

EFFECTS OF LEAF-LITTER ADDITION ON CARABID BEETLES IN A NON-NATIVE NORWAY SPRUCE PLANTATION

MAGURA, T., TÓTHMÉRÉSZ, B.* and ELEK, Z.*

Hortobágy National Park Directorate, H-4002 Debrecen, P.O. Box 216, Hungary

Present address: Department of Zoology, University of Debrecen

H-4010 Debrecen, P.O. Box 3, Hungary, E-mail: magura@www.hnp.hu

**Department of Ecology, University of Debrecen, H-4010 Debrecen, P.O. Box 71, Hungary*

To study the short-term effect of leaf-litter manipulation on the structure of carabid assemblage in a 50-year-old Norway spruce plantation in Hungary, pitfall samples from leaf-litter plots (leaf-litter addition) and control plots (no manipulation) were compared during the growing season in 2000. The most frequent species, *Pterostichus oblongopunctatus*, was significantly more numerous in the leaf-litter samples than in the control ones, indicating the leaf-litter preference of this species. Leaf-litter addition had no significant effect on the abundance of the other four dominant carabid species (*Carabus violaceus*, *Cychrus caraboides*, *Abax parallelepipedus*, *Molops piceus*). Difference in the number of collected carabid individuals, species richness and the Shannon diversity between the control and the manipulated plots were not significant. The observed leaf-litter preference of *Pterostichus oblongopunctatus* could be explained with the microhabitat variations and/or the interspecific interactions. Leaf-litter addition altered the microclimatic conditions (lower ground temperature, higher amount of prey items) and produced favourable microhabitat conditions that could influence the spatial distribution of *Pterostichus oblongopunctatus*. Moreover, the number of carabid larvae was significantly higher in the leaf-litter plots, indicating that the leaf-litter plots with their favourable conditions may be advantageous egg-laying sites.

Key words: carabid beetles, leaf-litter addition, habitat heterogeneity, spatial distribution, environmental conditions, interspecific interactions

INTRODUCTION

In Hungary, during the last centuries, large areas of native deciduous forests were reforested with non-native conifer trees, due to changes in forestry practice. Non-native Norway spruce (*Picea abies*) was preferred during reforestation, because of its quick growth and economic value. After the clear-cutting of a forest, mechanical soil preparation (grubbing and deep loosening) preceded the spruce reforestation. The reforestation following clear-cutting and soil preparation drastically altered the microclimatic, abiotic and biotic conditions and lead to the spatial homogenization of these reforested habitats (MÁTYÁS 1996). Ground-dwelling carabid beetles (*Coleoptera: Carabidae*) are especially sensitive to the soil disturbance, the changes in environmental conditions and to the homogenisation of their habitat (SAMWAYS 1994, NIEMELÄ 1997, 1999, DESENDER *et al.* 1999, MAGURA

et al. 1997, 2001, 2002, 2003, KOIVULA 2002, KOIVULA *et al.* 2002). Several previous studies demonstrated that assemblages of carabid beetles change remarkably after reforestation and in the monocultures, just the habitat generalist and forest generalist carabid species were abundant (SZYSZKO 1987, DAY & CARTHY 1988, EYRE *et al.* 1990, BAGUETTE & GÉRARD 1993, NIEMELÄ *et al.* 1993, BUTTERFIELD *et al.* 1995, SPENCE *et al.* 1996, FAHY & GORMALLY 1998, INGS & HARTLEY 1999, BIRD *et al.* 2000, WERNER & RAFFA 2000, ELEK *et al.* 2001).

In the boreal coniferous forests KOIVULA *et al.* (1999) showed that artificial leaf-litter addition increased the habitat heterogeneity and affected the carabid-assemblage structure by increasing the total carabid abundance and the abundance of three out of the four most common carabid species. Our previous study (MAGURA *et al.* 2000a) demonstrated that nature management that encourages the recolonisation by native deciduous plants and the accumulation of leaf litter, significantly contributes to the maintenance of carabid diversity in non-native Norway spruce plantations 30 years after management. There were two main objectives of the study: (1) does leaf-litter addition affect the structure of the carabid assemblages, namely does the number of collected carabid individuals, species richness and the Shannon diversity increase in the leaf-litter plots? (2) does leaf-litter addition influence the spatial distribution of the dominant carabid species? Moreover, based on the result we make proposals for silvicultural management.

MATERIAL AND METHODS

Study area and sampling

The study was performed in the North Hungarian Mountain Range, in a 50-year-old Norway spruce stand. The stand was established after clear-cutting of a beech forest and its area was 12 hectares. In the studied stand, three treated and three control square plots, each of 25 m² area, were established randomly. Distances between the plots and to the nearest forest edge were at least 30 m in order to provide adequate statistical independence for plots (DIGWEED *et al.* 1995) and to avoid edge effect (BEDFORD & USHER 1994, KOTZE & SAMWAYS 1999, MAGURA *et al.* 2000b, 2001b, MAGURA 2000, 2002, MOLNÁR *et al.* 2001). In the treated plots, leaf litter originating from the neighbouring beech forest was added before the commencement of trapping in late February. A random sample (10 litre) from the added leaf litter was examined in the laboratory and neither carabid adults nor larvae were found in the leaf litter. In each plot, nine pitfall traps (2 m apart) were placed in a three-by-three grid to collect carabid beetles. The pitfall traps were unbaited, consisting of plastic cups (diameter 100 mm, volume 500 ml) containing ethylene-glycol as a killing-preserving solution. The traps were covered with bark pieces to protect them from litter and rain (SPENCE & NIEMELÄ 1994). Trapped beetles were collected monthly from March to November in 2000. For the numerical analyses we pooled samples from the different months. Several authors (BAARS 1979, LOREAU 1992, HELIOLA *et al.* 2001) showed that the total capture of a species over the whole sampling period gave an estimate of

the ecological importance of each species in a habitat if the sampling period was long enough to cover the most of the beetles' activity period.

