

Research article

Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary

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Abstract

Responses of carabid beetles (Coleoptera: Carabidae) to urbanisation were studied along an urban-suburban-rural gradient representing decreasing intensities of human disturbance. Carabids were collected by pitfall trapping during their activity period in lowland oak forest patches in the city of Debrecen, Eastern Hungary. The average number of carabid species was significantly higher in the rural and urban areas compared to the suburban one. The high overall species richness in the urban area was due to the presence of species preferring open habitats. The species richness of forest specialist carabids significantly increased along the urban-rural gradient. The overall carabid abundance was significantly higher in the rural than the other two areas. The results did not support the hypothesis that overall diversity should decrease in response to habitat disturbance. They also contradicted the intermediate disturbance hypothesis: species richness was not the highest in the moderately disturbed suburban area. In the urban area, opportunistic species dominated. The average carabid body size was significantly larger in the rural and suburban areas than in the more disturbed urban area. Multivariate methods detected changes in species composition and abundance structure along the urban-rural gradient. Significant proportion of the variation in abundance and species richness was explained by the heterogeneity of environmental variables (ground temperature, surface temperature, humidity, cover of decaying wood material, herbs, canopy layer, and by the amount of prey).

Introduction

The large majority of human population lives in cities; urbanisation and the loss of biotic diversity have a vital direct and indirect influence on the biosphere (Vida 1978). Urban ecosystems are characterised by high-density human habitation, intense transport processes, and only remnants of natural habitats (McIntyre et al. 2001). To ensure that urban areas are managed both for the well-being of city-dwellers and nature, the knowledge of ecosystem responses to the influence of urbanisation is needed (McDonnell and Pickett 1990; Niemelä 1999). Central among these

considerations is the maintenance of diversity, which is an important indicator of the functional state of ecosystems (Probst and Crow 1991; Naeem et al. 1994; Scott and Anderson 2002). Since urban development is both spreading and intensifying, knowledge about the functioning of urban ecosystems has vital importance in planning future urban development in order to minimize its negative environmental impacts (McIntyre et al. 2001; Niemelä 1999).

Recently, a multi-national research framework to assess and compare the influence of urbanisation using a single group of invertebrates and standardised field methods has been initiated (GlobeNet, Niemelä

et al. 2000). Carabid beetles (coleoptera: Carabidae) were selected as the focal taxon since they are sufficiently varied both taxonomically and ecologically, abundant and sensitive to the changes of the microenvironment and human disturbance (Scott and Anderson 2002). Carabids are regarded as a reliable monitoring group (Rainio and Niemelä 2003), and they have been widely studied in relation to land use throughout the world (e.g., Stork 1990; Eyre and Luff 2002). In the first GlobeNet project, three kinds of forested habitats (urban parks, suburban forested area, and rural forest), representing different levels of human disturbance, were selected in three countries, Bulgaria, Canada, and Finland (Niemelä et al. 2002). The patterns and responses of carabid assemblages along this urbanisation gradient may help guide urban management practices. Other taxa (ants, spiders) are also studied within the GlobeNet framework (Alaruikka et al. 2003).

The effects of urbanisation can be explored through investigations of biotic and abiotic changes along urban-to-rural gradients (McDonnell et al. 1997; Niemelä 1999; Niemelä et al. 2000). Such gradients, from densely built inner cities to increasingly rural surroundings, reflect diminishing intensities of human influence. Urban forests are exposed to unique features with respect to suburban and rural forests, including higher air pollution and disturbance intensity, the heat island phenomenon and the presence or greater abundance of exotic species (Spence and Spence 1988; McDonnell et al. 1997; Pouyat et al. 1997). The floristic richness of many urban habitats frequently exceeds that of less urbanised areas (Tonteri and Haila 1990), reflecting the diverse, mosaic nature of urban habitats and the presence of introduced plants. The city-forest ecotone also plays an important role in maintaining this diversity (Godefroid and Koedam 2003).

