



## Diversity and composition of carabids during a forestry cycle

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**Abstract.** Carabids (Carabidae, Coleoptera) were studied for 2 years to explore changes in their diversity and composition during a forestry cycle in the Hungarian Mountain Range. Native beech forest was clear-cut and replanted with Norway spruce. Recently planted (5 years old), young (15 years old), middle-aged (30 years old) and old spruce plantations (50 years old) were studied using pitfall traps. Our results showed that the species richness of carabids was significantly lower in the plantations than in the native beech forest. Species composition was homogeneous in the beech forest.  $\beta$ -Diversity of the 15–30 year old plantations was also low, and it increased slightly towards ageing. Heterogeneity of the species composition of the 5 year old plantation was higher than that of the others, which reflected the patchiness of the young plantation. The main tendencies of the compositional changes were as follows. Deciduous forest specialists decreased significantly in abundance in the plantations; they appeared in high abundance only in the beech forest. Species characteristic of open habitats increased remarkably in abundance in the recently established plantation. Multiple linear regression between the diversity of carabids and of 12 environmental variables shows that the pH and compaction of the soil, and the cover of leaf litter had a significant effect in determining diversity of carabids.

### Introduction

In Hungary 12% of the land surface was forested in 1925. In the 1990s this area has expanded to 18%. However, the majority (ca. 75%) of the forested area is under economical exploitation (Mátyás 1996). Economical forests mainly consist of non-native tree species (e.g. black locust, Norway spruce, Scotch fir, black pine, poplar, etc.). In the hilly region of Hungary due to the modern forestry practices during the years 1940–1960 many native, deciduous forests were clear-felled and these habitats were reforested with non-native conifer trees, mainly with Norway spruce (*Picea abies*). Norway spruce was preferred during the reforestation because of its high productivity and its quick growth. After the clear-cutting of a forest, grubbing and deep loosening precede the spruce reforestation. These practices drastically change the microclimatic, abiotic and biotic conditions of the area. These changes, however, heavily damage the native biota. Ground-dwelling invertebrates are especially sensitive to these alterations (Samways 1994). Several previous studies (Eyre et al. 1990; Niemelä 1990; Luff et al. 1992; Niemelä et al. 1993, 1996; Loreau

1994; Lövei and Sunderland 1996; Ings and Hartley 1999; Bird et al. 2000; Magura et al. 2000a; Werner and Raffa 2000) demonstrated that surface-active carabid beetles (Coleoptera: Carabidae) are also highly sensitive to habitat changes. Furthermore, carabid beetles are appropriate organisms to study the impacts of habitat alteration, because they are sufficiently varied both taxonomically and ecologically; moreover, they are abundant and their ecology and systematics are relatively well known (Niemelä et al. 2000).

Research has been published concerning the effects of conifer plantations on the composition and diversity of carabids from North-America (Niemelä et al. 1993, 1994; Spence et al. 1996), Finland (Niemelä et al. 1996), the UK (Butterfield et al. 1995; Butterfield 1997), Ireland (Day and Carthy 1988), and from Western Europe (Baguette and Gérard 1993). Data from Eastern Europe concerning the same topic are rather limited (Šustek 1981; Szyszko 1983, 1987). Therefore, the aim of our study, conducted in Eastern Europe, was to examine changes in the diversity and composition of the carabid assemblages with the forestry cycle. The cycle studied represented consecutive stages in the forestry practice: a native beech forest was clear-felled and after mechanical soil treatment was reforested with Norway spruce. Overall, the aim of this study was: (1) to examine changes in the diversity of carabids during the forestry cycle, and (2) to study the changes in the species composition after the reforestation.

## Materials and methods

### *Study area and sampling*

The study area was located in the North Hungarian Mountain Range. The studied forestry cycle represented different stages of the forestry practice; a few structural characteristics are given in Table 1. Stages of the forestry cycle are as follows:

1. Beech forest; beech (*Fagus sylvatica*) was the dominant tree species in the canopy. Hornbeam (*Carpinus betulus*), maple (*Acer campestre*, *A. pseudo-platanus*) and ash (*Fraxinus excelsior*) were also present. The shrub layer was sparse, while the herb layer was moderate. This is the most widespread, typical forest of the region.
2. 5 year old spruce plantation with open canopy; due to grubbing and deep loosening before the reforestation, weeds, grasses and other species typical of the open habitats were dominant in the dense herb layer. The shrub layer was moderate.
3. 15 year old spruce plantation; the herb and shrub layer were sparse because of the closed canopy layer.
4. 30 year old spruce plantation; the undergrowth vegetation was entirely missing because of the shading of the closed canopy.
5. 50 year old spruce plantation; the canopy closure decreased due to the falling of trees caused by windstorm. Decreasing of the canopy closure resulted in a moderate herb layer.

