

## Carabid beetle (Coleoptera: Carabidae) communities in a woodland habitat in Hungary

Rita Andorkó & Ferenc Kádár

Andorkó, R. & Kádár, F. 2006: Carabid beetle (Coleoptera: Carabidae) communities in a woodland habitat in Hungary. — *Entomol. Fennica* 17: 221–228.

Carabid communities were investigated in a woodland area within the long-term framework of the MAB project in Hungary, in 1985–86 and in 1993–94, using pitfall trapping. The structural characteristics of the carabid communities and the habitat preferences of the most abundant species were studied in a beech wood, an oak forest, a transition zone and an ecotone. Altogether 7,636 carabid individuals were collected, representing 39 species. The value of Shannon diversity and the equitability consistently peaked in the transition zone. Further statistical analysis showed that the studied habitats were remarkably differentiated from each other.

*R. Andorkó, Department of Systematic Zoology and Ecology, Eötvös Loránd University, Faculty of Sciences, Budapest, H-1117, Pázmány Péter sétány 1/C, Hungary; E-mail: andorko.rita@freemail.hu; arita@ludens.elte.hu*  
*F. Kádár, Plant Protection Institute, Hungarian Academy of Sciences, Budapest, H-1525, P. O. Box 102, Hungary; E-mail: aptinus@freemail.hu*

*Received 28 December 2005, accepted 18 May 2006*

### 1. Introduction

In 1982, the Man and the Biosphere (MAB) project was initiated in the Pilis Biosphere Reserve (PBR), a woodland region in northern Hungary. This project combined general ecological, coenological and faunistical studies among others, including several studies on arthropods (Berczik 1984). The examination of carabid species at different spatial and temporal scales was also carried out.

Carabids respond to habitat-related differences at several ecological spatial scales, and relatively distinct carabid assemblages characterize forest communities (Niemelä *et al.* 1992). Kádár and Szél (1999) studied ground beetle assemblages at 15 topographically different sites of the PBR at landscape scale and showed that the ma-

jority of the most abundant species were found only in one or two forest habitats during each study year. Thus, at macrohabitat scale, the forest is a patchy environment for carabids (Niemelä *et al.* 1992). At a smaller scale, such as the microhabitat scale (within trapping grids), the occurrence of ground beetles has also been shown to be aggregated (Niemelä *et al.* 1986). Other studies also suggest that habitat fragmentation at a small spatial scale may lead to aggregated distributions of ground beetles within patches of similar habitat (Luff 1986, Niemelä *et al.* 1986, 1992, Hengeveld 1987).

The aim of the present study was to determine whether the composition of ground beetle communities and the abundance of the most abundant carabid species vary among different woodland habitats in the short-term (one or two years)

and/or in the long-term (eight and nine years) temporal scales. We also studied the habitat preferences of the most abundant carabid species. We examined the differences in composition and diversity of the ground beetle communities in different habitats at the macro-habitat scale. To assess the relationships between species and their habitats, we investigated the presence/absence of species and/or their relative densities within the different habitats. Thus, we were mainly interested in how distinctive habitat associations different species showed, based on their abundance in pitfall catches.

## 2. Material and methods

### 2.1. Study area and sampling

The study area was located in the PBR, near the Danube river, about 50 km from Budapest, northern Hungary (47°59'N, 18°54'E; 267 m a.s.l.). The study was done in the following four sites, treated as macro-habitats:

- (1) Beech wood (*Melittio-Fagetum*). Associated plant species were the tree *Carpinus betulus* and, in within-stand patches, the herb *Impatiens noli-tangere*;
- (2) Oak forest (*Quercu petraeae-Carpinetum*) situated on the other side of the stream from the beech forest; the altitude was approximately the same in both forests.
- (3) Transition zone that was about 40 m x 8 m, situated between the previously mentioned two habitats, i.e., bordered on one side by beech wood and on the other side by an oak forest, and dominated by *Asarum europaeum*, *Urtica dioica*, *Fragaria vesca* and nitrofil weeds. A deep ditch with periodic water-flow separated the transition zone and the oak forest. The shrub layer was absent, and the canopy layer was open.
- (4) Ecotone with area-wise dimensions similar to the transition zone, located between the transition zone and the beech wood. The characteristic plant was *Carex pilosa*, and the other associated plants were the same as in the adjacent habitats. The shrub layer was moderate, dominated by saplings of *Carpinus betulus*.

The canopy layer was slightly open. This habitat type was not sampled during 1985–86.