Several hypotheses try to explain the effects of disturbance on biotic communities. The *intermediate disturbance hypothesis* (IDH) predicts the increase in diversity at intermediate levels of disturbance (Connell 1978). This implicitly incorporates the *increased disturbance hypothesis*, according to which the species richness should decrease under higher levels of disturbance (Gray 1987, 1989). As increasing disturbance affects primarily the forest specialists, we hypothesised that abundance and species richness of forest specialists should decrease from the rural area to the urban one (*habitat specialist hypothesis*). At high level of disturbance opportunistic species are

predicted to gain dominance (Gray 1989). We call this the *opportunistic species hypothesis*. Gray (1989) also suggested that in habitats affected by (increased) disturbance the mean size of the species present should decrease (*decreasing mean body size hypothesis*).

In this paper, we tested the following predictions for carabids in urban environments: (1) diversity should be the highest in the suburban area (intermediate disturbance hypothesis); (2) diversity should decrease from a high value in the rural area to a low one in the urban area (increasing disturbance hypothesis); (3) the abundance and species richness of the forest-specialist species should increase from the more disturbed urban area to the less disturbed rural one (habitat specialist hypothesis); (4) opportunistic species should gain dominance in the urban area (opportunistic species hypothesis); (5) the mean body size of the species should decrease with increasing disturbance level, in our case from the rural to the urban area (mean body size hypothesis). We also investigated the changes of the carabid assemblages along the urbanisation gradient, identified the characteristic and/or key species across this gradient, and correlated certain environmental variables with the observed pattern of carabid abundance and species richness.

Material and methods

Study area

The study areas were in the city of Debrecen (Eastern Hungary), the second largest city of the country (Figure 1). Three forested sampling areas were selected along an urbanisation gradient within the boundaries of the city, and in the surrounding forest reserve. This represented urban, suburban and rural areas, according to the GlobeNet study requirements (Niemelä et al. 2000). All sampling sites were in continuous patches of forest dominated by English oak (*Quercus robur*) and covering at least an area of 6 ha. Distance among the studied areas was at least 1 km. In the urban park area, there were several asphalt-covered paths and the shrub layer was strongly thinned, while in the suburban area the fallen trees were removed. The urban-rural gradient extended over a distance of approximately 6 km, from the city centre (47° 32' N 21° 38' E), through the suburbs to the neighbouring Nagyerdo Forest Reserve (47° 35' N 21° 37' E). The typical, native forest association of