We studied eight environmental factors that may affect the distribution of carabids (THIELE 1977, LÖVEI & SUNDERLAND 1996). Ground temperature at 2 cm depth, air temperature on the surface and relative humidity were measured adjacent to each trap. We also estimated the cover of leaf litter, herbs, shrubs and canopy around the traps within a circle with a diameter of 1 m. We also counted the number of other invertebrates (other Coleoptera, Chilopoda, Collembola, Diplopoda, Gastropoda, Isopoda) in the traps, which were potential prey for carabids (SERGEEVA 1994). Moreover, we analysed the spatial distribution of the carabid larvae of the studied plots. The average values of the measured environmental factors are shown by Table 1 for the studied plantation.

Data analyses

The number of individuals, the species richness and the Shannon diversity index of the trapped carabids, as well as the abundance of the five most common species between the leaf-litter and control plots, were examined by analysis of variance (ANOVA). The cover of herbs was significantly different between the leaf-litter and control plots (see Table 1). This difference is not due to the leaf-litter addition and so could affect the carabid catches (e.g. KOIVULA *et al.* 2002). Therefore, we included the cover of herbs in the ANOVA model. Also, the data were analysed by performing a factorial ANOVA with leaf-litter treatment as a fixed factor and the coverage of the herbs as a covariate. Normal distribution of the data was achieved by $\log(x+1)$ transformation (SOKAL & ROHLF 1981). We examined the relationships between the environmental measurements and the abundance of selected carabid species by forward and backwards stepwise multiple linear regression analysis; forward stepwise multiple linear regression analysis provided a better fit. The analyses were done by the SPSS-PC program. Non-metric multidimensional scaling (NMDS) using the Bray-Curtis index was applied to display the similarity of pitfall catches of the plots (LEGENDRE & LEGENDRE 1998); calculations were done by the NuCoSA package (TÓTHMÉRÉSZ 1993).

Table 1. Average values (\pm S. E.) of the studied environmental factors in the study plots. Different letters indicate significant ($p < 0.05$) differences by ANOVA

	Control plot	Leaf-litter plot
Ground temperature at 2 cm depth (°C)	16.5444 \pm 0.1584 ^a	16.1037 \pm 0.1080 ^b
Air temperature on the surface (°C)	21.2259 \pm 0.1324 ^a	21.1889 \pm 0.0865 ^a
Relative humidity (%)	66.8889 \pm 0.7286 ^a	67.4815 \pm 0.4282 ^a
Cover of leaf litter (%)	0.2222 \pm 0.1233 ^a	91.6667 \pm 2.0149 ^b
Cover of herbs (%)	14.2222 \pm 1.8166 ^a	6.0000 \pm 1.3514 ^b
Cover of shrubs (%)	4.0741 \pm 1.1259 ^a	1.5926 \pm 0.7459 ^a
Canopy cover (%)	76.1111 \pm 2.6194 ^a	77.0741 \pm 2.9015 ^a
Number of prey items	114.8148 \pm 5.1052 ^a	135.3704 \pm 6.1181 ^b
Number of carabid larvae	1.9259 \pm 0.3154 ^a	2.8148 \pm 0.3021 ^b

RESULTS

The carabid catches consisted of 825 individuals representing 23 species (Table 2). The most numerous species both in the control and leaf-litter plots were *Pterostichus oblongopunctatus*, *Molops piceus*, *Abax parallelepipedus*, *Cychrus caraboides* and *Carabus violaceus*. These five carabid species made up 75.12% of the total catch. Four species were caught exclusively in the leaf-litter plots, while one species exclusively in the control plots (Table 2).

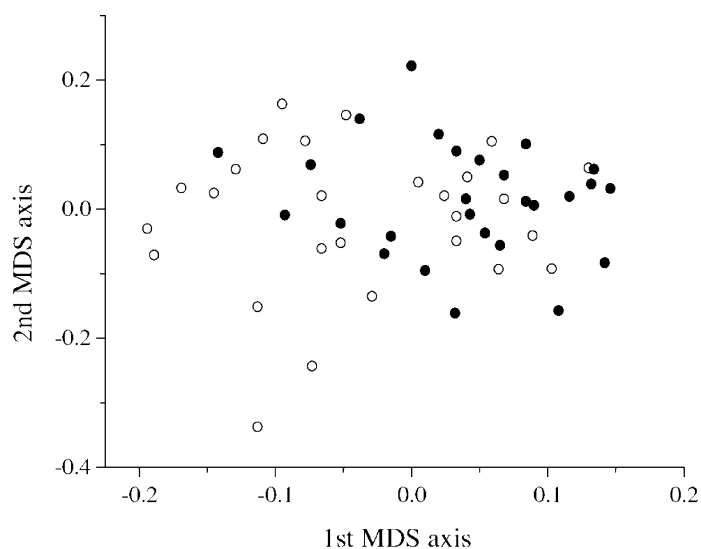
Table 2. The catches of carabid beetles in the control and the leaf-litter plots. n = number of individuals caught, (t) = number of traps wherein the species was captured