Table 1. Structural characteristics of the studied habitats.

	Beech forest	Norway spruce plantations (age in years)			
		5	15	30	50
Age of trees (years)	70	5	15	30	50
Tree height (m)	30	2.5	9	15	25
Trees/ha	250	2500	1000	600	400
Cover of leaf litter (%)	100	0	0	0	0
Cover of herbs (%)	40	60	4	0	10
Cover of shrubs (%)	1	20	2.5	0	2
Canopy cover (%)	90	20	80	80	75

Each of the plantations was established after clear-cutting of a beech forest. All of the study locations were on a northwestern slope of the same valley (48°05' N, 20°37' E); the distance between them was more than 1 km, and their area was 5–20 ha. Originally the valley was covered by a continuous beech forest. The base rock was limestone in all studied habitats. Unbaited pitfall traps (diameter 100 mm, volume 500 ml) containing ethylene glycol were used to collect carabid beetles. There were 10 traps in each stand. Two trapping stations were established in each stand by placing five traps randomly (ca. 5–10 m apart from each other) to provide replications. Trapping stations were set at least 50 m from each other to provide adequate statistical independence for pitfall samples (Digweed et al. 1995), and they were set at 100–150 m from the edge of the stand in order to avoid edge effects (e.g. Bedford and Usher 1994; Magura et al. 2000b, 2001a, b; Molnár et al. 2001). Trapped individuals were collected monthly from March 1998 to November 1999. The traps were not emptied during the winter period (from December–February), as they were covered with snow. For the numerical analyses we pooled samples from different months because several authors (Baars 1979; Loreau 1992) 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' active period.

We have measured 12 environmental factors that may be relevant controlling the distribution of carabids (Thiele 1977; Lövei and Sunderland 1996). They were measured monthly on a typical sunny day in the morning. The statistical analyses were based on averages. The temperature of the soil at a depth of 2 cm, the temperature at the soil surface, relative air humidity, soil pH, soil compaction, CaCO<sub>3</sub> content, and organic matter content were measured next to each trap. We also estimated the cover of leaf litter, herbs, shrubs and canopy around each trap in a circle of radius 1 m. We counted the number of other invertebrates (other Coleoptera, Chilopoda, Collembola, Diplopoda, Gastropoda, Isopoda, Orthoptera) in the traps, which were potential prey of carabids (Sergeeva 1994).

#### *Data analyses*

The simplest, and sometimes the most appropriate measure of species richness is the number of species. The habitats studied were characterized by the average number

of species in the traps and the minimum and maximum of the number of species. The heterogeneity of the species composition was measured by Whittaker's  $\beta$ -diversity, which was defined as the ratio of the total number of species and the average number of species minus one (Tóthmérész 1998). One-way ANOVA and Tukey-type multiple comparisons were used to determine differences in carabid species richness per trap between the habitats. One-way ANOVA depends on the assumption that the data follow a Gaussian distribution and that the samples were drawn from populations with the same variance. The Gaussian distribution of the data was tested by a Kolmogorov–Smirnov test. The equal variance of the samples was analysed by a Bartlett test. Multiple linear regression analyses were used to determine the relationships between the 12 environmental factors and the species richness of carabids (Sokal and Rohlf 1981). The analyses were carried out using the SPSS-PC program.

Characteristic species of the habitats were identified using the Indicator Value (IndVal) procedure (Dufrene and Legendre 1997). This method derives indicator species and species assemblages from a site classification. We obtained the site classification by hierarchical cluster analysis using Bray–Curtis dissimilarity for abundance and the Ward fusion method. Based on this site classification, IndVal identified the indicator species corresponding to the various groups. Indicator species were defined as the most characteristic of each group, found mostly in a single group and present in the majority of the pitfall traps belonging to that group. Thus, the IndVal method took both specificity and fidelity into account. The method is robust to differences in absolute abundances of both the different taxa and the same taxon in different habitats. Furthermore, it is possible to assess the statistical significance of the species indicator values using a Monte Carlo permutation test.