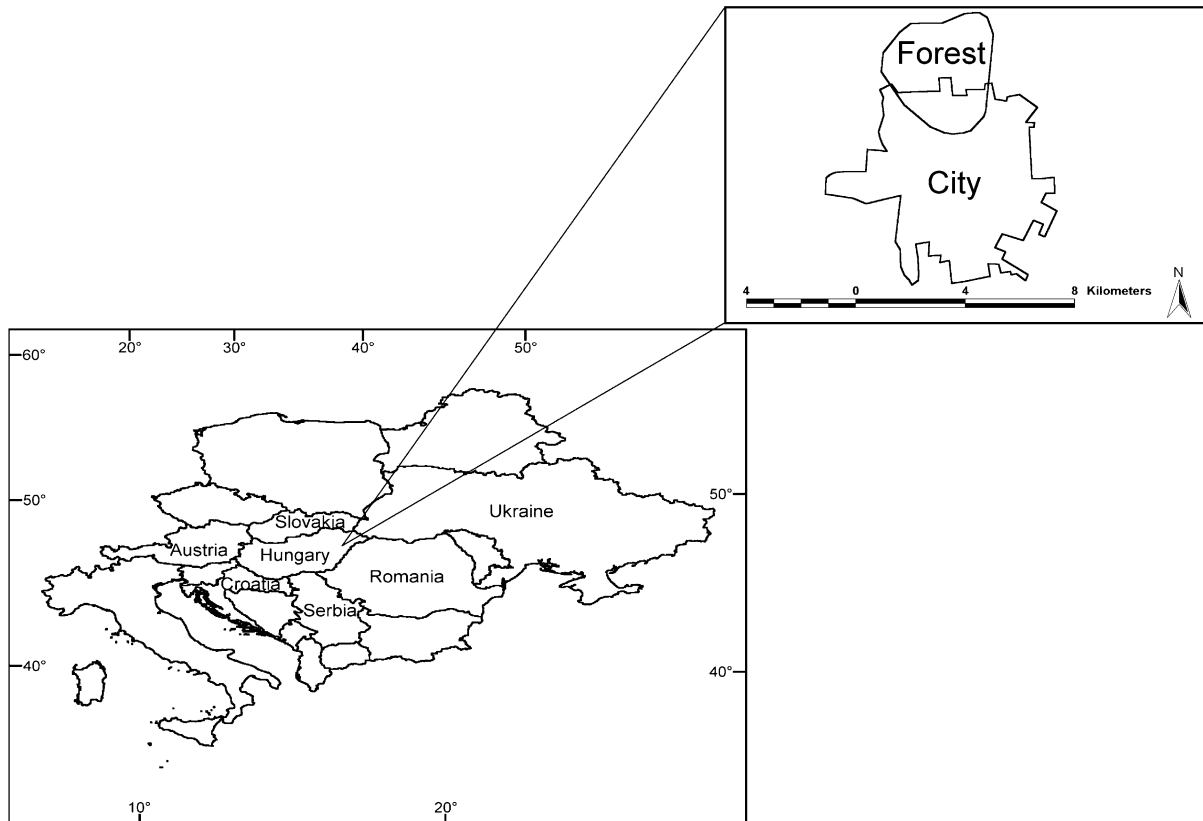


Figure 1. The sampling area in Eastern-Hungary and the location of the studied forest. The gradient is ranging from the city centre (47° 32' N 21° 38' E) towards the rural area (47° 35' N 21° 37' E).

the sampling sites was an oak forest (*Convallario-Quercetum roboris*).

Sampling design

Four sites, at least 50 m from each other, were selected within each sampling area (urban, suburban, and rural). Carabid beetles were collected at each site using pitfall traps, randomly placing ten traps at least 10 m apart from each other. This resulted in a total of 120 traps scattered along the urban-rural gradient (3 area \times 4 sites \times 10 traps). The pitfall traps were unbaited, consisting of plastic cups (diameter 65 mm, volume 250 ml) containing 75% ethylene glycol as a killing-preserving solution. The traps were covered with bark pieces to protect them from litter and rain (Spence and Niemelä 1994). Trapped beetles were collected fortnightly from the end of March to the end of November, 2001. For analysis we pooled samples from the whole year.

Nine environmental factors were measured that can affect the distribution of carabids (Thiele 1977; Lövei and Sunderland 1996). Ground temperature at 2 cm depth, air temperature on the surface and relative humidity on the surface were measured adjacent to each trap monthly on the morning of a typical sunny day. The statistical analyses were based on averages. We also estimated the percentage cover of leaf litter, decaying wood material, herbs, shrubs and canopy around the traps within a circle of 2 m diameter. We also counted the number of other invertebrates (other Coleoptera, Chilopoda, Collembola, Diplopoda, Gastropoda, and Isopoda) in the traps as a measure of the amount of potential prey for carabids (Sergeeva 1994).

