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Impacts of leaf-litter addition on carabids in a conifer plantation

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Abstract. As a fine-scale, manipulative model experiment leaf litter was added in plots to increase habitat heterogeneity in a 50-year-old Norway spruce plantation, established after the clear-cutting of a native beech forest, during a 2-year period in the Hungarian Mountain Range. Pitfall trap catches of carabids from leaf-litter plots were compared with those from control plots to explore the effect of leaf-litter addition. Difference in the species composition was revealed by ordination; scores of the samples of the two plot types were significantly separated along the first MDS axis. The most numerous species (*Pterostichus oblongopunctatus*) was significantly more abundant in the leaf-litter plots. However, there were no significant differences for the other most frequently obtained species. Habitat generalist species were the most abundant, followed by forest generalists, then forest specialists, and there were some open habitat species. Enhanced habitat heterogeneity (leaf-litter addition) in homogeneous plantations influenced the spatial distribution and composition of carabids, through altered abiotic (lower ground temperature in the leaf-litter plots) and biotic (more prey items) factors. Differences in abundance, species richness and Shannon diversity were not significant between the control and the manipulated plots, although carabid catch was higher in the leaf-litter plots during both years. Forestry practices to increase habitat heterogeneity should be considered to enhance biodiversity in managed forests.

Key words: Carabid beetles, Diversity, Environmental conditions, Habitat heterogeneity, Nature management

Introduction

As in many other European countries, large areas of native deciduous forests have been reforested in Hungary during the 20th century. Non-native Norway spruce (*Picea abies*) was a preferred tree species used in reforestation because of its quick growth and high productivity. After the clear-cutting of native forests, soil in felled areas was often mechanically prepared for seedlings by grubbing and deep loosening. Clear-cutting, soil preparation and the creation of even-aged monocultures of conifers drastically alter the microclimatic, abiotic and biotic conditions, and contribute to the spatial homogenisation of the reforested habitats (Mátyás 1996). Small-scale heterogeneity within forest stands considerably enhances local species richness and supports the existence of specialist species, so spatial heterogeneity is recognized as an important factor promoting the diversity of ecological systems (Pickett and White 1985; Niemelä 1997).

The distribution patterns and composition of ground-dwelling carabid beetles were related to habitat heterogeneity at various spatial scales (Niemelä et al. 1992, 1996; Loreau and Nolf 1993; Niemelä and Spence 1994; Penev 1996; Magura et al. 2000b). Carabids are especially sensitive to soil disturbance, changes in environmental conditions and the homogenisation of their habitat (Niemelä 1997, 1999; Magura et al. 1997, 2001a, 2002, 2003; Desender et al. 1999; Koivula 2002; Koivula et al. 2002). Carabid assemblages change remarkably after reforestation, with several hardwood forest specialists declining or disappearing, leaving only the habitat generalist and forest generalist carabid species being abundant (Baguette and Gérard 1993; Niemelä et al. 1993; Butterfield et al. 1995; Spence et al. 1996; Butterfield 1997; Ings and Hartley 1999; Bird et al. 2000; Elek et al. 2001). At the local, within-habitat scale spatial heterogeneity of environmental variables is considered to be an important factor influencing species distribution and the abundance of carabids (e.g., Eyre and Luff 1994; Niemelä 1999; Magura et al. 2003). In 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 encouraged the recolonization by native deciduous plants and the accumulation of leaf litter, significantly contributed to the enhancement of carabid diversity in a non-native Norway spruce plantation in an area where oak-hornbeam was the typical forest. Therefore, we were interested in studying the effect of artificial leaf-litter addition on the spatial pattern of carabids in a non-native conifer monoculture and comparing our results with those of Koivula et al. (1999) carried out in native boreal forests. Our objectives were to: (1) Determine if leaf-litter addition affects the structure of carabid assemblages (i.e., determine if real carabid abundance, species richness and Shannon diversity increase in the leaf-litter plots?); (2) Determine if leaf-litter addition influences species composition of the carabid assemblages; and (3) Determine the impact of leaf-litter addition on the spatial distribution of the most numerous carabid species. Finally, based on our results we make proposals for modern silvicultural management. We wanted to demonstrate in a fine-scale manipulative experiment that the addition of the leaf litter of the trees of the native forest improves the diversity of the carabid beetles.

