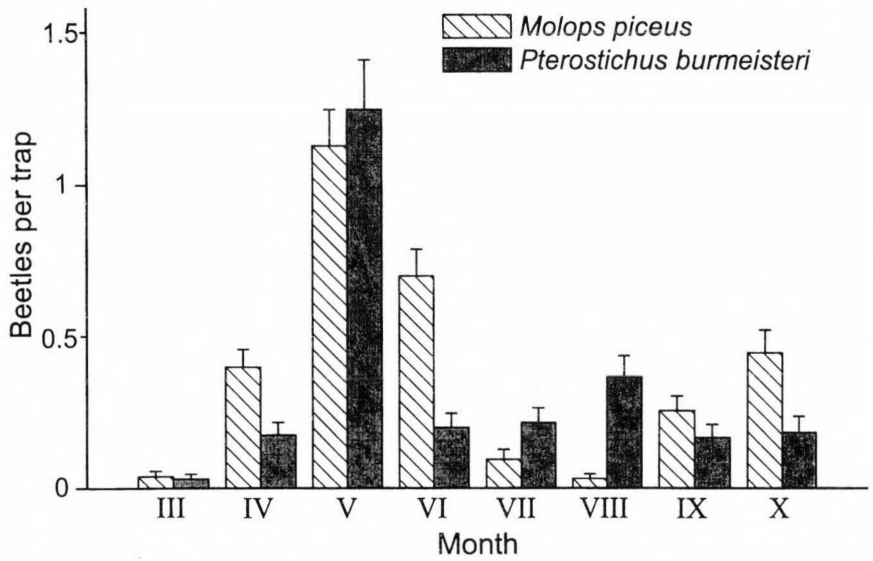

Fig. 2. Seasonal dynamics of the average number of individuals per trap of *Molops piceus* and *Pterostichus burmeisteri* based on 126 traps

ship between the cover of shrubs and the carabids' catch was significant for two species (*Abax parallelepipedus* (PILLER et MITTERPACHER, 1783) and *Molops piceus* (PANZER, 1793)). Canopy cover was a significant positive predictor for *Abax parallelepipedus* (PILLER et MITTERPACHER, 1783). Abundance of carabids' preys was a significant positive predictor for three carabids (*Carabus*

Table 3. The value of Kruskal-Wallis non-parametric ANOVA (*H*) and its statistical significance (*ns*: not significant. *: $p<0.05$. **: $p<0.01$ and ***: $p<0.001$) for the variation among the habitat types and for the variation among transects within habitat types. The result of Tukey-type multiple comparison among habitat types is given by indicating significant or not significant (=) differences; the significance level is $p<0.05$. Legends: F – forest interior, E – forest edge and G – grass.

Species	Variation among habitat types	Result of a Tukey-type comparison among habitat types	Variation among transects within the grass	Variation among transects within the forest edge	Variation among transects within the forest interior
ALL HABITATS (habitat generalists)					
Abax parallelepipedus	72.11 ***	F>E>G	9.72 **	8.99 *	13.58 **
Molops piceus	11.18 **	F=E, E=G, F>G	0.92 ns	3.51 ns	7.15 *
Carabus convexus	3.01 ns	F=E=G	3.23 ns	1.64 ns	9.68 **
Carabus nemoralis	0.15 ns	F=E=G	4.98 *	0.20 ns	4.97 *
Carabus intricatus	1.93 ns	F=E=G	1.21 ns	2.07 ns	2.15 ns
GRASS SPECIES					
Pterostichus melanarius	78.15 ***	F=E<G	1.19 ns	2.10 ns	4.10 ns
Synuchus vivalis	70.43 ***	F=E<G	15.39 ***	1.03 ns	–
Carabus violaceus	42.48 ***	F=E<G	3.40 ns	7.69 *	0.36 ns
Harpalus rufipes	45.85 ***	F=E<G	21.69 ***	2.00 ns	2.00 ns
Carabus arcensis	15.93 ***	F=E<G	18.54 ***	1.84 ns	2.10 ns
Carabus montivagus	19.85 ***	F=E<G	10.05 **	1.03 ns	8.63 *
EDGE SPECIES					
Carabus coriaceus	13.99 ***	F=G<E	2.16 ns	2.65 ns	8.04 *
FOREST INTERIOR AND EDGE SPECIES (forest generalists)					
Pterostichus oblongo-punctatus	93.44 ***	F>E>G	–	0.08 ns	24.78 ***
Pterostichus burmeisteri	87.50 ***	F>E>G	2.10 ns	0.29 ns	11.34 **
Carabus hortensis	47.36 ***	F=G<E	3.10 ns	4.14 ns	3.90 ns
FOREST INTERIOR SPECIES (forest specialists)					
Aptinus bombarda	67.70 ***	F>E=G	2.00 ns	2.10 ns	7.07 *
Abax ovalis	54.05 ***	F>E=G	6.61 *	1.26 ns	15.52 ***
Abax parallelus	14.21 ***	F>E, E=G, F=G	4.33 ns	2.10 ns	0.08 ns