Non-metric multidimensional scaling was used to display the similarity of the pitfall catches in the stages of the forestry cycles. The Rogers–Tanimoto index was used to measure the similarity in species composition and the Bray–Curtis index was used to assess similarity in abundances (Legendre and Legendre 1998).

## Results

Altogether 2768 specimens of carabids were trapped during the two years, belonging to 35 species. The species richness per trap in all of the trapping stations followed a Gaussian distribution and the variances of the samples were equal (for all Kolmogorov–Smirnov tests  $KS > 0.2$  and  $P > 0.1$ ; while Bartlett's statistic = 15.97 and  $P = 0.068$ ). It was demonstrated by ANOVA that there was a significant difference between the habitats in the average number of carabid species per trap ( $H = 16.11$ ,  $df = 9, 49$ ,  $P < 0.0001$ , Figure 1). The average number of species of carabids was significantly lower ( $P < 0.05$ ) in the spruce plantations than in the beech forest. The same pattern was shown by the minimum and the maximum number of species in the traps (Table 2). Both the minimum and the maximum of the number of sampled species in a trap was much larger in the beech forest. All the

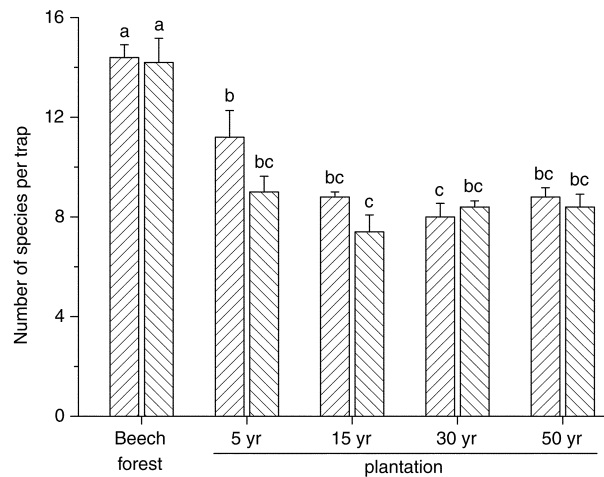


Figure 1. Average number of species per trap (with SE) in the studied habitats. Different letters indicate significant difference in the means ( $P < 0.05$ ).

Table 2. Diversity characteristics of the carabids per trap.

	Beech forest	Norway spruce plantations (age in years)			
		5	15	30	50
Average number of species	14.3	10.1	8.1	8.2	8.6
Min. number of species	11	7	6	7	7
Max. number of species	17	13	10	10	10
$\beta$ -Diversity	0.54	1.87	0.85	1.07	1.21
Number of individuals	1031	239	587	552	359

The last row is the total for the forest type.

Norway spruce plantations were very close regarding the minimum and maximum of the number of species per trap.

Carabid beetles were most abundant in the beech forest and contributed more than one third of the total catch (see Table 2).  $\beta$ -Diversity was the lowest in the beech forest; it was roughly twice as much or more in the Norway spruce plantations.  $\beta$ -Diversity of the 5 year old plantation was higher than for the other Norway spruce plantations.

The cluster analysis and the IndVal procedure suggested four characteristic groups of carabid species (Figure 2): (1) generalists that occurred in all habitat types; (2) generalists of forests with closed canopy. These species occurred in the habitat with closed canopy layer (beech forest, 15, 30 and 50 year old spruce plantation); (3) deciduous forest specialists; these species were abundant only in the deciduous beech forest, although they were also present in other habitats in small numbers; (4) species of the open habitats that were characteristic to those habitats, where the canopy layer was still open; i.e., they occurred in the 5 year old spruce plantation. The general patterns of similarity of the carabids of the studied habitats

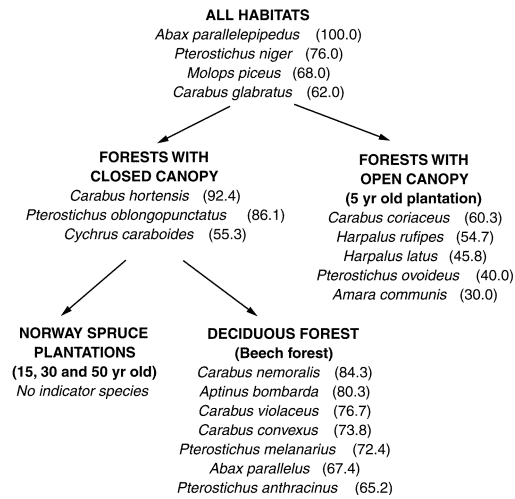


Figure 2. Tree diagram of the habitat types with the associated indicator species. The figure in parentheses shows the species indicator value for the habitat type. All of the indicator values are statistically significant ( $P < 0.05$ ).