Materials and methods

Study area and sampling

The study was performed in the North Hungarian Mountain Range, in a 50-year-old Norway spruce plantation (12 ha). The Norway spruce plantation was established after clear-cutting of a beech forest. Norway spruce is not a native species in Hungary. Three treated and three control square plots, each of 25 m^2 area, were established randomly in the study area. Distances between the plots and to the nearest forest edge were at least 30 m in order to provide adequate statistical independence (Digweed et al. 1995) and to avoid edge effects (Kotze and Samways 1999; Magura et al. 2000b, 2001b; Magura 2002; Molnár et al. 2002). In the treated plots, leaf litter collected from the neighbouring beech forest was added in the beginning of November 1999. The thickness of the added leaf litter was at least 15 cm in order to uniformly cover the plots. We again added leaves to each leaf-litter plot in late November 2000 to imitate natural leaf fall. Ten samples of 1 l of the leaf litter used were put in bags and examined in the laboratory for presence of ground beetle larvae and adults; none were found. In each plot, nine pitfall traps (2 m apart) were placed in a three-by-three grid to collect carabid beetles. The beetles were collected with unbaited pitfall traps consisting of plastic cups (diameter 100 mm, volume 500 ml) partly filled with 70% ethylene-glycol and detergent. The traps were covered with bark pieces to protect them from litter and rain (Spence and Niemelä 1994). Trapped beetles were collected monthly from April 2 to November 30 in both 2000 and 2001. For the numerical analyses we pooled samples from the different months. Several authors (Baars 1979) 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 most of the beetles' activity period.

In both years, we studied eight environmental factors that may affect the distribution of carabid species (Thiele 1977; Lövei and Sunderland 1996). (1) Ground temperature at 2 cm depth, (2) air temperature on the surface, and (3) relative humidity on the surface were measured monthly near each trap. The statistical analyses were based on averages. We also estimated (4) the cover of leaf litter, (5) herbs, (6) shrubs and (7) canopy around the traps within a 1 m-diameter circle. We also counted (8) the number of other invertebrates (other Coleoptera, Chilopoda, Collembola, Diplopoda, Gastropoda, and Isopoda) in the traps which could be taken as potential prey for carabids (Sergeeva 1994). Moreover, we analysed the spatial distribution of the carabid larvae of the studied plots. Table 1 shows the average values of the environmental factors.

Table 1. Average values of the studied environmental factors in the study plots based on the measures of the two study years.

	Control plot	Leaf-litter plot	Statistics (df = 1,52)
Ground temperature at 2 cm depth (°C)	16.64a	16.20b	$F = 5.83$, $P = 0.026$
Air temperature on the surface (°C)	21.53a	21.26a	$F = 0.05$, $P = 0.816$
Relative humidity (%)	67.02a	67.83a	$F = 0.49$, $P = 0.486$
Leaf litter cover (%)	0.19a	93.70b	$F = 4769$, $P < 0.0001$
Herb cover (%)	14.19a	6.43b	$F = 12.4$, $P = 0.0009$
Shrub cover (%)	4.02a	2.01a	$F = 3.38$, $P = 0.072$
Canopy cover (%)	76.16a	77.14a	$F = 0.06$, $P = 0.806$
Number of prey items/trap	105.61a	125.65b	$F = 6.12$, $P = 0.017$
Number of carabid larvae/trap	1.87a	2.93b	$F = 9.13$, $P = 0.004$

Different letters indicate significant ($P < 0.05$) differences by repeated measures ANOVA.

The only tree species was the Norway spruce (*Picea abies*). The shrub layer was almost entirely missing. Small gaps in the canopy allowed sporadic presence of other species, mainly elderberry (*Sambucus nigra*), more rarely hornbeam (*Carpinus betulus*), or beech (*Fagus sylvatica*). The sparce herbaceous layer was composed of seedlings of the above shrubs, of *Acer pseudoplatanoides* and *A. platanoides*, plus weeds and shade-tolerant generalists: *Ajuga reptans*, *Carex pilosa*, *Cucubalus baccifera*, *Dactylis glomerata*, *Epilobium montanum*, *Impatiens noli-tangere*, *Glechoma hirsuta*, *Mycelis muralis*, *Oxalis acetosella*, *Fragaria vesca*, *Lamium purpureum*, *Senecio nemorensis*, and *Rubus* spp.

Data analysis

The values of the environmental variables between the leaf litter and the control plots were examined by repeated measure analysis of variance. Also number of individuals, species richness and the Shannon diversity index of the trapped carabids, and the abundance of the five most numerous species (exceeding 5% of the total catch) between the two plot types were examined by repeated measure analysis of variance. The cover of herbs was significantly different between the leaf-litter and control plots (Table 1). This difference was not due to the leaf-litter addition. A dense herb layer potentially correlates negatively with carabid catches (Koivula et al. 2002). Therefore, we included the cover of herbs as a covariate in the ANOVA model. Normal distribution of the data was achieved by $\log(x + 1)$ transformation (Sokal and Rohlf 1981). The analyses were carried out using the SPSS-PC program. Non-metric multidimensional scaling (MDS) was used to display the similarity of the pitfall catches from the leaf-litter plots and from the control ones in both years. The Bray–Curtis index was used to measure the similarity in abundances (Legendre and Legendre 1998); calculations were done using the NuCoSA package (Tóthmérész 1993). The scores of pitfall catches on axes 1 and 2 were analysed by repeated measures ANOVA in order to determine whether pitfall catches from the two plot types were significantly different.

Results

Results of the repeated measures ANOVA showed that leaf-litter addition altered the microclimatic conditions of the plots. The ground temperature was significantly lower in the leaf litter plots compared to the control plots (Table 1). There was significantly more prey in the leaf-litter plots than in the control (Table 1; repeated measures ANOVA). Similarly, the carabid larvae were significantly more numerous in the leaf-litter plots than in the control plots (Table 1; repeated measures ANOVA).