Carabids were collected using pitfall traps (plastic jars of 80 mm diameter, 300 ml volume) containing 4% formaldehyde as a killing and preserving agent, and having a metal lid above the traps. The traps were emptied weekly from the end of April to early September in two consecutive years, in 1985 and 1986 and in 1993 and 1994. Five traps placed at least 5 m apart were placed in a row within each area at the same sites each year. In 1985 and in 1986, trapping was conducted only at the first three sites.

### 2.2. Statistical analyses

Following species identifications, the quantitative carabid data were analysed using hierarchical classification method to explore differences among the studied habitat types, using Ward's method with Manhattan distances (Podani 1997). Species diversity in each habitat was estimated using Shannon-Wiener index ( $H'$ ) (Magurran 1988). The average number of individuals, the mean number of species, the mean values of the Shannon-Wiener indices, and the mean values of the equitabilities of  $H'$  among the different habitats were tested using Kruskal-Wallis test and subsequent Mann-Whitney  $U$  test (Sokal & Rohlf 1981). The Statistica program package was used for statistical calculations (StatSoft 2000).

## 3. Results

### 3.1. Species composition

Altogether 7636 individuals were caught during the four years, representing 39 species (Table 1). The most common species were large or medium large, whereas most of the rare species were small to medium large. The most abundant carabid species was *Aptinus bombardus* (>37% of all carabids caught during the four years), being about four times more abundantly caught than the second and third most abundant species *Abax parallelepipedus* and *Pterostichus melanarius*. The following four most abundant species were repre-

Table 1. Data on the carabid community structure in 1985–86 and in 1993–94 in the Pilis Biosphere Reserve, Hungary.

Variable	1985	1986	1993	1994	Total
Number of species	32	35	26	23	39
Mean±SE	10.4±0.92	11.87±0.76	12.25±0.64	12.4±0.68	
Number of individuals	1,169	1,249	3,034	2,184	7,636
Mean±SE	77.93±11.43	83.27±9.34	151.7±14.94	109.2±12.46	
Diversity ( $H'$ )±SE	1.42±0.18	1.59±0.12	1.61±0.10	1.96±0.07	
Equitability±SE	0.61±0.06	0.65±0.04	0.65±0.04	0.79±0.02	

Table 2. Ground beetle species collected in the Pilis Biosphere Reserve, Hungary, in 1985–86 and in 1993–94 (see also footnote). Frequency = mean relative frequency.

Species	Frequency (%)	Total catch
<i>Aptinus bombarda</i> (Illiger, 1800)	37.32	2,850
<i>Abax parallelepipedus</i> (Piller et Mitterpacher, 1783)	8.00	611
<i>Pterostichus melanarius</i> (Illiger, 1789)	7.89	603
<i>Pterostichus melas</i> (Creutzer, 1799)	7.67	586
<i>Platynus assimilis</i> (Paykull, 1790)	7.58	579
<i>Carabus ullrichi</i> Germar, 1824	7.23	552
<i>Carabus scheidleri</i> Panzer, 1799	6.06	463
<i>Pterostichus oblongopunctatus</i> (Fabricius, 1787)	3.84	294
<i>Abax carinatus</i> (Duftschmid, 1812)	3.82	292
<i>Carabus nemoralis</i> Müller, 1764	2.38	182
<i>Carabus coriaceus</i> Linnaeus, 1758	1.83	140
<i>Trechus pilisensis</i> Csiki, 1918	1.17	89

Further species collected: *Carabus convexus* Fabricius, 1775, *Molops piceus* (Panzer, 1793), *Abax ovalis* (Duftschmid, 1812), *Pterostichus niger* (Schaller, 1783), *Leistus rufomarginatus* (Duftschmid, 1812), *Pterostichus ovoideus* (Sturm, 1824), *Notiophilus rufipes* Curtis, 1829, *Abax parallelus* (Duftschmid, 1812), *Harpalus rufipes* (De Geer, 1774), *Harpalus marginellus* Dejean, 1828, *Harpalus atratus* Latreille, 1804, *Cychrus caraboides* (Linnaeus, 1758), *Amara saphyrea* Dejean, 1828, *Stomis pumicatus* (Panzer, 1796), *Platynus dorsalis* (Pontoppidan, 1763), *Synuchus vivalis* (Illiger, 1789), *Nebria brevicollis* (Fabricius, 1792), *Carabus intricatus* Linnaeus, 1761, *Pterostichus strenuus* (Panzer, 1797), *Calosoma inquisitor* (Linnaeus, 1758), *Platyderus rufus* (Duftschmid, 1812), *Bembidion lampros* (Herbst, 1784), *Licinus hoffmannseggii* (Panzer, 1797), *Harpalus pumilus* Sturm, 1818, *Brachinus explodens* Duftschmid, 1812, *Carabus violaceus* Linnaeus, 1758, *Amara convexior* Stephens, 1828.

sented in almost the same number of individuals (6–7%): *P. melas*, *Platynus assimilis*, *Carabus ullrichi* and *C. scheidleri*. The mean relative frequency and the total number of individuals of the more frequent twelve species are given in Table 2. Twenty-two common species occurred during the four examined years.