	Control plot		Leaf-litter plot		Total	
	n	(t)	n	(t)	n	(t)
<i>Pterostichus oblongopunctatus</i> (FABRICIUS, 1787)	86	(23)	153	(26)	239	(49)
<i>Molops piceus</i> (PANZER, 1793)	67	(22)	73	(23)	140	(45)
<i>Abax parallelepipedus</i> (PILLER et MITTERPACHER, 1783)	40	(18)	42	(19)	82	(37)
<i>Cychrus caraboides</i> (LINNAEUS, 1758)	39	(20)	43	(20)	82	(40)
<i>Carabus violaceus</i> LINNAEUS, 1758	46	(18)	31	(14)	77	(32)
<i>Carabus glabratus</i> PAYKULL, 1790	26	(15)	22	(14)	48	(29)
<i>Carabus hortensis</i> LINNAEUS, 1758	31	(14)	13	(11)	44	(25)
<i>Abax parallelus</i> (DUFTSCHMID, 1812)	25	(15)	11	(8)	36	(23)
<i>Notiophilus biguttatus</i> (FABRICIUS, 1799)	10	(7)	5	(4)	15	(11)
<i>Aptinus bombardus</i> (ILLIGER, 1800)	8	(7)	5	(4)	13	(11)
<i>Carabus nemoralis</i> O. F. MÜLLER, 1764	4	(4)	5	(4)	9	(8)
<i>Harpalus latus</i> (LINNAEUS, 1758)	1	(1)	7	(5)	8	(6)
<i>Platyderus rufus</i> (DUFTSCHMID, 1812)	2	(2)	6	(5)	8	(7)
<i>Pterostichus niger</i> (SCHALLER, 1783)	4	(3)	2	(2)	6	(5)
<i>Carabus coriaceus</i> LINNAEUS, 1758	3	(3)	2	(2)	5	(5)
<i>Harpalus marginellus</i> DEJEAN, 1829	1	(1)	2	(2)	3	(3)
<i>Carabus convexus</i> FABRICIUS, 1775	2	(2)	0	(0)	2	(2)
<i>Pterostichus melanarius</i> (ILLIGER, 1798)	1	(1)	1	(1)	2	(2)
<i>Synuchus vivalis</i> (ILLIGER, 1798)	1	(1)	1	(1)	2	(2)
<i>Bembidion properans</i> (STEPHENS, 1828)	0	(0)	1	(1)	1	(1)
<i>Carabus intricatus</i> LINNAEUS, 1761	0	(0)	1	(1)	1	(1)
<i>Harpalus distinguendus</i> (DUFTSCHMID, 1812)	0	(0)	1	(1)	1	(1)
<i>Leistus piceus</i> FRÖLICH, 1799	0	(0)	1	(1)	1	(1)
Number of individuals	397		428		825	
Number of species	19		22		23	

Table 3. ANOVA results for the number of individuals, species richness and the Shannon diversity of carabids. Leaf-litter addition (Treatment) as a factor and cover of herbs (Herbs) as a covariate

Variable	Source	SS	df	MS	F	p
Number of individuals	Treatment	0.0373	1	0.0373	0.8140	0.3710
	Herbs	0.0247	1	0.0247	0.5400	0.4660
	Error	2.3380	51	0.0460		
Number of species	Treatment	0.0042	1	0.0042	0.2940	0.5900
	Herbs	0.0004	1	0.0004	0.0280	0.8690
	Error	0.7330	51	0.0144		
Shannon diversity	Treatment	0.0042	1	0.0042	1.1880	0.2810
	Herbs	0.0003	1	0.0003	0.1100	0.7410
	Error	0.1800	51	0.0035		

The total number of individuals and the number of species were higher in the leaf-litter plots than in the control plots (Table 2), nevertheless the results of the ANOVA shows that leaf-litter addition had no effect on the structure of carabid assemblages, as there were no significant differences in the number of individuals, species and the Shannon diversity between the plots (Table 3). The result of the ordination also showed that leaf-litter addition had no effect on the structure of carabid assemblages, because samples from the control and the leaf-litter plots were weakly separated from each other (Fig. 1)

**Fig. 1.** Ordination (NMDS) of the pitfall catches based on the Bray-Curtis similarity index. ○: Traps of the control plots and ●: Traps of the leaf-litter plots

Leaf-litter addition was found to have no effect on the spatial distribution of four out of the five dominant carabid species (*Carabus violaceus*, *Cychrus caraboides*, *Abax parallelepipedus*, *Molops piceus*), while *Pterostichus oblongopunctatus* was more numerous in the leaf-litter samples as compared to the control samples (Table 4, Fig. 2).

Although difference in the percentage cover of herbs was significant between the control and leaf-litter plots (ANOVA; $F = 13.1878$, $df = 1, 52$, $p = 0.0006$), neither the number of carabid individuals, species richness, diversity nor the abundance of the five dominant carabid species indicated a correlation with the cover of herbs (Table 3 & 4). Ground temperature was significantly lower in the leaf-litter plots compared to the control plots (ANOVA; $F = 5.2862$, $df = 1, 52$, $p = 0.0255$), suggesting that leaf-litter material offers more stable temperature conditions. Moreover, the amount of prey items was significantly higher in the leaf-litter plots than in the control (ANOVA; $F = 6.6547$, $df = 1, 52$, $p = 0.0128$), indicating the leaf-litter preference of other ground-dwelling invertebrates and/or the fact that the leaf-litter layer may offer shelter against predators and desiccation. Similarly, the carabid's larvae were also more numerous in the leaf-litter plots than in the control ones (ANOVA; $F = 4.1416$, $df = 1, 52$, $p = 0.0469$), suggesting that leaf-litter layer may offer shelter against predators and desiccation and/or the fact that adults may prefer leaf-litter plots during egg-laying.