The total carabid catch consisted of 1656 individuals representing 24 species (Table 2). Although the dominance order of the species varied slightly in the two trapping years, the total number of trapped individuals was nearly the same in both years (825 and 831 individuals, respectively, see Table 2). The most numerous species were *Pterostichus oblongopunctatus*, *Abax parallelepipedus*, *Molops piceus*, *Carabus glabratus* and *Carabus hortensis*. These five carabid species made up 72.5% of the total catch. Three species were caught exclusively in the leaf-litter plots, while one species was caught exclusively in the control plots during the 2-year study (Table 2). The number of habitat generalist individuals was the highest, followed by forest generalists, forest species and finally the individuals of open habitat species (768, 643, 216 and 29 individuals, respectively; Table 2).

The total number of individuals was higher in the leaf-litter plots than in the control plots in both years. The total number of species was also higher in the leaf-litter plots compared to the control ones in 2000, although no difference was observed the following year. However, both the total number of individuals and species were higher in the leaf-litter plots when data from both years were pooled (Table 2).

There were no statistically significant differences in the number of individuals, species richness or Shannon diversity between leaf-litter and control plot (Table 3).

Table 2. The catches of carabid beetles and their habitat preference in the studied region according to Magura et al. (2002).

Species	Habitat preference	2000		2001	
		Control	Leaf-litter	Control	Leaf-litter
Pterostichus oblongopunctatus (F.)	ForGen	86	153	40	100
Abax parallelepipedus (Pill. et Mitt.)	HabGen	40	42	95	89
Molops piceus (Panz.)	HabGen	67	73	28	56
Carabus glabratus Payk.	HabGen	26	22	90	52
Carabus hortensis L.	ForGen	31	13	51	46
Cychrus caraboides (L.)	ForGen	39	43	6	18
Carabus violaceus L.	ForSpec	46	31	13	15
Pterostichus niger (Schall.)	HabGen	4	2	35	37
Abax parallelus (Dft.)	ForSpec	25	11	16	14
Aptinus bombarda (Ill.)	ForSpec	8	5	3	3
Notiophilus biguttatus (F.)	ForGen	10	5	1	0
Carabus nemoralis O. F. Müll.	ForSpec	4	5	3	1
Harpalus latus (L.)	Open	1	7	2	1
Platyderus rufus (Dft.)	HabGen	2	6	0	1
Carabus convexus F.	ForSpec	2	0	6	0
Carabus coriaceus L.	Open	3	2	0	1
Zabrus tenebrioides (Goez.)	Open	0	0	5	1
Harpalus marginellus Dej.	Open	1	2	0	0
Pterostichus melanarius Ill.	ForSpec	1	1	0	1
Carabus intricatus L.	ForSpec	0	1	1	0
Synuchus vivalis Ill.	Open	1	1	0	0
Bembidion properans (Steph.)	HabGen	0	1	0	0
Harpalus distinguendus (Dft.)	Open	0	1	0	0
Leistus piceus Fröl.	ForGen	0	1	0	0
Total number of individuals		397	428	395	436
Total number of species		19	22	16	16

HabGen = habitat generalist, ForGen = forest generalist, ForSpec = forest specialist and Open = open habitat species.

The result of MDS ordination shows that leaf-litter addition had an effect on the composition of carabid assemblages, as samples from the control and the leaf-litter plots separated from each other along the first axis in both years

Table 3. The results of repeated measures ANOVA for the number of individuals, species richness and the Shannon diversity of carabids captured in Norway spruce plantation with and without leaf-litter addition; No/traps, 2000–2001.

Variable	Source	SS	df	MS	*F*	*P*
Number of individuals	*Within-subjects effects*					
	Year	0.0008	1	0.0008	0.0200	0.8880
	Year × Treatment	0.0002	1	0.0002	0.0050	0.9470
	Year × Herbs	0.0000	1	0.0000	0.0000	0.9980
	Error	1.9070	51	0.0374		
	Between-subjects effects					
	Treatment	0.0677	1	0.0677	1.0050	0.3210
	Herbs	0.0498	1	0.0498	0.7380	0.3940
	Error	3.4380	51	0.0674		
Number of species	*Within-subjects effects*					
	Year	0.0230	1	0.0230	2.5050	0.1200
	Year × Treatment	0.0016	1	0.0016	0.1790	0.6740
	Year × Herbs	0.0041	1	0.0041	0.4450	0.5080
	Error	0.4670	51	0.0092		
	Between-subjects effects					
	Treatment	0.0027	1	0.0027	0.1500	0.7010
	Herbs	0.0013	1	0.0013	0.0720	0.7900
	Error	0.9050	51	0.0177		
Shannon diversity	*Within-subjects effects*					
	Year	0.0047	1	0.0047	1.6300	0.2070
	Year × Treatment	0.0014	1	0.0014	0.4740	0.4940
	Year × Herbs	0.0004	1	0.0004	0.1550	0.6950
	Error	0.1470	51	0.0029		
	Between-subjects effects					
	Treatment	0.0030	1	0.0030	0.5980	0.4430
	Herbs	0.0000	1	0.0000	0.0090	0.9240
	Error	0.2560	51	0.005		

Year = the effect of study year (2000 and 2001); Treatment (leaf-litter addition), and Herbs (cover of herbs) were used as covariates.