In 1985–86, *A. parallelepipedus* was only the sixth (1985) and seventh (1986) most abundant species with about 40 individuals in each year. In 1993–94, it was the second (1993) and the fourth (1994) most abundant species (227 and 307 individuals, respectively). In 1986, *C. scheidleri* was collected in high numbers (332 individuals). In contrast, during the other three years this species occurred only in low numbers. While *C. ullrichi*

was hardly represented in the 1985–86 samples, it was the second most abundant carabid species in 1994, and the fourth one in 1993, with more than 200 individuals.

### 3.2. Hierarchical classification

The results of the cluster analysis for the pitfall trap catches are given in Figs. 1–2. The clusters formed three groups of habitat; these were well separated from each other at macro-scale in 1985 (Fig. 1). However, in 1993, the oak forest and beech wood formed isolated groups, and little overlap occurred between the transition zone and the ecotone at a smaller scale (Fig. 2).

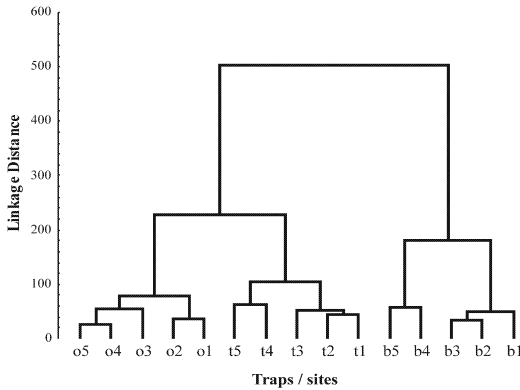


Fig. 1. The 15 traps in three sites in the Pilis Biosphere Reserve, Hungary, clustered according to the distances of their carabid communities (data from 1985; Ward's method, Manhattan distances). b1–b5: beech wood, t1–t5: transition zone, o1–o5: oak forest).

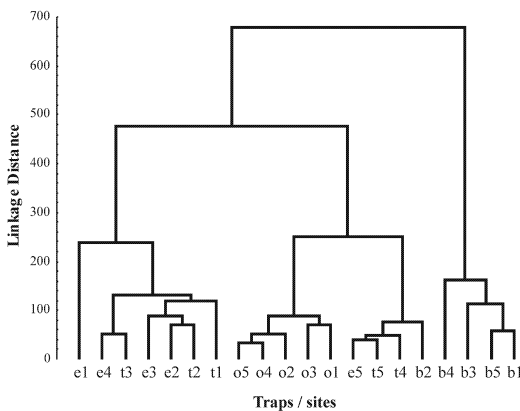


Fig. 2. The 20 traps in four sites in the Pilis Biosphere Reserve, Hungary, clustered according to the distances of their carabid communities (data from 1993; Ward's method, Manhattan distances). b1–b5: beech wood, t1–t5: transition zone, o1–o5: oak forest, e1–e5: ecotone).

**3.3. Community structural indices**

The Kruskal-Wallis test indicated significant differences among the different habitats in structural indices of each community over the four years (Table 3). There was a significant difference among the number of species of the three studied habitats during 1985–86. The number of individuals of the different habitats did not vary significantly in 1985 or in 1993–94; indeed, there was a detectable significant difference only in 1986.

The Shannon-Wiener diversity index for different habitats varied significantly among habitats in 1985–86, and also in 1993–94. Moreover, there was a significant difference among the equitabilities of the different habitats in 1985–86 and in 1993, but not in 1994.

The changes in the structural indices for the communities in time are shown in Table 1. The number of species of each habitat decreased to 1993–94, but otherwise the mean number of species slightly increased. The mean number of individuals, on the other hand, was higher in 1993–94 and peaked in 1993. The diversity index and the equitability increased during the four years, and peaked in 1994.

**3.4. Habitat preference**

The different habitats were clearly separated by abundance among the most frequent species (Figs. 3–5). *Aptinus bombarda* was associated with the beech forest (Fig. 3), and Kruskal-Wallis test indicated a significant abundance difference of *A. bombarda* among the studied habitats in 1985–86. There was also a significant difference among the four habitats based on the abundance in 1993–94.