Table 4. ANOVA results for the catches of the five dominant carabid species. Leaf-litter addition (Treatment) as a factor and cover of herbs (Herbs) as a covariate

Species	Source	SS	df	MS	F	p
<i>Abax parallelepipedus</i>	Treatment	0.0665	1	0.0665	0.982	0.3260
	Herbs	0.1020	1	0.1020	1.5100	0.2250
	Error	3.4510	51	0.0677		
<i>Carabus violaceus</i>	Treatment	0.1090	1	0.1090	1.3630	0.2480
	Herbs	0.0069	1	0.0069	0.0870	0.7690
	Error	4.0640	51	0.0797		
<i>Cychrus caraboides</i>	Treatment	0.0097	1	0.0097	0.1600	0.6910
	Herbs	0.0185	1	0.0185	0.3050	0.5830
	Error	3.0860	51	0.0605		
<i>Molops piceus</i>	Treatment	0.0316	1	0.0316	0.4060	0.5270
	Herbs	0.0162	1	0.0162	0.2070	0.6510
	Error	3.9740	51	0.0779		
<i>Pterostichus oblongopunctatus</i>	Treatment	0.6370	1	0.6370	6.5420	0.0140
	Herbs	0.0105	1	0.0105	0.1080	0.7440
	Error	4.9660	51	0.0974		

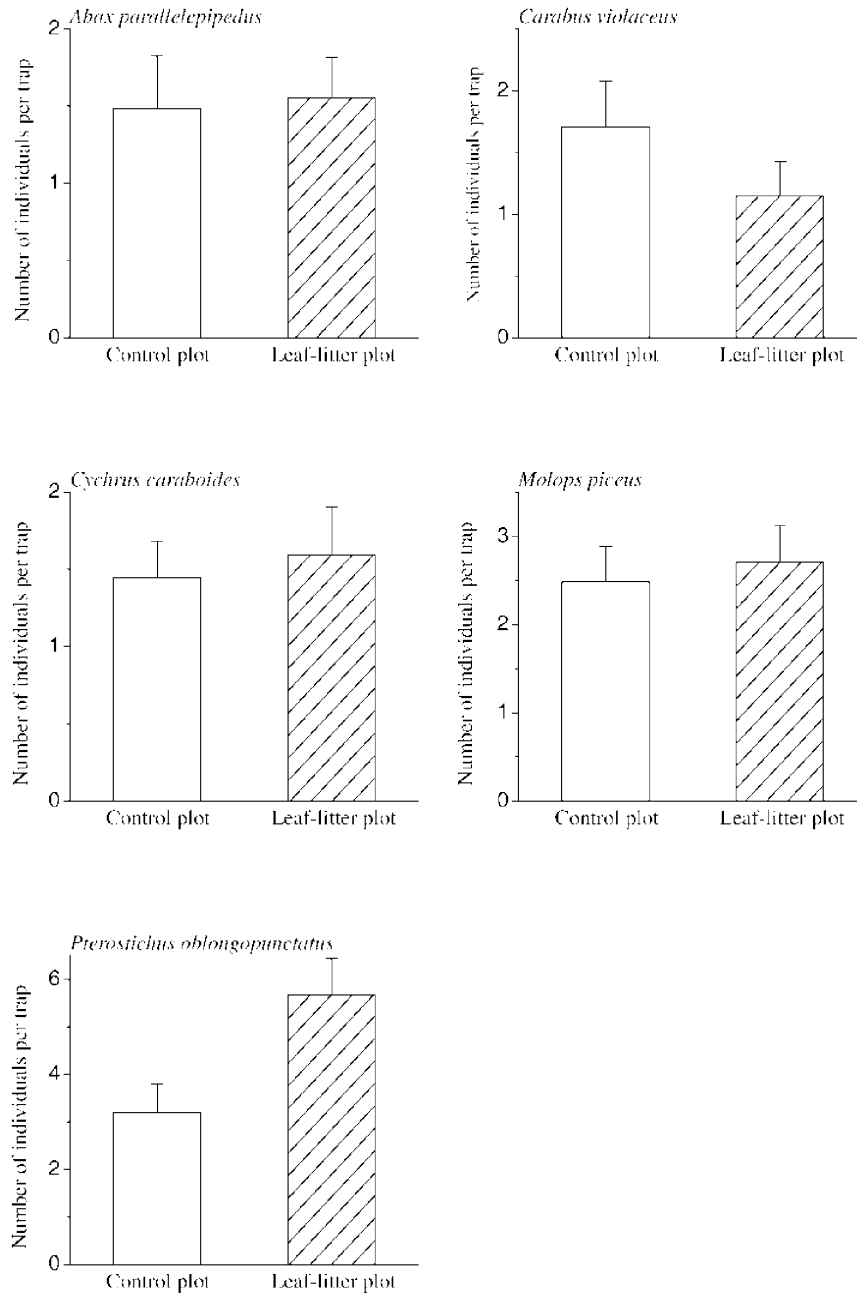


Fig. 2. The mean numbers (\pm S. E.) of the five dominant carabid species in the control and leaf-litter plots. Note different scales in the vertical axes

Forward stepwise multiple linear regression analysis showed that there were significant positive correlations between the cover of leaf-litter and the abundance of *Pterostichus oblongopunctatus*, between the number of *P. oblongopunctatus* and *Abax parallelepipedus* and between the number of *P. oblongopunctatus* and *Cychrus caraboides*, while the other studied environmental factors had no significant effects on the abundance of *P. oblongopunctatus* ($F = 5.5859$; $df = 4, 49$; $p = 0.0009$; $r = 0.5596$).

Figure 3 shows that both *Pterostichus oblongopunctatus* and *Abax parallelepipedus* have similar patterns of seasonal activity, as their number of individuals are the highest in spring and early summer, while during the rest of the season it is gradually decreasing.