(Figure 1). Results of the repeated measures ANOVA also confirmed that the scores of the pitfall catches on axis 1 were significantly different between the leaf-litter and control plots and showed that there was a change in the pitfall

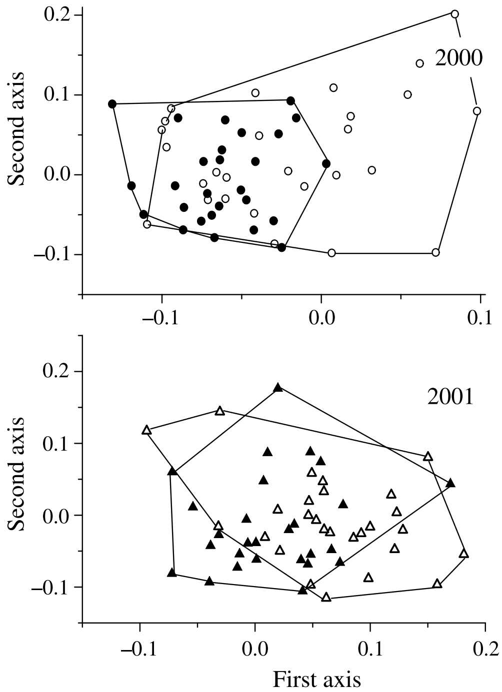

Figure 1. Ordination (MDS) of the pitfall catches based on the Bray–Curtis similarity index. Notations: empty circles and empty triangles – traps in the control plots; bullets and black triangles – traps in the litter enhanced plots.

catches between the two years (Table 4). There was no significant difference in the scores of pitfall traps on axis 2 either between the plot types, or between the study years (Table 4).

Pterostichus oblongopunctatus was more numerous in the leaf-litter plots as compared to the control ones (Figure 2 and Table 5). The abundance of the other four most numerous carabid species (*Abax parallelepipedus*, *Molops piceus*, *Carabus glabratus*, *C. hortensis*) did not differ significantly between the two plot types (Figure 2 and Table 5). Year was a significant source of variation in the repeated measures ANOVA in the case of *A. parallelepipedus* and *C. glabratus*, while it was marginally significant in the case of *P. oblongopunctatus*, indicating changes in abundance of these species between the study years (Figure 2 and Table 5).

Although difference in the percentage cover of herbs was significant between the control and leaf-litter plots (Table 1; repeated measures ANOVA), neither the number of carabid individuals, species richness, diversity nor the abundance of the five most numerous carabid species indicated a correlation with the cover of herbs (Tables 3 and 5).

Table 4. The results of ANOVA with repeated measures for the scores of pitfall catches both on the first and second axis.

Variable	Source	SS	df	MS	*F*	*P*
First coordinate	*Within-subjects effects*					
	Year	0.1820	1	0.1820	61.9290	0.0000
	Year × Treatment	0.0006	1	0.0006	0.2210	0.6410
	Error	0.1530	52	0.0029		
	Between-subjects effects					
	Treatment	0.0577	1	0.0058	21.1530	0.0000
	Error	0.1420	52	0.0027		
Second coordinate	*Within-subjects effects*					
	Year	0.0119	1	0.0119	3.4420	0.0690
	Year × Treatment	0.0039	1	0.0039	1.1250	0.2940
	Error	0.1800	52	0.0035		
	Between-subjects effects					
	Treatment	0.0083	1	0.0083	1.6520	0.2040
	Error	0.2600	52	0.0050		

Year = the effect of study year (2000 and 2001), Treatment = the leaf-litter addition.