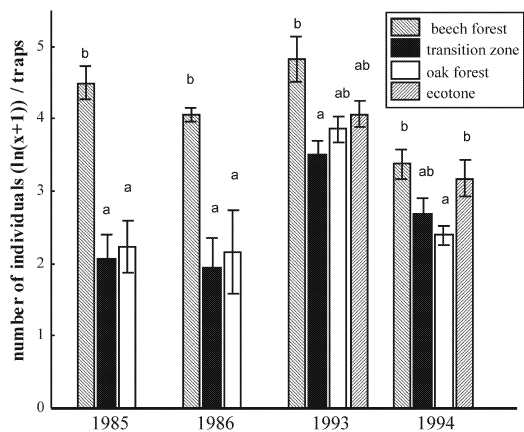


Fig. 3. The habitat associations of *Aptinus bombardata* in the Pilis Biosphere Reserve, Hungary, based on mean ( $\pm$ SE) abundance data. Different letters indicate significant differences within the given years by Mann-Whitney *U* test ( $p < 0.05$ ). Kruskal-Wallis test; 1985:  $H_2 = 9.57, p < 0.05, n = 15$ ; 1986:  $H_2 = 9.61, p < 0.05, n = 15$ ; 1993:  $H_3 = 8.17, p < 0.05, n = 20$ ; 1994:  $H_3 = 8.68, p < 0.05, n = 20$ .

Table 3. Data on community structure of carabids of different habitats in 1985 and 1986 (upper part) and in 1993 and 1994 (lower part) in the Pilis Biosphere Reserve, Hungary (mean  $\pm$  SE; lower-case letters indicate significant ( $p < 0.05$ ) differences by Mann-Whitney  $U$  test). The Ecotone habitat was not sampled in 1985–86. Beech = beech forest; Transition = transition zone; Oak = oak forest; Ecotone = ecotone habitat; K-W test = Kruskal-Wallis test (with  $H_2$  and  $p$  values).

	1985				K-W test	1986				K-W test
	Beech	Transition	Oak	(Ecotone)		Beech	Transition	Oak	(Ecotone)	
Mean no. species	9 $\pm 0.84$ a	14 $\pm 1.05$ b	8.2 $\pm 1.46$ a		$H_2=8.96$ ; $p=0.011$	10.8 $\pm 0.86$ a	15 $\pm 0.95$ b	9.8 $\pm 0.73$ a		$H_2=9.34$ ; $p=0.009$
Mean no. individuals	115.2 $\pm 24.05$ b	67.2 $\pm 11.94$ ab	51.4 $\pm 9.91$ a		$H_2=5.46$ ; $p=0.065$	76 $\pm 5.29$ a	120.4 $\pm 14.44$ b	53.4 $\pm 9.94$ a		$H_2=10.52$ ; $p=0.005$
Diversity ( $H'$ )	0.71 $\pm 0.12$ a	2.22 $\pm 0.06$ c	1.31 $\pm 0.17$ b		$H_2=11.58$ ; $p=0.003$	1.06 $\pm 0.08$ a	1.95 $\pm 0.09$ b	1.78 $\pm 0.13$ b		$H_2=9.92$ ; $p=0.007$
Equitability	0.32 $\pm 0.05$ a	0.85 $\pm 0.02$ c	0.66 $\pm 0.05$ b		$H_2=12.52$ ; $p=0.002$	0.45 $\pm 0.04$ a	0.72 $\pm 0.02$ b	0.78 $\pm 0.04$ b		$H_2=10.82$ ; $p=0.004$
	1993				K-W test	1994				K-W test
	Beech	Transition	Oak	Ecotone		Beech	Transition	Oak	Ecotone	
Mean no. species	12 $\pm 0.77$ b	15 $\pm 1.52$ b	9.4 $\pm 0.6$ a	12.6 $\pm 0.68$ b	$H_2=12.83$ ; $p=0.005$	11 $\pm 0.89$ a	14.8 $\pm 0.2$ b	8.8 $\pm 0.49$ a	15 $\pm 0.95$ b	$H_2=14.49$ ; $p=0.002$
Mean no. individuals	194.4 $\pm 28.85$ a	126.4 $\pm 22.62$ a	110 $\pm 13.29$ a	176 $\pm 38.99$ a	$H_2=4.83$ ; $p=0.185$	83.2 $\pm 11.3$ a	95.4 $\pm 15.22$ a	77.6 $\pm 7.86$ a	180.6 $\pm 28.02$ b	$H_2=7.72$ ; $p=0.052$
Diversity ( $H'$ )	1.07 $\pm 0.19$ a	2.09 $\pm 0.05$ c	1.46 $\pm 0.07$ a	1.81 $\pm 0.09$ b	$H_2=15.79$ ; $p=0.001$	1.75 $\pm 0.11$ a	2.25 $\pm 0.1$ b	1.65 $\pm 0.05$ a	2.18 $\pm 0.05$ b	$H_2=13.19$ ; $p=0.004$
Equitability	0.43 $\pm 0.08$ a	0.78 $\pm 0.02$ c	0.66 $\pm 0.03$ b	0.72 $\pm 0.03$ bc	$H_2=12.41$ ; $p=0.006$	0.74 $\pm 0.04$ a	0.84 $\pm 0.04$ b	0.76 $\pm 0.01$ ab	0.81 $\pm 0.02$ ab	$H_2=6.79$ ; $p=0.079$