DISCUSSION

Our results indicate that leaf-litter addition did not affect the structure of carabid assemblages, as there were no significant differences in the number of individuals, number of species and the Shannon diversity (Table 3), and the species

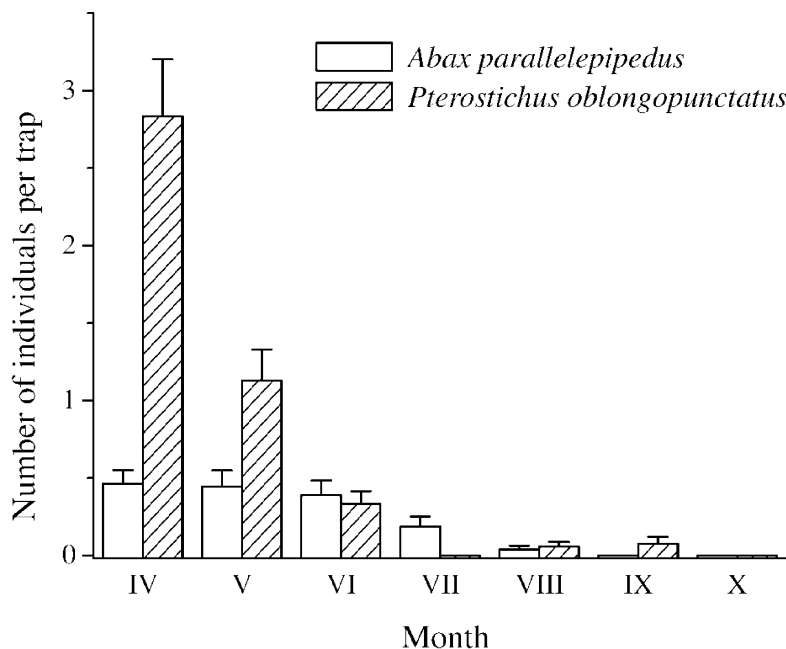


Fig. 3. Seasonal dynamics of the average number of individuals per trap for the two species (\pm S. E.)

composition between the plots were only slightly different as indicated by the NMDS (Fig. 2). However, both the total number of carabid individuals and species showed a weak increase in the leaf-litter plots (Table 2). Moreover, leaf-litter addition was found to have no significant effect on the spatial distribution of four out of the five dominant carabid species, although the number of individuals per trap of *Abax parallelepipedus*, *Cychrus caraboides* and *Molops piceus* were somewhat higher, while that of *Carabus violaceus* was slightly lower in the leaf-litter plots than in the control ones (Fig. 2 and Table 4). The fifth dominant carabid species (*Pterostichus oblongopunctatus*) was significantly more numerous in the leaf-litter samples as compared to the control samples (Fig. 2, Table 4). KOIVULA *et al.* (1999) examining the effect of leaf-litter addition on carabid beetles in a four-year experiment in a boreal coniferous forest, reported similar results, as they did not detect any significant leaf-litter effects on the number of species or the Shannon diversity. Their results, however, indicated that both the number of carabid individuals and the catches of three out of the four most common species increased in the litter plots as compared to the control ones (KOIVULA *et al.* 1999). Two dominant carabid species were the same in the study of KOIVULA *et al.* (1999) and in our investigation, namely *Cychrus caraboides* and *Pterostichus oblongopunctatus*. *Pterostichus oblongopunctatus* showed similar, leaf-litter preferring spatial distribution pattern in both experiments. During their long-term study KOIVULA *et al.* (1999) pointed out that *Cychrus caraboides* was significantly more abundant in the leaf-litter plots. In our short-term study *Cychrus caraboides* also showed a weak leaf-litter preference. In the study of KOIVULA *et al.* (1999) the number of individuals of *Cychrus caraboides* was only by five individuals higher in the leaf-litter plots than in the control plots in the first year immediately after the leaf-litter addition, so the difference in the first year after the treatment was not yet significant. Perhaps *Cychrus caraboides* responds later to the leaf-litter addition, therefore we cannot detect any significant effects of leaf-litter treatment on the spatial pattern of this species in our short-term study. KOIVULA *et al.* (1999) examined the effect of leaf-litter addition in the boreal coniferous forest, where there are deciduous trees as an admixture in the canopy layer; therefore, fallen leaf litter could accumulate on the ground surface at some sites. Carabid species living in this forest system adapted to this environment with leaf-litter patches and some carabid species may actively search and select the most favourable microhabitats (like the leaf-litter sites) in their environment. In our research, the studied Norway spruce stand was created after the clear-cutting of a beech forest and there are no deciduous trees in the canopy layer. In this non-native spruce plantation only habitat generalists and forest generalist carabid species can survive and maintain viable populations (ELEK *et al.* 2001, MAGURA *et al.* 2003). Habitat generalists may be poorly adapted to liv-

ing in habitats with leaf-litter patches. On the contrary the abundance of habitat generalist carabid species could decrease by increasing the amount and thickness of leaf-litter as showed by GUILLEMAIN *et al.* (1997). MAGURA *et al.* (2003) examining carabid assemblages of a beech forest and clear-cut originated succession of non-native Norway spruce stands in the same region of this study, identified *Abax parallelepipedus* and *Molops piceus* as habitat generalist species, and *Cychrus caraboides* and *Pterostichus oblongopunctatus* as forest generalist species and *Carabus violaceus* as a deciduous forest specialist species. According to the results of GUILLEMAIN *et al.* (1997) the catches of habitat generalist carabids, *Abax parallelepipedus* and *Molops piceus* may decrease in the leaf-litter plots. In the present study, however, there was no difference in the number of individuals caught in the leaf-litter and control plots, suggesting that these species can find their optimal habitat requirements in the leaf-litter dominated patches, too. *Carabus violaceus*, a deciduous forest specialist survived in low density in the Norway spruce plantations during the clear-cut originated succession (MAGURA *et al.* 2003). Examining an old beech stand and an adjacent old Norway spruce plantation ŠUSTEK (1984) also reported that forest specialists could survive in the monocultures. In contrast with the assumption that deciduous forest specialist species prefer leaf-litter plots in conifer stands, in our study the catches of *Carabus violaceus* was slightly smaller in the leaf-litter plots than in the control ones (Fig. 2).