Table 4. Environmental variables and other carabids contributing significantly (negatively or positively) as predictors for all the dominant and subdominant species by multiple regression analysis. Carabid species abbreviations: C arce=*Carabus arcensis*, C conv=*Carabus convexus*, C cori=*Carabus coriaceus*, C mont=*Carabus montivagus*, C nemo=*Carabus nemoralis*, H rufi=*Harpalus rufipes*, Pt bur=*Pterostichus burmeisteri*, Pt mel=*Pterostichus melanarius*, Pt obl=*Pterostichus oblongopunctatus*, Mo pic=*Molops piceus*, A ater=*Abax parallelepipedus*, A para=*Abax parallelus*, A oval=*Abax ovalis*, Sy viv=*Synuchus vivalis*, Ap bom=*Aptinus bombarda*.

	C arce	C conv	C cori	C mont	C nemo	H rufi	Pt bur	Pt mel	Pt obl	Mo pic	A ater	A para	A oval	Sy viv	Ap bom
R^2	0.3059	0.3543	0.3430	0.3286	0.2018	0.5840	0.7278	0.5807	0.7171	0.3691	0.6223	0.2467	0.5768	0.4930	0.4781
F	2.0633	2.5687	2.4446	2.2918	1.1837	6.5736	12.515	6.4839	11.869	2.7395	7.7140	1.5331	6.3814	4.5530	4.2890
$p<$	0.010	0.001	0.010	0.010	ns	0.001	0.001	0.001	0.001	0.001	0.001	ns	0.001	0.001	0.001
cover of litter											–				–
cover of herbs			+												
cover of shrubs										+	+				
canopy cover											+				
carabids' prey		+				+								+	
C arce						–								–	
C conv			+												
C cori		+													
C mont						–									
C nemo										+					
H rufi	–			–											
Pt bur									+	–					
Pt mel														+	
Pt obl							+			+			+		
Mo pic					+		–		+						
A para													+		
A oval									+			+			
Sy viv	–							+							

convexus FABRICIUS, 1775, *Harpalus rufipes* (DE GEER, 1774) and *Synuchus vivalis* (PANZER, 1797)). There were eleven significant relationships between the distribution of particular carabid species and the occurrence of other carabids. The majority of these relationships were positive. A notable exception was the pair *Molops piceus* (PANZER, 1793) (body length 11–15 mm) and *Pterostichus burmeisteri* HEER, 1841 (12–14.5 mm), which have nearly identical body sizes and seasonal activity (Fig. 2), and showed negative association in abundance. In the case of three species (*Carabus hortensis* LINNAEUS, 1758, *Carabus intricatus* LINNAEUS, 1761, *Carabus violaceus* LINNAEUS, 1758) we have found no significant correlations between their distribution and the environmental variables and occurrence of other carabids.