were similar, both for the species composition and for the abundance data (Figure 3). It is shown (Figure 3A) that the heterogeneity of the species composition is larger for the 5 and 50 year old Norway spruce plantations than for the other stands. The differences of the carabid assemblages of the stages were demonstrated by ordination based on the abundances (Figure 3B); pitfall traps of the different habitats were well separated.

The multiple linear regression between the number of carabid species and the environmental variables showed that the pH of the soil, compaction of the soil and cover of the leaf litter were the most important factors controlling the number of carabid species in the studied habitats (Table 3).

## Discussion

### *Carabid diversity and the forestry cycle*

We have pointed out that there are dramatic changes in the diversity and composition of carabids during the forestry cycle. Diversity of the carabid beetles decreased significantly after reforestation of the native beech forest with non-native Norway spruce, and the composition of the carabid beetles also changed remarkably. Diversity of carabids remained low during the growth of the plantations, even 50 years after the establishment (Figure 1). In the Czech Republic (Middle Bohemian highland), Šustek (1984), studying the carabids along a transect running from a beech forest into the neighbouring Norway spruce plantation, observed that the diversity of carabids decreased rapidly in the Norway spruce monoculture.

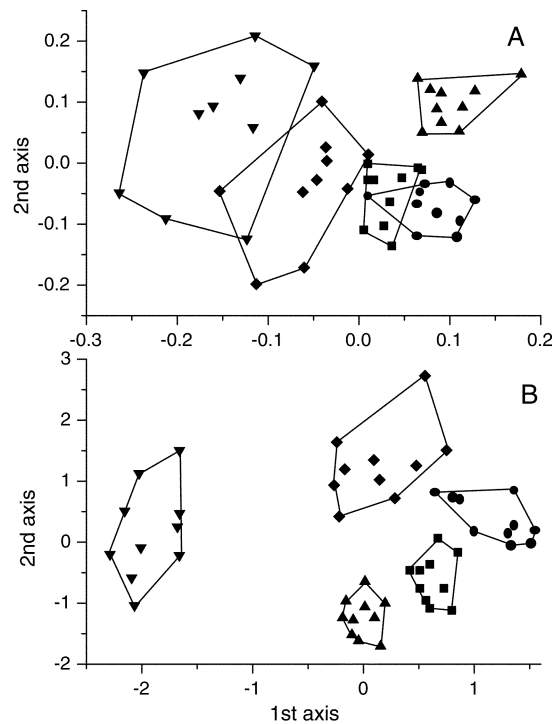


Figure 3. Ordination (NMDS) of the pitfall catches based on the species composition (A) and on the abundance (B). ■: beech forest; plantations: ▼ 5, ▲ 15, ● 30, and ◆ 50 year old.

Research of Butterfield et al. (1995), carried out in Sitka spruce (*P. sitchensis*) plantations in northern England, also showed that the carabid species richness was less in the plantations than in the deciduous forests. The change of diversity presented in this paper is in agreement with the results obtained by Fahy and Gormally (1998), who showed that carabid diversity was significantly less in a conifer plantation than in the nearby oak woodland. Mader (1986), Niemelä et al. (1988, 1993) and Niemelä (1990, 1999) also demonstrated that increased homogeneity of the groundflora contributed to a decrease in carabid diversity.

Results of the multiple linear regression showed that the pH of the soil, compaction of the soil, and cover of the leaf litter were the most important factors in determining diversity of carabids (Table 3). The significant positive correlation between the species richness of carabids and the pH of the soil was explained by the absence of species preferring acid conditions (Thiele 1977; Lindroth 1985–1986). Earlier studies (Paje and Mossakowski 1984; Butterfield and Benitez Malvido 1992; Butterfield 1997) also emphasized that the spatial distribution and habitat preference of carabids were influenced by the soil pH. This relationship may also be related to the fact that the eggs and larvae (the most sensitive stage of the development) of carabids are very sensitive to the environmental conditions (Thiele 1977; Lövei and Sunderland 1996). Furthermore, the majority of the carabid's prey were also very

Table 3. Multiple linear regression between the number of species per trap and the studied environmental variables for each year.