Data analyses

To test differences in the overall carabid abundance, species richness, the ratio of the opportunistic (generalist) carabid species to the total number of

individuals, body size, and dominance structure among the three sampling areas (urban, suburban and rural), and among the 12 sites, nested analyses of variance (ANOVA) were performed using data from the individual traps (sites nested within the sampling areas). Data on body size were obtained from Hürka (1996). Further, carabid beetles were divided into three ecological groups according to their habitat preference (Hürka 1996): forest species, generalist species and open-habitat species. Differences in the number of individuals and species richness in the three groups were also tested by nested ANOVA. The distribution of data used in the ANOVA model was normal (tested by the Kolmogorov-Smirnov test, Sokal and Rohlf 1995). When ANOVA revealed a significant difference between the means, an LSD (least significant difference) test was performed for multiple comparison among means.

The composition of the carabid assemblages along the urban-rural gradient was compared at site level by cluster analysis based on presence-absence data using the Sørensen index of similarity and the group average fusion algorithm. Multidimensional scaling (MDS) was applied to display resemblances in the abundance of carabids among the sites using the Bray-Curtis index of dissimilarity (Legendre and Legendre 1998).

Characteristic species of the urban, suburban and rural areas were identified by the IndVal (Indicator Value) procedure (Dufrière and Legendre 1997). This method identifies quantitatively the characteristic species of the studied habitat types, and generates a significance value (p -value) for the strength of association using a randomised computerised resampling technique. The characteristic value (IndVal) of a species is expressed as a product of the specificity and fidelity measures. It receives its maximum (100) when all individuals of a species are found in a single type of sites (high specificity) and when the species occurs at all sites of that type (high fidelity) (Dufrière and Legendre 1997). The characteristic species is defined as the most characteristic species of each habitat type, found mostly in that habitat and present in the majority of sites belonging to that habitat. This proved to be a useful method to identify the characteristic carabid species in several habitats (Elek et al. 2001; Magura et al. 2000a, 2001b, 2003).

The relationships between the environmental measurements and the abundance and species richness of carabids were examined by forward and backwards stepwise multiple linear regression analyses. Forward

stepwise multiple linear regression analysis provided a better fit; thus, we used this method as suggested by Kutner et al. (1996).

Results

Carabid diversity along the urban-rural gradient

The total carabid catch consisted of 2140 individuals representing 50 species; 477 individuals belonging to 43 species were captured in the urban area, 26 species and 457 individuals in the suburban area, and 25 species and 1206 individuals in the rural area.

Analysing the trap-level data by ANOVA we found that the overall carabid abundance was significantly higher in the rural than in the urban and suburban areas (Table 1). The number of individuals of the forest species was also the highest in the rural area, while significantly more individuals of open-habitat species were collected from the urban than from the suburban or rural areas (Figure 2A-C, Table 1).

The average number of collected carabid species was significantly higher in the rural (6.4 species/trap) and the urban (5.8) areas than in the suburban (4.8) one (Table 1). However, the species richness of forest carabids increased significantly from the urban to the rural area. Furthermore, the number of open-habitat species was significantly higher in the urban than in the suburban or rural areas. All these results indicated that there was a pronounced change in the carabid assemblages along the gradient (Figure 2A-F, Table 1).

Dominance structure and body size along the urban-rural gradient

The ratio of the number of individuals of the opportunistic (generalist) carabid species to the total number of individuals was significantly higher in the urban area than in the suburban and rural areas (Figure 3A, Table 1).

Our results were also coherent with the mean body size hypothesis (Blake et al. 1994, Gray 1989): the mean carabid body size was significantly higher in the less disturbed rural and suburban areas than in the more disturbed urban area (Figure 3B, Table 1).

Table 1. Nested ANOVA showing differences in carabid abundance, species richness, ratio of generalists to overall abundance, and in average carabid body size along the urban-suburban-rural gradient and among the 12 sites.