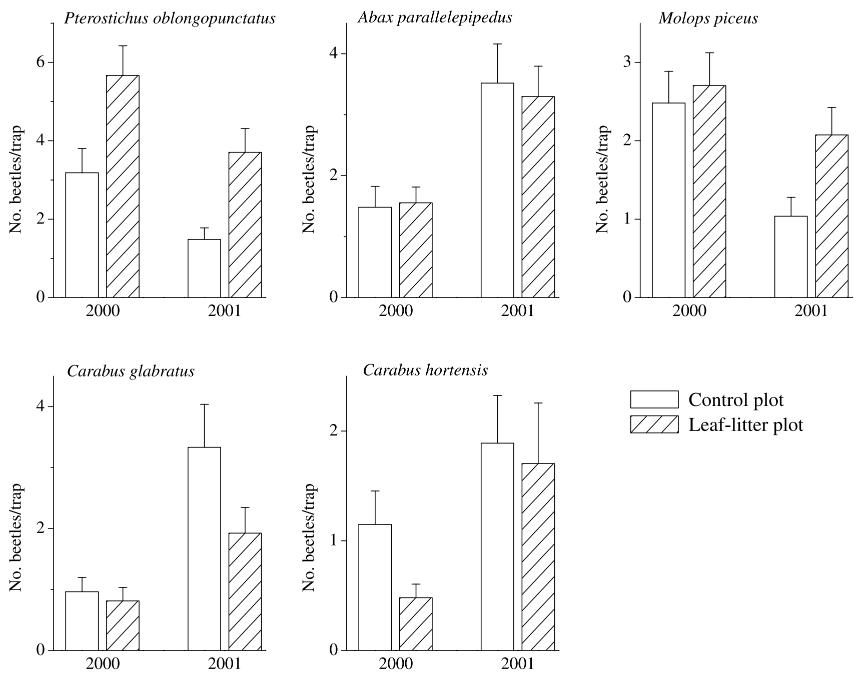

Figure 2. The mean numbers (±S.E.) of the five most numerous carabid species in the control and leaf-litter plots. Note different scales on the vertical axes.

Table 5. The results of ANOVA with repeated measures for the catches of the five most numerous carabid species.

Variable	Source	SS	df	MS	*F*	*P*
Pterostichus oblongopunctatus	*Within-subjects effects*					
	Year	0.2830	1	0.2830	3.9630	0.0520
	Year × Treatment	0.0054	1	0.0054	0.0760	0.7840
	Year × Herbs	0.0029	1	0.0029	0.0400	0.8420
	Error	3.6350	51	0.0713		
	Between-subjects effects					
	Treatment	1.4450	1	1.4450	13.5530	0.0010
	Herbs	0.0084	1	0.0084	0.0780	0.7810
	Error	5.4390	51	0.1070		
Abax parallelepipedus	*Within-subjects effects*					
	Year	0.8590	1	0.8590	11.7280	0.0010
	Year × Treatment	0.0459	1	0.0459	0.6260	0.4320
	Year × Herbs	0.0625	1	0.0625	0.8520	0.3600
	Error	3.7360	51	0.0733		
	Between-subjects effects					
	Treatment	0.0226	1	0.0226	0.2600	0.6120
	Herbs	0.0409	1	0.0409	0.4700	0.4960
	Error	4.4340	51	0.0869		
Molops piceus	*Within-subjects effects*					
	Year	0.1160	1	0.1160	2.0380	0.1590
	Year × Treatment	0.0527	1	0.0527	0.9300	0.3400
	Year × Herbs	0.0377	1	0.0377	0.6650	0.4190
	Error	2.8930	51	0.0567		
	Between-subjects effects					
	Treatment	0.2320	1	0.2320	2.6580	0.1090
	Herbs	0.0002	1	0.0002	0.0020	0.9610
	Error	4.4430	51	0.0871		
Carabus glabratus	*Within-subjects effects*					
	Year	1.1360	1	1.1360	15.8160	0.0000
	Year × Treatment	0.2540	1	0.2540	3.5410	0.0660
	Year × Herbs	0.1600	1	0.1600	2.2230	0.1420
	Error	3.6620	51	0.0718		

Table 5. Continued

Variable	Source	SS	df	MS	*F*	*P*
	Between-subjects effects					
	Treatment	0.2760	1	0.2760	3.7480	0.0580
	Herbs	0.0265	1	0.0265	0.3590	0.5520
	Error	3.7610	51	0.0737		
Carabus hortensis	*Within-subjects effects*					
	Year	0.0745	1	0.0745	0.9360	0.3380
	Year × Treatment	0.0909	1	0.0909	1.1430	0.2900
	Year × Herbs	0.0692	1	0.0692	0.8700	0.3550
	Error	4.0560	51	0.0795		
	Between-subjects effects					
	Treatment	0.1920	1	0.1920	3.1630	0.0810
	Herbs	0.0867	1	0.0867	1.4280	0.2380
	Error	3.0970	51	0.0607		

Year = the effect of study year (2000 and 2001), Treatment = the leaf-litter addition, and Herbs = cover of herbs which was used as a covariate.

Discussion

Species characteristics and spatial distribution

Carabid beetles, like most organisms, are generally non-randomly distributed at the local, within-habitat scale (Niemelä et al. 1992; Niemelä and Spence 1994; Magura et al. 2000b). This non-random carabid occurrence is determined by the heterogeneous distribution of both abiotic and biotic factors and because they actively select the most favourable microhabitat within the habitat patch (Niemelä et al. 1992). Studying the variation in abundance of carabid beetles in connection with abiotic factors, Guillemain et al. (1997) showed that the abundance of habitat generalist carabid species decreases, while the abundance of forest species increases by the thickness of leaf litter. Habitat generalists may be less adapted to living in habitats with leaf-litter patches than the forest specialists. In Finland, artificially created leaf-litter patches in a boreal coniferous forest with deciduous trees as an admixture caused the second most numerous species, *Pterostichus oblongopunctatus*, to be significantly more numerous in the leaf-litter plots than in the control ones (Koivula et al. 1999). We also detected a significant leaf-litter effect on this species. *P. oblongopunctatus* is a forest generalist species both in Finland (Lindroth 1986) and in the Hungarian region (Magura et al. 2003), and appears to favour habitat with leaf-litter patches. Results of Koivula et al. (1999) also indicated that both the catches of *Calathus micropterus* and those of *Cychrus caraboides* increased in the leaf-litter plots as compared with the control ones. In Finland all these species are also forest generalists (Lindroth 1985, 1986).