	Number of species	
	1998	1999
Soil temperature	<i>ns</i>	<i>ns</i>
Ground air temperature	<i>ns</i>	<i>ns</i>
Relative air moisture	<i>ns</i>	<i>ns</i>
Soil pH	+**	+*
Soil compaction	-**	-*
CaCO <sub>3</sub> content of soil	<i>ns</i>	<i>ns</i>
Organic matter content	<i>ns</i>	<i>ns</i>
Cover of leaf litter	+*	<i>ns</i>
Cover of herbs	<i>ns</i>	<i>ns</i>
Cover of shrubs	<i>ns</i>	<i>ns</i>
Canopy cover	<i>ns</i>	<i>ns</i>
Number of carabids' prey	<i>ns</i>	<i>ns</i>
$r^2$	0.8868	0.7301
$F$	24.162	8.339
$df$	12, 37	12, 37
$P <$	0.0001	0.0001

*ns*: not significant. \*  $P < 0.05$ ; \*\* $P < 0.001$ .

sensitive to soil pH, and thus could also influence the species richness of carabids. The significant negative correlation between the soil compaction and the species richness of carabids may also be explained by the habitat preferences of carabids. In the habitat patches with greater soil compaction, egg laying and digging into the soil during aestivation and hibernation would have been more difficult. Many carabid species need to dig holes to deposit their eggs, some even building chamber holes below the soil surface and exhibiting caves (Thiele 1977). This digging requirement explains the negative relationship between carabid diversity and increasing soil compaction. Moreover, previous studies (Thiele 1977) have shown that species of the genus *Abax* dug holes in which they cared for their eggs. The result of the multiple linear regression between the number of carabid species in 1998 and the environmental factors showed that leaf litter had a positive effect on carabid species richness. Leaf litter had been shown to increase the number of carabid species through producing favourable microsites for carabids (Niemelä 1990; Niemelä et al. 1992a, b; Niemelä and Spence 1994). Loreau (1987) demonstrated that carabid beetles had a separated vertical distribution in the litter layer, which may lead to decreased intra- and inter-specific competition (Müller 1987; Loreau 1988). Moreover, leaf litter may contribute to the heterogeneity of the habitats. Niemelä et al. (1996) and Butterfield (1997) also pointed out that species richness of carabids was related to habitat heterogeneity.

#### *β-Diversity and/or the heterogeneity of species composition*

β-Diversity characterizes the heterogeneity of the species composition of an

assemblage. It is frequently induced by the patchiness of the habitat. Although it is usually mentioned as a kind of diversity, in many respects it is related to the spatial pattern of the community. The floor of the beech forest in the present study was very monotonous. Both the carabid and herb species composition of the beech forest were also homogeneous. Most species were sampled by each trap within the beech forest. Therefore, the dominant and subdominant species of the forest were relatively uniformly distributed.

$\beta$ -Diversities of the 15–30 year old plantations were similar, with a slight increase towards ageing (Table 2). The actual value of  $\beta$ -diversity means that roughly half of the species pool were present in a trap. Therefore, this was a very homogeneous assemblage. The  $\beta$ -diversity was much higher for the 5 year old plantation, suggesting a large heterogeneity of the species composition, i.e. roughly three times higher than for the beech forest. Approximately a quarter of the species pool were present in a trap. Therefore, the species composition changed from trap to trap to a greater extent than in the other habitats. This was induced by the large patchiness of the young plantation. The canopy was not closed and patches of the Norway spruce, shrubs, mixed herbaceous vegetation, and grassland composed a patchy environment. It facilitated the survival and persistence of both the closed canopy forest species after the clear-cutting and the species of the open habitats. Niemelä et al. (1996), studying species composition using a similarity index in conifer forests with different age, also demonstrated considerable within-stand variation in species composition in the young successional stages. They also explained this variation by differences in the environmental conditions on a microscale.