*Pterostichus melanarius* was mainly found in the transition zone and in the ecotone during the four years (Fig. 4), as was *P. oblongopunctatus*. The abundance of *P. melanarius* in the studied habitats differed significantly in 1985–86. Based on abundance, there was also a significant difference among the four habitats in 1993–94.

*Pterostichus melas* was caught almost exclusively in the oak forest each year (Fig. 5). There were significant differences among the abundances of *P. melas* in the studied habitats in 1985–86, and the abundance also significantly varied among the four habitats in 1993–94.

*Abax parallelepipedus* was collected in a higher number in 1993–94 (534 individuals), and only 34 individuals were found in the oak forest.

Many more individuals of *P. assimilis* were collected in 1993–94 (479) than in 1985–86 (100), and mainly from the ecotone and the tran-

sition zone. A similar pattern was found for *C. ullrichi* that had fewer individuals collected in the beech forest. Out of the 332 collected *C. scheidleri* individuals, 248 were collected in the transition zone.

## 4. Discussion

### 4.1. Variation within ecological scales

In the only published investigation on ground beetle communities of this area (Kádár & Szél 1999), the composition and the occurrence of carabid species were examined between 1982 and 1984 at the landscape scale. At the scale of forest habitat patches, such as at the macro-habitat scale, soil moisture appears an important determinant of carabid distribution (Thiele 1977, Epstein

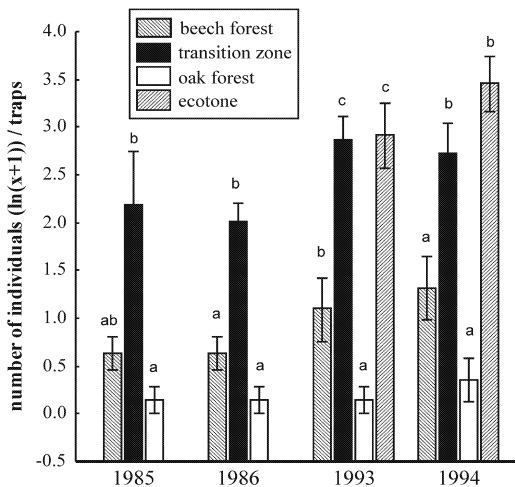


Fig. 4. The habitat associations of *Pterostichus melanarius* in the Pilis Biosphere Reserve, Hungary, based on mean ( $\pm$ SE) abundance data. Different letters indicate significant differences within the given years by Mann-Whitney  $U$  test ( $p < 0.05$ ). Kruskal-Wallis test; 1985:  $H_2 = 6.66$ ,  $p < 0.05$ ,  $n = 15$ ; 1986:  $H_2 = 11.26$ ,  $p < 0.05$ ,  $n = 15$ ; 1993:  $H_3 = 14.80$ ,  $p < 0.05$ ,  $n = 20$ ; 1994:  $H_3 = 14.91$ ,  $p < 0.05$ ,  $n = 20$ .

& Kulman 1990). Forest carabid species are associated with micro-sites with a particular kind of environment heterogeneity, such as favourable microclimate (soil temperature, ground air temperature, relative air moisture), the presence of dead and decaying trees, and the cover of leaf litter, shrubs and herbs (Desender *et al.* 1999). Other biotic and abiotic ecological factors also influence the composition of the carabid assemblages and distribution, such as soil pH, soil compactness,  $\text{CaCO}_3$  content, and the amount of prey items (Magura *et al.* 2002).

According to our results, the studied habitat types were segregated (Figs. 1–2). We suggest that the main cause of this segregation was soil moisture. This environmental factor influences e.g. egg and larval development (Thiele 1977).