The observed leaf-litter preference of *Pterostichus oblongopunctatus* could be explained with the microhabitat variations and/or the interspecific interactions. Leaf-litter addition could alter the microclimatic conditions (humidity, temperature, food availability etc.) and produce favourable microhabitat conditions that could influence the spatial distribution of *Pterostichus oblongopunctatus*. Indeed, ground temperature was significantly lower, while amount of prey items was significantly higher in the leaf-litter plots compared to the control plots (Table 1). We did not find significant differences in the relative humidity between the two plot types (Table 1), but we may have found significant differences if we had measured it not on the surface of the leaf litter but under it. *Pterostichus oblongopunctatus* is a forest generalist species and a generalist predator (LINDROTH 1985–86). Consequently it could aggregate in microhabitats with favourable environmental conditions (lower ground temperature and higher amount of prey items). Moreover, the leaf-litter plots with their favourable conditions may be advantageous egg-laying sites that provide shelter against predators and desiccation for the most vulnerable life stages (eggs and larvae) of carabids. This can explain the revealed higher number of carabid larvae in the leaf-litter plots (Table 1). HEESSEN (1980) showed that females of *Pterostichus oblongopunctatus* preferred laying their eggs in the coarser leaf litter.

Analysing crop contents of carabids, GRÜM (1971) showed that less than 15% of the individuals in a natural population were satiated and this proportion increased more than five-fold through food supplementation. HEESSEN (1980), BAARS and VAN DIJK (1984) and BRUNSTING and HEESSEN (1984) examining the fecundity of carabids, all concluded that the egg production and the number of eggs laid were largely determined by the amount of food and the adult density, that is the fecundity was greater if the food supplies became better or if the density of breeding animals was lower. The most probable cause for these relationships is the competition for food. All these results indicate that food for carabids is generally limited in the field and these findings support the fact that there are density-dependent regulations in carabid assemblages. LENSKI (1982) also supposed that carabid species competed for limiting food in the field. LOREAU (1990, 1994), testing the significance of the competition in a carabid beetle assemblage, suggests that dominant species in a forest habitat are affected by competitive interactions. Therefore, in our case, it is presumed that dominant species compete for the foods with each other. However, we showed that there were significant positive correlations between the amount of *Pterostichus oblongopunctatus* and *Abax parallelepipedus* and between the number of *P. oblongopunctatus* and *Cychrus caraboides*. How can the abundance of these dominant species increase if the food is limited and we suppose that they compete for food? It is unlikely that *Pterostichus oblongopunctatus* and *Cychrus caraboides* compete for food, since their dietary do not overlap. *Pterostichus oblongopunctatus* is a generalist predator, while *Cychrus caraboides* is an oligophagous predator, it specialises on hunting snails as it is reflected in its body structure (THIELE 1977). However, both *Pterostichus oblongopunctatus* and *Abax parallelepipedus* are generalist predators foraging nocturnally and their dietary considerably overlaps (THIELE 1977). The competition for food between *Pterostichus oblongopunctatus* and *Abax parallelepipedus* could be avoided by different temporal or spatial distribution. But *Pterostichus oblongopunctatus* and *Abax parallelepipedus* have similar patterns of seasonal activity, as their number of individuals are the highest in spring and early summer, while during the rest of the season it is gradually decreasing (Fig. 3). However, leaf-litter layer may offer new niches, for example by providing space for the vertical separation of the coexisting species. *Abax parallelepipedus* are active on the surface of the leaf litter, while *Pterostichus oblongopunctatus* within the leaf litter (LOREAU 1987, SERGEEVA 1994). In the present situation, the coexistence of the dominant carabid species can be explained by their different vertical distribution. *Pterostichus oblongopunctatus* within the leaf-litter could avoid interspecific competition with the above mentioned dominant carabid species. The leaf-litter preference of

Pterostichus oblongopunctatus could be also due to the avoidance of the interspecific competition with *Abax parallelepipedus*.

Creating conifer plantations has direct and indirect harmful effects on forest carabids (MAGURA *et al.* 2000a, FAHY & GORMALLY 1998). Both the clear-cutting of the native forest, the mechanical soil preparation (grubbing and deep loosening) before the reforestation and the establishment of even-aged conifer stands without deciduous trees as an admixture contribute to the homogenisation of the previously heterogeneous habitat. All these practices directly cause destruction of the forest specialist carabids. However, creating plantations also influences carabids indirectly. The earlier continuous landscape is fragmented by inhospitable habitats (plantations) for forest specialists, hereby the patch-to-patch dispersal of the forest specialists and maintenance of meta-populations become more difficult or even impossible. Our short-term study, and/or the other long-term research (KOIVULA *et al.* 1999) also demonstrate that artificially enhanced microhabitat heterogeneity (leaf-litter addition) in relatively homogenous habitats increases the number of total carabid individuals and that of the dominant species.