DISCUSSION

In our study the aggregated distribution pattern was typical for the carabids; there were 19 cases where the statistical test was applicable and 18 distribution patterns out of 19 were significantly aggregated (Table 2). Non-random spatial distributions were commonly reported for carabids (LUFF 1986, NIEMELÄ 1988*a*, NIEMELÄ *et al.* 1992*ab*). The analyses of indicator species and the variation in carabid catches among traps and habitats (Tables 1 and 3) also show that the collected carabid species have a clear habitat and microsites preferences with specific environmental conditions. The causes of the variation in catches among traps and habitats are unclear (LUFF 1986, NIEMELÄ *et al.* 1986). One difficulty is that descriptions of the environment are rarely accurate enough to support inferences about determinants of spatial distribution (NIEMELÄ & SPENCE 1994). In the literature, four not mutually exclusive factors are mentioned that might explain the spatial distribution of carabid beetles (NIEMELÄ 1988*a*, NIEMELÄ *et al.* 1985, 1988, 1996): (1) differences in environmental conditions (e.g. habitat heterogeneity, food resources, microclimate), (2) autecological characteristics of the species, (3) small-scale dispersal, and (4) interspecific interactions.

Our analyses showed that a significant proportion of the variation in catch was associated with a particular kind of environmental heterogeneity reflected by the cover of leaf litter, herbs, shrubs, canopy layer and by the distribution of carabids' preys (Table 4). This may be a fairly general pattern among carabids because clear preferences for microsites defined by ground vegetation and litter have also been detected elsewhere (THIELE 1977, NIEMELÄ 1990, NIEMELÄ *et al.* 1992*a*). Multiple regression analyses showed that canopy layer was a significant positive predictor for *Abax parallelepipedus* (PILLER et MITTERPACHER, 1783). *Abax parallelepipedus* (PILLER et MITTERPACHER, 1783) is a habitat generalist (Table 1), but significantly more individuals were captured in the forest interior than in the other habitats (Table 3), suggesting the importance of microsites preference within the movement area. The significant negative association between leaf litter and *Abax parallelepipedus* (PILLER et MITTERPACHER, 1783) and *Aptinus bombarda* (ILLIGER, 1800) is surprising. LOREAU (1987) reported that *Abax parallelepipedus* (PILLER et MITTERPACHER, 1783) is active mainly on the surface of the litter. Perhaps this species can move easier in a habitat with limited litter layer. The same may be supposed for *Aptinus bombarda* (ILLIGER, 1800). Since many carabid species are generalist predators, scavangers or omnivorous, the amount of available prey may influence location of foraging (HENGEVELD 1985, NIEMELÄ *et al.* 1986, LOREAU 1987) and carabids may aggregate in habitats with a high amount of prey (BRYAN & WRATTEN 1984). This may explain the positive relationships between the abundance of carabids' preys and the four carabid species (Table 4). Behavioural responses (e.g. mating behaviour, involving sexual pheromones) may also lead to aggregations in pitfall traps (LUFF 1986).

Similarly to NIEMELÄ and SPENCE (1994) we also found significant positive correlation between the number of individuals and the degree of aggregation for the eighteen studied species. This may be interpreted as more abundant species are more aggregated. It may also be regarded as a simple statistical rule. Indeed, it is evident that both the mean and the variance are dependent on density, even when the pattern is not random. BARTLETT (1936) suggested that the relative variance was likely to be a linear function of the mean. Zoologists frequently attribute a similar statement to IWAO (1968) for the relationship of Morisita index and the mean. The Morisita index is closely related to the index of dispersion. TAYLOR *et al.* (1978) studied the pattern and density relationship for a huge variety of different species, and they concluded that the multiplicative law, suggested by TAYLOR (1961) provides a better fit between variance and mean. This relationship is usually mentioned as Taylor's power law (SOUTHWOOD 1978). The observed relationship during our study is clearly a variant of the Taylor's power law. We used non-parametric rank correlation, therefore the result does not depend on the exact shape of the curve, just on the monotony of the relationship.

On the studied spatial scale the different habitats (grass, forest edge, forest interior) are not independent of each other and there appears to be movement between the adjacent habitats (NIEMELÄ 1988*b*, NIEMELÄ and HALME 1992). Although the majority of the species showed clear differences in abundance between the habitat types, most species were also found outside their optimal environment (Table 1). Small-scale dispersal between habitat patches may be caused by density-dependent processes (GRÜM 1971), and also by movement between reproduction habitat and hibernation habitat (WALLIN 1986, ANDERSEN 1997).