#### 4.2. Community differences among the compared habitats

The number of species and individuals of the less humid habitat, viz. oak forest, was much lower than those of more humid sites (Table 3). In the oak forest, diversity and equitability of the assemblages of the beech forest were always the lowest,

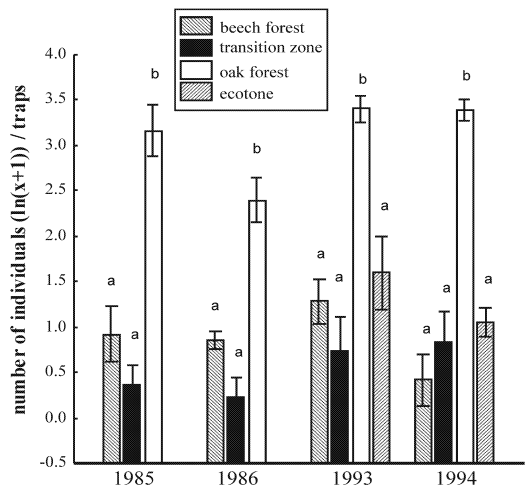


Fig. 5. The habitat associations of *Pterostichus melas* in the Pilis Biosphere Reserve, Hungary, based on mean ( $\pm$ SE) abundance data. Different letters indicate significant differences within the given years by Mann-Whitney  $U$  test ( $p < 0.05$ ). Kruskal-Wallis test; 1985:  $H_2 = 10.37$ ,  $p < 0.05$ ,  $n = 15$ ; 1986:  $H_2 = 11.18$ ,  $p < 0.05$ ,  $n = 15$ ; 1993:  $H_3 = 12.63$ ,  $p < 0.05$ ,  $n = 20$ ; 1994:  $H_3 = 12.84$ ,  $p < 0.05$ ,  $n = 20$ .

whereas in the transition zone they were always the highest, except in 1986 (Table 3). This zone is occupied by species characteristic of both adjacent habitats; this “adjacency effect” explains the species richness of this site. Ground beetles probably use these habitats during dispersal, hibernating and reproduction periods (Bommarco & Fagan 2002). The community structural indices of the ecotone showed the supposed compositional and structural similarities to the adjacent habitats in 1993–94; ecotones often contain relatively high biodiversity (Murcia 1995, Risser 1995). Small-scale movements of carabids between habitats may modify ground beetle assemblages of neighbouring habitat patches (Niemelä & Halme 1992). That is why the number of species increases and their relative abundances change in the adjacent habitats. The transition zones and the ecotones can contribute to the maintenance of the diversity of carabid communities.

#### 4.3. Changes of the communities in time

One year prior to our sampling, the forests were selectively thinned, which may have influenced



the composition of the carabid assemblages we found, for example by increasing the diversity and the equitability during the ten years in each habitat (Table 3). For example, *A. parallelepipedus* increased in 1993–94 probably because of the cessation of the forest management. There were also more individuals in the beech forest during these two years, but this is an ambiguous consequence because of the lack of continuous survey between the periods 1985–86 and 1993–94. The “natural” fluctuation of *A. parallelepipedus* population could be another reason behind this phenomenon. This common species is well adapted to many environmental conditions, but its distribution might change at a larger scale, for example following large-scale forest harvesting (Loreau & Nolf 1994). Such changes might have taken place in our study site, too. *Carabus scheidleri* is associated with disturbed, human-modified areas (Andorkó *et al.* 2003), which may explain why this species was found in high numbers in 1985–86 but was missing in 1993–94. *Carabus ullrichi* occurs in more stable forests, possibly explaining its distribution in 1993–94.

#### 4.4. Habitat associations

All the abundant species showed associations to particular habitats. The distribution of the most abundant species, *A. bombardard*, is well known (Brandmayr 1974, Casale & Vigna Taglianti 1983, Pravisani & Torossi 1987, Fazekas *et al.* 1992). This species has been found only in the *Seslerio-Quercetum* patch with an extremely high dominance value (Brandmayr *et al.* 1980). It is a typical forest-dwelling species in Hungary (Kádár & Szél 1993). In our study it was most abundant in the beech forest, similarly to Magura *et al.* (2002). The second most abundant species in our study, *A. parallelepipedus*, was also among the most abundant species captured by Kádár and Szél (1993, 1999), and Magura *et al.* (2002). This carabid is typically an opportunistic species and has a good adaptation ability to various habitat types (Kádár & Szél 1993). That is why it is a dominant species in different habitats (Chemini & Werth 1982, Contarini 1986, Pravisani & Torossi 1987).