It is expected that forest generalist species which are adapted to living in habitats with leaf-litter patches would actively search the most favourable microsites, and show leaf-litter preference. In our case, however, the studied habitat was an aged non-native Norway spruce plantation without deciduous trees. In such a situation mainly habitat generalists and forest generalist carabid species can survive (Elek et al. 2001; Magura et al. 2003). Three out of the five most numerous species in our study were habitat generalists (*Abax parallelepipedus*, *Molops piceus*, *Carabus glabratus*) and two were forest generalists (*P. oblongopunctatus*, *Carabus hortensis*). We detected leaf-litter effects only on the most numerous forest generalist (*P. oblongopunctatus*). According to the results of Guillemain et al. (1997) the catches of habitat generalist carabids (*A. parallelepipedus*, *M. piceus*, *Carabus glabratus*) decreased in the leaf-litter plots. Indeed, in our study the catches of *Carabus glabratus* were marginally significantly lower in the leaf-litter plots, and the catches of *A. parallelepipedus* were almost the same in the two plot types. In contrast, *M. piceus* individuals were somewhat more numerous in the leaf-litter plot than in the control. These findings indicate that habitat generalists respond variously to leaf litter, suggesting that these species are poorly adapted to living in habitats with leaf-litter patches, or other factors not measured may influence them.

In agreement with our results, data from Koivula et al. (1999) also show that the catches of *Carabus glabratus* (a forest generalist in Finland; Lindroth 1985) decreased (but not significantly) in the leaf-litter plot. Light intensity and humidity could be the prime determinants of distribution of this carabid species (Lindroth 1985), consequently, it can find its microhabitat requirements in every dark, moist habitat irrespective of the types of litter cover, contrary to expectations. Contrary to expectations *C. hortensis* (a forest generalist species in the studied region; Magura et al. 2003) decreased in the leaf-litter plot in the first year, while its catch was nearly the same in the leaf-litter and control plots in the second year. The study of Koivula et al. (1999) also showed that the catches of *C. hortensis* (a forest generalist species in Finland; Lindroth 1985) were not different between the leaf-litter and the control plots. The most important factor for the spatial distribution of this carabid species may be the humus-rich and dry soil (Lindroth 1985); litter cover could be of less importance.

In Finland, addition of litter significantly increased carabid catches (Koivula et al. 1999), unlike in our study. The possible cause of this difference is the difference in proportion of forest species: 99.8% in Finland versus 51.9% in Hungary. The higher proportion of habitat generalists in Hungary is an effect of reforestation when in the even-aged monocultures mostly generalists can be abundant (Elek et al. 2001; Magura et al. 2003).

Microhabitat heterogeneity and spatial pattern

The more frequent occurrence of *Pterostichus oblongopunctatus* in the leaf-litter plots and the different composition of carabids between the leaf-litter plots and the control ones may be attributed to variations in abiotic factors which are important factors determining the spatial pattern of carabids (Thiele 1977). Leaf-litter addition could alter the microclimatic conditions (e.g., temperature, humidity, food availability, etc.) and produce favourable microhabitat conditions that could influence the spatial pattern of *P. oblongopunctatus* and the composition of carabids. Leaf litter creates more stable temperature and humidity conditions. Ground temperature was significantly lower, humidity somewhat higher and the soil under the leaf litter was always moister in leaf addition then in control plots (Magura et al. 2005).

Pterostichus oblongopunctatus, as a generalist predator, may gather in microhabitats with a higher amount of prey items. Although the amount of prey items was significantly higher in the leaf-litter plots, we did not detect significant positive correlation between the catches of prey items and the catches of *P. oblongopunctatus*. However, our previous data indicate that there was a significant positive correlation between the total catches of prey items and that of carabid individuals (Magura et al. 2005). Moreover, data from the same plantation show that Diplopoda (potential prey for carabids) were significantly more numerous in the leaf-litter plots than in the control plots and there was a significant positive correlation between the number of diplopods and the number of carabid individuals (Magura et al. 2005). In fact, there was a positive (although not significant) correlation between the number of diploids and *P. oblongopunctatus* (Magura et al. 2005). The leaf-litter preference of the other ground-dwelling invertebrates suggests that the leaf-litter layer may also act as a favourable microhabitat for other invertebrates by providing shelter against desiccation. The positive relationship between the abundance of carabids and that of prey items emphasizes that the amount of prey items can influence the location of carabid foraging (Loreau 1988; Chen and Wise 1999) and carabid species aggregate at microsites with a high amount of prey (Bryan and Wratten 1984; Niemelä et al. 1996; Guillemain et al. 1997).