At the studied spatial scale, the occurrence of other carabids was a significant predictor of the abundance of a particular dominant and subdominant species (Table 4). Most of the correlations were positive, suggesting similar response to habitat properties. Previous works (NIEMELÄ *et al.* 1992*b*, NIEMELÄ & SPENCE 1994) also reported some negative relationships. These relationships were usually between species of clearly different body sizes or seasonal activities, or both, and are probably better attributed to different microhabitat preferences than to effects of interspecific interactions. In our study there was a negative relationship between the spatial distribution of the small *Synuchus vivalis* (PANZER, 1797) and the much larger *Carabus arcensis* HERBST, 1784 which also showed maximum activities at different times of the season. For similar reasons interspecific competition is not a likely explanation for the other pairs of species showing a significant negative relationship: *Carabus arcensis* HERBST, 1784 and *Harpalus rufipes* (DE GEER, 1774); *Carabus montivagus* PALLIARDI, 1825 and *Harpalus rufipes* (DE GEER, 1774)

Interspecific competition may be suspected to contribute to the negative relationship between *Molops piceus* (PANZER, 1793) and *Pterostichus burmeisteri* HEER, 1841 (Table 4) which are of similar size and showed similar habitat preference (Table 1) and similar patterns of seasonal activity (Fig. 2). Other data sets (MAGURA & MOLNÁR 1997, MAGURA & TÓTHMÉRÉSZ 1997, MAGURA *et al.* 1997, 1998*a*, *b*) suggest that negative interactions are not a general feature of these two species. NIEMELÄ (1988*a*) and NIEMELÄ and SPENCE (1994) also reported two carabid species with similar size and seasonal activity which showed negative interaction in a forest habitat, while these species in other forest associations showed a high overlap in spatial distribution and in seasonal activity (NIEMELÄ *et al.* 1992*b*, NIEMELÄ & HALME 1992) or there were no correlation between the occurrence of the two species (NIEMELÄ *et al.* 1993). These facts suggest that the type of relationships between the occurrence of carabids may not be a general feature. The interactions can vary among habitat types with different environmental attributes. Further manipulative and non-manipulative studies are necessary to prove the presence of competition between *Molops piceus* (PANZER, 1793) and *Pterostichus burmeisteri* HEER, 1841 because distributional data (spatially non-overlapping distribution) are just the first step to evaluate the mechanism of interspecific competition.

Overall, our results suggest that carabids are useful as an indicator group to asses the environmental variation, as they show different habitat choices. Our study implies that distribution of carabids is determined not only by abiotic environmental factors, like soil types and soil properties (LUFF *et al.* 1989, 1992, NIEMELÄ *et al.* 1992*b*, BAGUETTE 1993, EYRE & LUFF 1994, ŠUSTEK 1994), microclimatic conditions (NIEMELÄ *et al.* 1986, MÜLLER-MOTZFELD 1989, SPENCE *et al.* 1996), heterogeneity of vegetation (NIEMELÄ 1990, BLAKE *et al.*

1996), cover of decaying woods and leaf litter (NIEMELÄ *et al.* 1992*a*, EYRE & LUFF 1994) but also by biotic factors, like distribution of other ground-dwelling animals (e.g. ants; NIEMELÄ *et al.* 1992*a*), abundance of carabids' preys (NIEMELÄ *et al.* 1986, HALME & NIEMELÄ 1993, GUILLEMAIN *et al.* 1997), intraspecific competition (MÜLLER 1986, LOREAU 1990) and interspecific competition (LENSKI 1982, 1984, LOREAU 1989). THIELE (1977) and DEN BOER (1980, 1985) emphasize the priority of abiotic factors in the determination of carabid distribution and in the organisation. Our result stresses that a synthesis is needed, which integrates competition with other abiotic and biotic ecological factors. This synthesis would help a lot in understanding community organisation of carabids, but in this respect, we are still at the beginning (NIEMELÄ 1993).

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