In our study, *P. melanarius* was associated

with the transition zone and the ecotone, i.e., habitats with high level of soil moisture and dense shrub vegetation. It can be found in relatively high numbers in quite different habitats, too; for example, it is common in agricultural landscapes (Thiele 1977) and riverside woodlands (Baguette 1993). *Pterostichus melanarius* has also occurred in high numbers in various other environment types, such as fields, pastures, abandoned fields, and in forests in Finland (Niemelä and Halme 1992). Although this species is favoured by human activity, our study and that of Niemelä and Spence (1991) also showed that it was not solely restricted to disturbed habitats.

*Pterostichus melas* also showed a clear habitat association, as it was found mainly in the oak forest every year. It is characteristic for different kinds of oak forests such as *Quercus-Ostryetum* (Contarini 1986) and *Querceto-petraeae cerris* (Fazekas *et al.* 1992). *Platynus assimilis* was only occasionally found in the PBR between 1982 and 1984 (Kádár & Szél 1999), whereas in our study it was commonly caught. Similarly to our study, it is reported to occur in wet, shady forests (Kleinert 1983). In the present study, *Carabus ullrichi* was captured from each habitat. It has also been collected in the PBR between 1982 and 1984, but in low numbers (Kádár & Szél 1999). It occurs in wet and shady but also in dry and light forests in Slovakia (Kleinert 1983). *Carabus scheidleri* is common in lowlands and hills in mixed forests, and is associated with fields, meadows, gardens, hedges, watersides and various types of forests (Hürka 1996). It has also been found in an abandoned agricultural field (Andorkó *et al.* 2003).

Our results emphasize that carabids are appropriate organisms for ecological studies both at macro-scale and landscape levels. We conclude that carabid beetles are good indicators of site type, quality and conservation status (Eyre & Rushton 1989).

*Acknowledgements.* The authors are grateful to Á. Szentesi for critical comments and improving the English of the manuscript. The authors thank the reviewers for comments on this manuscript. We thank the Middle-Danube-Valley Environmental, Nature and Water Inspectorate to approve the permission for the investigations. This work was supported partly by the Hungarian National Scientific Research Foundation (No. OTKA TO48434).