Implications for management

Creating non-native conifer plantations after the clear-cutting of native forests has several unfavourable effects on carabid beetles (Fahy and Gormally 1998;

Magura et al. 2000a). The clear-cutting, the mechanical soil preparation (grubbing and deep loosening) before the reforestation as well as the establishment of even-aged conifer plantations without deciduous trees contribute to the homogenisation of the previously heterogeneous habitats. All of these practices influence the forest specialist carabids directly. Carabid density also decreases. In Hungary, a native beech forest supports three times more beetles than a similar-aged Norway spruce (Magura et al. 2003). The larger year-to-year changes in the abundance of the dominant species also suggest unfavourable habitat conditions in the conifer plantation. Moreover, plantations also influence carabids indirectly. The earlier, more continuous landscape is fragmented by the plantations that are inhospitable habitats for forest specialists, making the patch-to-patch dispersal of forest specialists and the maintenance of metapopulations more difficult or even impossible (Den Boer 1990; Niemelä et al. 1993).

Our results suggest ways to improve the value of conifer plantations as habitat for forest biodiversity while allowing profitable forestry practices. We recommend that deciduous trees should also be planted in the conifer plantations, since they are crucial to maintaining heterogeneity through producing deciduous leaf litter. During the establishment of plantations, mechanical soil preparation (grubbing and deep loosening) should be omitted. Instead of the clear-cutting of the whole stand of the aged plantation, openings or gaps should be logged (Koivula 2002) into which the deciduous herbs, shrubs and trees can colonize. This kind of forestry practice is also supported by the result of another research study (Magura et al. 2000a). These patches enhance the habitat heterogeneity. They also provide refuges during logging of other gaps in the plantations. All the proposed methods contribute to the increase of habitat heterogeneity and ensure the enhancement of biodiversity, while they do not endanger profitable forestry activities.

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References

Baars M.A. 1979. Patterns of movement of radioactive carabid beetles. Oecologia 44: 125–140.

Baguette M. and Gérard S. 1993. Effects of spruce plantations on carabid beetles in southern Belgium. Pedobiologia 37: 129–140.

Bird S., Coulson R.N. and Crossley D.A. 2000. Impacts of silvicultural practices on soil and litter arthropod diversity in a Texas pine plantation. Forest Ecology and Management 131: 65–80.

Bryan K.M. and Wratten S.D. 1984. The responses of polyphagous predators to spatial heterogeneity: aggregation by carabid and staphylinid beetles to their cereal aphid prey. Ecological Entomology 9: 251–259.

Butterfield J. 1997. Carabid community succession during forestry cycle in conifer plantations. Ecography 20: 614–625.

Butterfield J., Luff M.L., Baines M. and Eyre M.D. 1995. Carabid beetle communities as indicators of conservation potential in upland forests. Forest Ecology and Management 79: 63–77.

Chen B.R. and Wise D.H. 1999. Bottom-up limitation of predaceous arthropods in a detritus-based terrestrial food web. Ecology 80: 761–772.

Den Boer P.J. 1990. The survival value of dispersal in terrestrial arthropods. Biological Conservation 54: 175–192.

Desender K., Ervynck A. and Tack G. 1999. Beetle diversity and historical ecology of woodlands in Flanders. Belgian Journal of Zoology 129: 139–156.

Digweed S.C., Currie C.R., Cárcamo H.A. and 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. and Tóthmérész B. 2001. Impacts of nonnative spruce plantation on carabids. Web Ecology 2: 32–37.

Eyre M.D. and Luff M.L. 1994. Carabid species assemblages of north-east England woodlands. In: Desender K. et al. (eds), Carabid Beetles: Ecology and Evolution. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 277–281.

Fahy O. and 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 Ecology and Management 110: 263–273.

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

Heessen H.J.L. 1980. Egg production of *Pterostichus oblongopunctatus* (Fabricius) (Col., Carabidae) and *Philonthus decorus* (Gravenhorst) (Col., Staphylinidae). Netherland Journal of Zoology 30: 35–53.

Ings T.C. and Hartley S.E. 1999. The effect of habitat structure on carabid communities during the regeneration of a native Scottish forest. Forest Ecology and Management 119: 123–136.

Koivula M. 2002. Alternative harvesting methods and boreal carabid beetles (Coleoptera, Carabidae). Forest Ecology and Management 167: 103–121.

Koivula M., Puntilla P., Haila Y. and Niemelä J. 1999. Leaf litter and the small-scale distribution of carabid beetles (Coleoptera, Carabidae) in the boreal forest. Ecography 22: 424–435.

Koivula M., Kukkonen J. and Niemelä J. 2002. Boreal carabid-beetle (Coleoptera, Carabidae) assemblages along the clear-cut originated succession gradient. Biodiversity and Conservation 11: 1269–1288.

Kotze D.J. and Samways M.J. 1999. Invertebrate conservation at the interface between the grassland matrix and natural Afromontane forest fragments. Biodiversity and Conservation 8: 1339–1363.