	Source of variation	df	MS	F	p
All species, number of individuals	Gradient	2	4598.77	4.80	< 0.05
	Sites	9	957.54	5.98	< 0.0001
	Error	108	159.99		
Forest species, number of individuals	Gradient	2	4453.81	11.17	< 0.005
	Sites	9	398.61	3.62	0.0006
	Error	108	110.14		
Open-habitat species, no. of individuals	Gradient	2	32.61	2.30	< 0.25
	Sites	9	14.16	3.81	0.0003
	Error	108	3.71		
Total number of species	Gradient	2	28.42	1.01	> 0.25
	Sites	9	28.09	5.83	< 0.0001
	Error	108	4.82		
Number of forest species	Gradient	2	21.76	19.26	< 0.001
	Sites	9	1.13	2.85	0.0048
	Error	108	0.40		
Number of open-habitat species	Gradient	2	6.47	5.48	< 0.05
	Sites	9	1.18	1.46	0.1725
	Error	108	0.81		
Generalists: all individuals	Gradient	2	1.59	13.25	< 0.0025
	Sites	9	0.12	3.13	0.0022
	Error	108	0.04		
Body size	Gradient	2	84.56	6.52	< 0.025
	Sites	9	12.97	1.41	0.1905
	Error	108	9.17		

Carabid assemblage composition along the urban-rural gradient

There was a marked separation among the sites along the urban-rural gradient. The four urban sites separated into a distinct cluster based on the species composition, while the suburban and rural sites formed the other cluster (Figure 4A). The MDS ordination based on the abundance data revealed a linear gradient: the carabid assemblages changed gradually from the rural area towards the urban area (Figure 4B). The heterogeneity of the carabid composition among the sites of the given area is highlighted by the size of the convex hull on the ordination graph. The larger size of the convex hull indicates a higher variability among the carabid composition of the sites (Figure 4B). The size of the convex hull of the sites decreased from the urban to the rural area, suggesting a decreased heterogeneity of the carabid composition along the urban-rural gradient.

Five groups of species were distinguished by habitat affinity (Table 2). We also identified quantitative character species by the IndVal procedure for the compared areas: (1) habitat generalists, numerous in all areas (character species: *Harpalus tardus*, *Cara-*

bus violaceus, *Platyderus rufus*); (2) species preferring the urban area, either recorded exclusively or being most abundant in the urban area (*Amara convexior*, *Pterostichus melanarius*, *Anisodactylus nemorivagus*); (3) species characteristic of suburban-rural areas (*Carabus convexus*, *Stomis pumicatus*, *Oxypselaphus obscurus*); (4) species preferring the suburban area; (*Harpalus luteicornis*, *Badister lacertosus*, *Amara consularis*); and (5) species characteristic of the rural area; (*Pterostichus oblongopunctatus*, *Ophonus nitidulus*, *Amara saphyrea*).

Environmental factors and carabids

Ground temperature was a significant positive predictor for the abundance of open-habitat species and for the overall species richness. Soil surface temperature was a negative determinant for the abundance of forest species and for the number of forest species, and a positive predictor for the number of open-habitat species. The relationships between relative humidity and the abundance of both total species and forest species were negative. The number of forest species increased, while the abundance and species richness of open-habitat species decreased as the amount of