#### *Species characteristic to the stages of the forestry cycle*

All of the carabid species in the present study showed clear habitat preferences (Figure 2). The 5 year old spruce plantation was characterised by species which preferred open habitats and their microclimatic conditions (*Carabus coriaceus*, *Harpalus rufipes*, *H. latus*, *Pterostichus ovoides*, *Amara communis*). These species usually disappeared at the closure of the canopy or they were reduced in abundance. Baguette and Gérard (1993) also found that *Am. communis* and *H. latus* were characteristic of young (1–5 years old) Norway spruce plantation. In our study *C. coriaceus* was characteristic of the 5 year old plantation, while Baguette and Gérard (1993) found it characteristic of old (50–70 years) plantations. However, in our study it was also present in the beech forest, suggesting that this species was more likely a species living in the beech forest which survived in the recently established plantation after the clear-cutting. Niemelä et al. (1996) and Spence et al. (1996), studying a lodgepole pine–white spruce (*Pinus contorta*–*P. glauca*) plantation at different ages, also reported that deciduous forest species survived in the spruce plantations. Szyszko (1987), studying the succession of carabid beetles after clear-felling in pine plantations, also demonstrated that some forest carabid species survived in the young plantations. The deciduous forest specialist species characteristic to the beech forest (see Figure 2) required the environmental conditions

specific to the deciduous forest with closed canopy (e.g. leaf litter, microclimate, etc.), and were either restricted to, or abundant only in the beech forest. However, some of these deciduous forest species can also survive in the plantations (Szyszko 1986; Niemelä et al. 1993; Spence et al. 1996). The generalists of closed forests (Figure 2) required closed canopy, regardless of the tree species in the canopy layer.

The result of the indicator species analysis showed that the species composition of the carabids altered drastically during the forestry cycle: (1) the clear-cutting of the native forest and the reforestation with non-native Norway spruce resulted in the disappearance or the dramatic reduction of the abundance of the specialists characteristic to the native beech forest (deciduous forest specialists). (2) The recently established plantation with open canopy layer was colonised by species typical of the open habitats. However, they disappeared or their abundance reduced significantly after the closure of the canopy. (3) In the aged monocultures, only the habitat generalists and the closed canopy forest generalists were abundant. The observed changes in the species composition of carabids during the forestry cycle were very similar to those observed by Niemelä et al. (1994). They showed that: (1) mature forest specialists either disappeared from the young forest or their abundance decreased considerably; (2) in the young forests after clear-cutting the abundance of the species characteristic to the open habitats increased; and (3) changes in the forest composition did not significantly influence the forest generalists. Szyszko (1987), investigating carabids in pine stands of different ages, emphasized that clear-cutting causes important changes in the carabid assemblages, as many forest specialist species disappeared, while species of open areas increased in abundance. Magura et al. (1997), studying carabid beetles in an oak-hornbeam forest, Norway spruce and black pine (*P. nigra*) plantation created after clear-cutting oak-hornbeam forests, also confirmed these responses of carabid beetles to reforestation.

#### *Management and monitoring*

Our results corroborated that significant changes in the carabid diversity and species composition appeared after reforestation. Moreover, it was also demonstrated that no recolonization of the species characteristic to the native deciduous forest occurred during the growth of the plantations, even 50 years after the establishment. Despite the evident negative influences of non-native Norway spruce plantations in this area, their removal is almost impossible because of economic demands. Immediate clearing of the plantations would cause financial loss to the timber company. Moreover, clear-cutting could have damaging effects on the environment and on the biota, so it might make the situation worse rather than improving it. It is possible to reduce these effects by nature management practice. Magura et al. (2000a) demonstrated that creating gaps in the Norway spruce plantations and facilitating the re-establishment of the native herbs, shrubs and deciduous trees enhanced the regeneration of the native carabid assemblage. However, monitoring the impacts of nature management practice was essential, as it includes early observation of structural changes, and re-arrangement of the assemblage. Moreover, observations on the regeneration and succession of such assemblages may provide

useful information for future management plans. Observed significant changes in the carabid diversity and species composition in this study were similar to many studies conducted in different regions (Šustek 1981; Szyszko 1983, 1986, 1987; Day and Carthy 1988; Baguette and Gérard 1993; Niemelä et al. 1993, 1994, 1996; Butterfield et al. 1995; Spence et al. 1996; Butterfield 1997; Magura et al. 1997, 2000a; Elek et al. 2001). Such studies illustrated that, despite the different carabid species pool of the various regions, the general patterns of their responses to anthropogenic disturbances were very similar (Niemelä et al. 2000). This suggested the possibility of using carabid beetles to monitor changes in terrestrial habitats (Eyre et al. 1990; Rushton et al. 1990; Luff et al. 1992).

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