Based on our results, using carabid beetles as a good indicator group, for the modern ecologically sound silvicultural management the following proposals could be made. Because of the financial interest of the forestry companies plantations of quick growth and with timber of good quality (like the Norway spruce in Hungary) will be established hereafter. However, in the spruce plantations deciduous trees as an admixture must be also planted, which are crucial to maintain heterogeneity, e.g. through producing fallen leaf litter. In the conifer stands dead and decaying trees must be left untouched, as they provide excellent hiding and overwintering sites for insects. Instead of the clear-cutting of the whole stand of the aged plantation, openings or gaps must be logged (see KOIVULA 2002), in which the deciduous herbs, shrubs and trees can colonise. The colonised deciduous plants firstly enhance the habitat heterogeneity, secondly provide refuges during logging of other gaps in the plantations. All of the proposed methods contribute to the increase of habitat heterogeneity, and ensure the enhancing of biodiversity.

*

Acknowledgements – Research was supported by the grants of the Hungarian Scientific Research Fund (OTKA research grant no. T32130).

REFERENCES

BAARS, M. A. (1979) Catches in pitfall traps in relation to mean densities of carabid beetles. *Oecologia* **41**: 25–46.

- BAARS, M. A. & VAN DIJK, Th. S. (1984) Population dynamics of two carabid beetles at a Dutch heathland. II. Egg production and survival in relation to density. *J. Anim. Ecol.* **53**: 389–400.
- BAGUETTE, M. & GÉRARD, S. (1993) Effects of spruce plantations on carabid beetles in southern Belgium. *Pedobiologia* **37**: 129–140.
- BEDFORD, S. E. & USHER, M. B. (1994) Distribution of arthropod species across the margins of farm woodlands. *Agr. Ecosyst. Environ.* **48**: 295–305.
- BIRD, S., COULSON, R. N. & CROSSLEY, D. A. (2000) Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. *Forest Ecol. Manag.* **131**: 65–80.
- BRUNSTING, M. H. & HEESSEN, H. J. L. (1984) Density regulation in the carabid beetle *Pterostichus oblongopunctatus*. *J. Anim. Ecol.* **53**: 751–760.
- BUTTERFIELD, J., LUFF, M. L., BAINES, M. & EYRE, M. D. (1995) Carabid beetle communities as indicators of conservation potential in upland forests. *Forest Ecol. Manag.* **79**: 63–77.
- DAY, K. R. & CARTHY, J. (1988) Changes in carabid beetle communities accompanying a rotation of Sitka spruce. *Agr. Ecosyst. Environ.* **24**: 407–415.
- DESENDER, K., ERVYNCK, A. & TACK, G. (1999) Beetle diversity and historical ecology of woodlands in Flanders. *Belg. J. Zool.* **129**: 139–156.
- DIGWEED, S. C., CURRIE, C. R., CÁRCAMO, H. A. & SPENCE, J. R. (1995) Digging out the digging-in effect of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia* **39**: 561–576.
- ELEK, Z., MAGURA, T. & TÓTHMÉRÉSZ, B. (2001) Impacts of non-native Norway spruce plantation on abundance and species richness of ground beetles (Coleoptera: Carabidae). *Web Ecology* **2**: 32–37.
- EYRE, M. D., LUFF, M. L. & RUSHTON, S. P. (1990) The ground beetle (Coleoptera, Carabidae) fauna of intensively managed agricultural grasslands in northern England and southern Scotland. *Pedobiologia* **34**: 11–18.
- FAHY, O. & GORMALLY, M. (1998) A comparison of plant and carabid beetle communities in an Irish oak woodland with a nearby conifer plantation and clearfelled site. *Forest Ecol. Manag.* **110**: 263–273.
- GRÜM, L. (1971) Spatial differentiation of the *Carabus* L. (Carabidae, Coleoptera) mobility. *Ekologia Polska* **19**: 1–34.
- GUILLEMAIN, M., LOREAU, M. & DAUFRESNE, T. (1997) Relationships between the regional distribution of carabid beetles (Coleoptera, Carabidae) and the abundance of their potential prey. *Acta Oecol.* **18**: 465–483.
- HEESSEN, H. J. L. (1980) Egg production of *Pterostichus oblongopunctatus* (Fabricius) (Col., Carabidae) and *Philonthus decorus* (Gravenhorst) (Col., Staphylinidae). *Neth. J. Zool.* **30**: 35–53.
- HELIOLA, J., KOIVULA, M. & NIEMELÄ, J. (2001) Distribution of Carabid Beetles (Coleoptera, Carabidae) across a Boreal Forest-Clearcut Ecotone. *Conserv. Biol.* **15**: 370–377.
- INGS, T. C. & HARTLEY, S. E. (1999) The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. *Forest Ecol. Manag.* **119**: 123–136.
- KOIVULA, M. (2002) Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). *Forest Ecol. Manag.* **167**: 103–121.
- KOIVULA, M., KUKKONEN, J. & NIEMELÄ, J. (2002) Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. *Biodivers. Conserv.* **11**: 1269–1288.
- KOIVULA, M., PUNTTILA, P., HAILA, Y. & NIEMELÄ, J. (1999) Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. *Ecography* **22**: 424–435.
- KOTZE, D. J. & SAMWAYS, M. J. (1999) Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. *Biodivers. Conserv.* **8**: 1339–1363.