## References

- Andorkó, R., Kádár, F. & Szekeres, D. 2005: Reproductive characteristics of *Carabus scheidleri* (Coleoptera, Carabidae) in Hungary. — In: Lövei, G. & Toft, S., European Carabidology 114: 9–16. DIAS Report. 401 pp.
- Baguette, M. 1993: Habitat selection of carabid beetle in deciduous woodlands of southern Belgium. — *Pedobiologia* 37: 365–378.
- Berczik, Á. 1984: A Pilis Bioszféra Rezervátum kutatási programja. (The research programme of the Pilis Biosphere Reserve). — *Állattani Közlemények* 71: 14–16.
- Bommarco, R. & Fagan, W. F. 2002: Influence of crop edges on movement of generalist predators: a diffusion approach. — *Agricultural and Forest Entomology* 4: 21–30.
- Brandmayr, P. 1974: Auto- und synökologische Untersuchungen über die Carabiden zweier Vegetationseinheiten des Slowenischen Küstenlandes: das *Carici (humilis)* – *Seslerietum juncifoliae* und das *Seslerio (autumnalis)* – *Fagetum* (Coleoptera, Carabidae). — *Acta Entomologica Jugoslavica* 10: 15–40.
- Brandmayr, P., Colombetta, G., Drovnik, B., Forti, F., Poldini, L. & Brandmayr, T. Z. 1980: Etude multidisciplinaire sur l'écologie de quelques carabides endogés (Coleoptera, Carabidae). — *Mem. Biospeol.* 7: 85–98. [In French.]
- Casale, A. & Vigna Taglianti, A. 1983: Il genere *Aptinus* Bonelli, 1810 (Coleoptera, Carabidae). — *Boll. Mus. Reg. Sci. Nat. Torino* 1: 21–58.
- Chemini, C. & Werth, F. 1982: Censimenti di Carabidi in tre ambienti forestali di Magré e Favogna (Provincia di Bolzano) (Insecta, Coleoptera, Carabidae). — *Studi Trentini Sci. Nat.* 59: 201–211.
- Contarini, E. 1986: Eco-profilo d'ambiente della Coleottero fauna di Romagna: 1. Il Quercio-Ostryetum dell'orizzonte submontano. — *Boll. Ass. Romana Entomol.* 41: 1–62.
- Desender, K., Eryvynck, A. & Tack, G. 1999: Beetle diversity and historical ecology of woodlands in Flanders. — *Belgian Journal of Zoology* 129: 139–156.
- Epstein, M. E. & Kulman, H. M. 1990: Habitat distribution and seasonal occurrence of carabid beetles in east-central Minnesota. — *American Midland Naturalist* 123: 209–225.
- Eyre, M. D. & Rushton, S. P. 1989: Quantification of conservation criteria using invertebrates. — *Journal of Applied Ecology* 26: 159–171.
- Fazekas, J., Kádár, F. & Lövei, G. 1992: Comparison of ground beetle assemblages (Coleoptera, Carabidae) of an abandoned apple orchard and the bordering forest. — *Acta Phytopathologica Hungarica* 27: 233–238.
- Hengeveld, R. 1987: Scales of variation: Their distinction and ecological importance. — *Annales Zoologici Fennici* 24: 195–202.
- Hürka, K. 1996: Carabidae of the Czech and Slovak Republics. — *Kabourek, Zlín*. 566 pp.
- Kádár, F. & Szél, Gy. 1993: Analysis of the distribution of ground beetles in different habitats of the Nagy-szénás Nature Reserve (Coleoptera, Carabidae). — *Folia Entomologica Hungarica* 54: 65–73.
- Kádár, F. & Szél, Gy. 1999: Species composition and occurrence of ground beetles (Coleoptera, Carabidae) in the Pilis Biosphere Reserve, Hungary: a pitfall trap study. — *Folia Entomologica Hungarica* 60: 205–212.
- Kleinert, J. 1983: Ground beetles (Coleoptera, Carabidae) in selected habitats of lowland in southeastern Slovakia. — *Biologia* 38 (10): 981–989.
- Loreau, M. & Nolf, C.-L. 1994: Spatial structure and dynamics of a population of *Abax ater*. — In: Desender, K. *et al.* (eds.), *Carabid Beetles: Ecology and Evolution*: 165–169. Kluwer Academic Publishers, the Netherlands. 492 pp.
- Luff, M. L. 1986: Aggregation of some Carabidae in pitfall traps. — In: den Boer, P. J., Luff, M. L., Mossakowski, D. & Weber, F. (eds.), *Carabid beetles, their adaptations and dynamics*: 385–397. Gustav Fischer, Stuttgart. 551 pp.
- Magura, T., Elek, Z. & Tóthmérész, B. 2002: Impacts of non-native spruce reforestation on ground beetles. — *European Journal of Soil Biology* 38: 291–295.
- Magurran, A. E. 1988: Ecological diversity and its measurements. — University Press, Cambridge. 179 pp.
- Murcia, C. 1995: Edge effects in fragmented forests: implications for conservation. — *Trends in Ecology and Evolution* 10: 58–62.
- Niemelä, J. & Halme, E. 1992: Habitat associations of carabid beetles in fields and forests on the Åland Islands, SW Finland. — *Ecography* 15: 3–11.
- Niemelä, J. & Spence, J. R. 1991: Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. — *Oikos* 62: 351–359.
- Niemelä, J., Haila, Y. & Ranta, E. 1986: Spatial heterogeneity of carabid beetle dispersion in uniform forests on the Åland Islands, SW Finland. — *Annales Zoologici Fennici* 23: 289–296.
- Niemelä, J., Spence, J. R. & Spence, D. H. 1992: Habitat associations and seasonal activity of ground-beetles (Coleoptera, Carabidae) in Central Alberta. — *Canadian Entomologist* 124: 521–540.
- Podani, J. 1997: Bevezetés a többváltozós biológiai adatfeldtárás rejtelmibe. (An introduction to methods of multivariate biological data processing and evaluating). — *Scientia Kiadó, Budapest*. 412 pp. [In Hungarian.]
- Pravisan, L. & Torossi, G. 1987: Coleotteri carabidi in alcune biocenosi dell'Alta Val Torre (Friuli). — *Atti. Mus. Friul. Stor. Nat.* 9: 169–200. [In Italian.]
- Risser, P. G. 1995: The status of the science examining ecotones. — *Bioscience* 45: 318–325.
- Sokal, R. R. & Rohlf, F. J. 1981: *Biometry*. Second edition. — W. H. Freeman and Co., New York. 859 pp.
- StatSoft 2000: *Statistica for Windows I–III*. — StatSoft Inc., Tulsa, OK.
- Thiele, H.-U. 1977: *Carabid beetles in their environment*. — Springer-Verlag, Berlin. 369 pp.