Legendre P. and Legendre L. 1998. Numerical Ecology. Elsevier, Amsterdam, The Netherlands.
Lindroth C.H. 1985. The Carabidae (Coleoptera) of Fennoscandia and Denmark, Part 1. Fauna Entomologica Skandinavica, Leiden, The Netherlands and Copenhagen, Denmark.
Lindroth C.H. 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark, Part 2. Fauna Entomologica Skandinavica, Leiden, The Netherlands and Copenhagen, Denmark.
Loreau M. 1988. Determinants of the seasonal pattern in the niche structure of a forest carabid community. Pedobiologia 31: 75–87.
Loreau M. and Nolf C.L. 1993. Occupation of space by the carabid beetle *Abax ater*. Acta Oecologica 14: 247–258.
Lövei G. and Sunderland K.D. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology 41: 231–256.
Magura T. 2002. Carabids and forest edge: spatial pattern and edge effect. Forest Ecology and Management 157: 23–37.
Magura T., Tóthmérész B. and Bordán Zs. 1997. Comparison of the carabid communities of a zonal oak-hornbeam forest and pine plantations. Acta Zoologica Academiae Scientiarum Hungaricae 43: 173–182.
Magura T., Tóthmérész B. and Bordán Zs. 2000a. Effects of nature management practice on carabid assemblages (Coleoptera: Carabidae) in a non-native plantation. Biological Conservation 93: 95–102.
Magura T., Tóthmérész B. and Molnár T. 2000b. Spatial distribution of carabids along grass–forest transects. Acta Zoologica Academiae Scientiarum Hungaricae 46: 1–17.
Magura T., Ködöböcz V. and Bokor Zs. 2001a. Effects of forestry practices on carabids (Coleoptera: Carabidae). Implication for nature management. Acta Phytopathologica et Entomologica Hungarica 36: 179–188.
Magura T., Tóthmérész B. and Molnár T. 2001b. Forest edge and diversity: carabids along forest–grassland transects. Biodiversity and Conservation 10: 287–300.
Magura T., Tóthmérész B. and Elek Z. 2002. Impacts of non-native spruce reforestation on ground beetles. European Journal of Soil Biology 38: 291–295.
Magura T., Tóthmérész B. and Elek Z. 2003. Diversity and composition of carabids during a forestry cycle. Biodiversity and Conservation 12: 73–85.
Magura T., Tóthmérész B. and Elek Z. 2005. Biotic interactions between carabids and other ground-dwelling invertebrates in a non-native Norway spruce plantation. Acta Zoologica Academiae Scientiarum Hungaricae (submitted).
Mátyás Cs. 1996. Forestry Ecology. Mezőgazda Kiadó, Budapest, Hungary (in Hungarian).
Molnár T. Magura T. and Tóthmérész B. 2002. Ground beetles (Carabidae) and edge effect in oak-hornbeam forest and grassland transects. European Journal of Soil Biology 37: 297–300.
Niemelä J. 1997. Invertebrates and boreal forest management. Conservation Biology 11: 601–610.
Niemelä J. 1999. Management in relation to disturbance in the boreal forest. Forest Ecology and Management 115: 127–134.
Niemelä J. and Spence J.R. 1994. Distribution of forest dwelling carabids (Coleoptera): spatial scale and the concept of communities. Ecography 17: 166–175.
Niemelä J., Haila Y., Halme E., Pajunen T. and Punttila P. 1992. Small-scale heterogeneity in the spatial distribution of carabid beetles in the southern Finnish taiga. Journal of Biogeography 19: 173–181.

Niemelä J., Langor D. and Spence J.R. 1993. Effects of clear-cut harvesting on boreal ground-beetle assemblages (Coleoptera: Carabidae) in western Canada. Conservation Biology 7: 551–561.

Niemelä J., Haila Y. and Punttila P. 1996. The importance of small-scale heterogeneity in boreal forests: variation in diversity in forest-floor invertebrates across the succession gradient. Ecography 19: 352–368.

Penev L. 1996. Large-scale variation in carabid assemblages, with special reference to the local fauna concept. Annales Zoologici Fennici 33: 49–63.

Pickett S.T.A. and White P.S. (eds) 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Orlando, Florida.

Sergeeva T.K. 1994. Seasonal dynamics of interspecific trophic relations in a carabid beetle assemblage. In: Desender K. et al. (eds), Carabid Beetles: Ecology and Evolution. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 367–370.

Sokal R.R. and Rohlf F.J. 1981. Biometry. W.H. Freeman, New York.

Spence J.R. and Niemelä J. 1994. Sampling carabid assemblages with pitfall traps: the madness and the method. Canadian Entomologist 126: 881–894.

Spence J.R., Langor D.W., Niemelä J., Cárcamo H.A. and Currie C.R. 1996. Northern forestry and carabids: the case for concern about old-growth species. Annales Zoologici Fennici 33: 173–184.

Thiele H.U. 1977. Carabid Beetles in Their Environments. Springer-Verlag, Berlin, Germany, 1977.

Tóthmérész B. 1993. NuCoSA 1.0: Number Cruncher for Community Studies and other Ecological Applications. Abstracta Botanica 17: 283–287.