- LEGENDRE, P. & LEGENDRE, L. (1998) *Numerical Ecology*. Elsevier, Amsterdam, 870 pp.
- LENSKI, R. E. (1982) Effects of forest cutting on two Carabus species: evidence for competition for food. *Ecology* **63**: 1211–1217.
- LINDROTH, C. H. (1985–86) *The Carabidae (Coleoptera) of Fennoscandia and Denmark*. Scandinavian Science Press, Leiden, 499 pp.
- LOREAU, M. (1987) Vertical distribution of activity of carabid beetles in a beech forest floor. *Pedobiologia* **30**: 173–178.
- LOREAU, M. (1990) Competition in a carabid beetle community: a field experiment. *Oikos* **58**: 25–38.
- LOREAU, M. (1992) Species abundance patterns and the structure of ground-beetle communities. *Ann. Zool. Fennici* **28**: 49–56.
- LOREAU, M. (1994) Ground beetles in a changing environment: determinants of species diversity and community assembly. Pp. 77–98. In BOYLE, T. J. & BOYLE, C. E. B. (eds.): *Biodiversity, temperate ecosystems and global change*. Springer Verlag, Berlin.
- LÖVEI, G. & SUNDERLAND, K. D. (1996) Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annu. Rev. Entomol.* **41**: 231–256.
- MAGURA, T. (2000) *Quantitative faunistical, biogeographical and ecological analyses of carabid assemblages*. Ph.D. thesis. Debrecen.
- MAGURA, T. (2002) Carabids and forest edge: spatial pattern and edge effect. *Forest Ecol. Manag.* **157**: 23–37.
- MAGURA, T., ELEK, Z. & TÓTHMÉRÉSZ, B. (2002) Impacts of non-native spruce reforestation on ground beetles. *Eur. J. Soil. Biol.* **38**: 291–295.
- MAGURA, T., KÖDÖBÖCZ, V. & BOKOR ZS. (2001a) Effects of forestry practices on carabids (Coleoptera: Carabidae) – Implication for nature management. *Acta Phytopath. Entomol. Hung.* **36**: 179–188.
- MAGURA, T., TÓTHMÉRÉSZ, B. & BORDÁN, ZS. (1997) Comparison of the carabid communities of a zonal oak-hornbeam forest and pine plantations. *Acta zool. hung.* **43**: 173–182.
- MAGURA, T., TÓTHMÉRÉSZ, B. & BORDÁN, ZS. (2000a) Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. *Biol. Conserv.* **93**: 95–102.
- MAGURA, T., TÓTHMÉRÉSZ, B. & ELEK, Z. (2003) Diversity and composition of carabids during a forestry cycle. *Biodiv. Conserv.* **12**: 73–85.
- MAGURA, T., TÓTHMÉRÉSZ, B., MOLNÁR, T. (2001b) Forest edge and diversity: carabids along forest-grassland transects. *Biodivers. Conserv.* **10**: 287–300.
- MAGURA, T., TÓTHMÉRÉSZ, B., MOLNÁR, T. (2000b) Spatial distribution of carabids along grass-forest transects. *Acta Zool. Acad. Sci. Hung.* **46**: 1–17.
- MÁTYÁS, CS. (1996) Erdészeti ökológia. (*Forestry ecology*.) Mezőgazda Kiadó, Budapest, 312 pp. [in Hungarian]
- MOLNÁR, T., MAGURA, T., TÓTHMÉRÉSZ, B. & ELEK, Z. (2001) Ground beetles (Carabidae) and edge effect in oak-hornbeam forest and grassland transects. *Eur. J. Soil. Biol.* **37**: 297–300.
- NIEMELÄ, J. (1997) Invertebrates and boreal forest management. *Conserv. Biol.* **11**: 601–610.
- NIEMELÄ, J. (1999) Management in relation to disturbance in the boreal forest. *Forest Ecol. Manag.* **115**: 127–134.
- NIEMELÄ, J., LANGOR, D. & SPENCE, J. R. (1993) Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. *Conserv. Biol.* **7**: 551–561.
- SAMWAYS, M. J. (1994) *Insect conservation biology*. Chapman and Hall, London, 358 pp.

- SERGEEVA, T. K. (1994) Seasonal dynamics of interspecific trophic relations in a carabid beetle assemblage. Pp. 367–370. In DESENDER, K., DUFRÈNE, M., LOREAU, M., LUFF, M. L. & MAELFAIT, J.-P. (eds): *Carabid beetles: ecology and evolution*. Kluwer Academic Publishers, Dordrecht.
- SOKAL, R. R. & ROHLF, F. J. (1981) *Biometry*. W. H. Freeman, New York, 310 pp.
- SPENCE, J. R. & NIEMELÄ, J. (1994) Sampling carabid assemblages with pitfall traps: the madness and the method. *Can. ent.* **126**: 881–894.
- SPENCE, J. R., LANGOR, D. W., NIEMELÄ, J., CÁRCAMO, H. A. & CURRIE, C. R. (1996) Northern forestry and carabids: the case for concern about old-growth species. *Ann. Zool. Fennici* **33**: 173–184.
- ŠUSTEK, Z. (1984) Carabidae and Staphylinidae of two forest reservations and their reactions on surrounding human activity. *Biologia* **39**: 137–162.
- SZYSZKO, J. (1987) How can the fauna of Carabidae be protected in managed pine forest? *Acta Phytopath. Entomol. Hung.* **22**: 293–303.
- THIELE, H. U. (1977) *Carabid beetles in their environments*. Springer, Berlin, 369 pp.
- TÓTHMÉRÉSZ, B. (1993) NuCoSA 1.0: Number Cruncher for Community Studies and other Ecological Applications. *Abstracta Botanica* **17**: 283–287.
- WERNER, S. M. & RAFFA, K. F. (2000) Effects of forest management practices on the diversity of ground-occurring beetles in mixed northern hardwood forests of the Great Lakes Region. *Forest Ecol. Manag.* **139**: 135–155.

Revised version received December 10, 2003, accepted August 19, 2004, published September 15, 2004