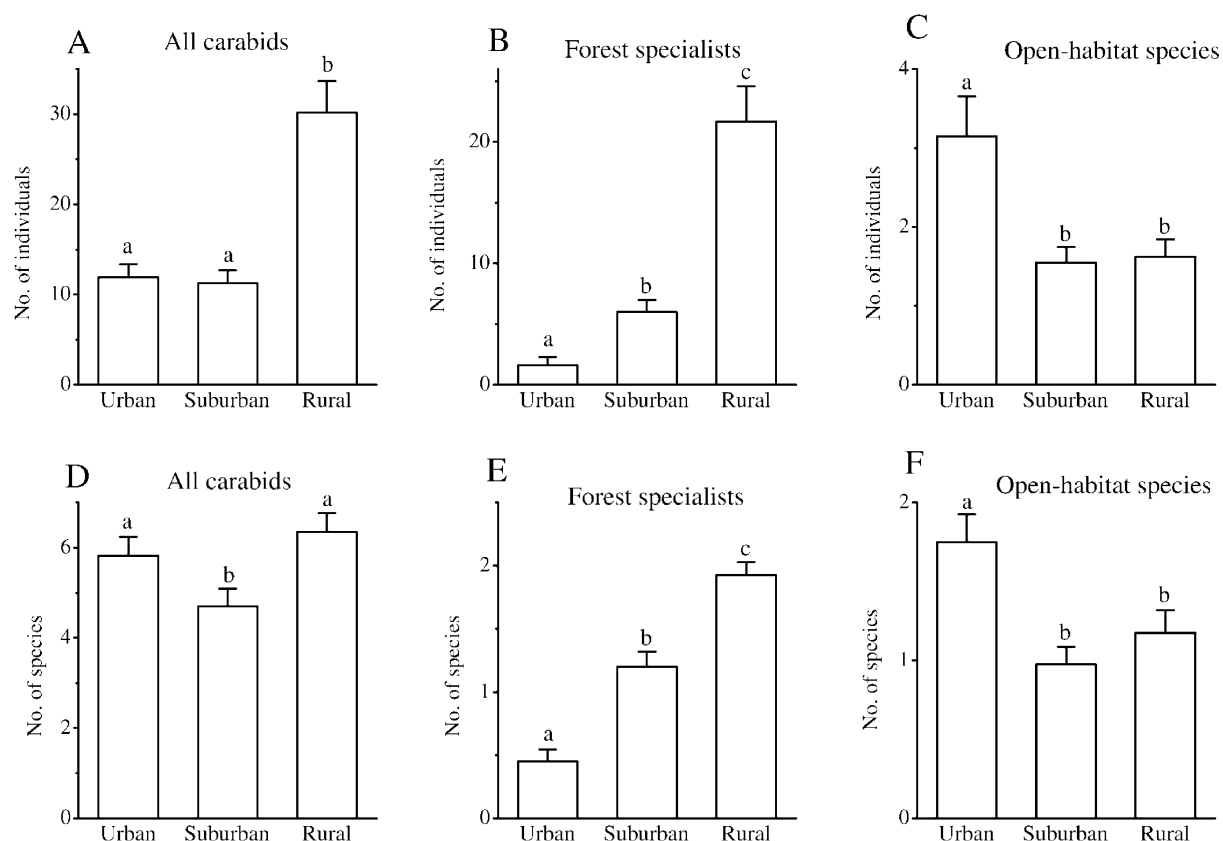


Figure 2. Average values (\pm SE) of (A) the overall carabid abundance, the abundance of (B) forest carabids, (C) open-habitat carabids, the (D) overall carabid species richness, the species richness of (E) forest carabids, (F) open-habitat carabids along the urban-suburban-rural gradient calculated for the traps. Different letters indicate significant ($p < 0.05$) differences based on the LSD (least significant difference) multiple comparison.

decaying wood material increased. Herb cover was a significant, positive predictor for all the studied carabid variables except for the number of open-habitat species. The overall carabid abundance, the abundance of forest species and the number of open-habitat species were negatively influenced by the extent of the canopy closure. The number of potential prey items was a significant positive predictor of the overall species richness and the number of forest species (Table 3).

Discussion

Responses of carabids to urbanisation

Urbanisation causes several forms of disturbance, such as alteration, fragmentation and isolation of indigenous habitats, changes of temperature, moisture

and edaphic conditions, and pollution (Gilbert 1989; Niemelä 1999). Gray (1989) hypothesised that in habitats influenced by disturbance, overall diversity should decrease, opportunistic (generalist) species should gain dominance and the mean body size of species should decrease. Our results did not support the hypothesis that overall diversity should decrease in disturbed habitats. The overall species richness of carabids was almost as high in the urban area as in the rural one.

Overall species richness increased with decreasing urbanisation both in Canada and Finland (Niemelä et al. 2002). The pattern of overall species richness of carabids in Bulgaria was the same as in our study. The different responses of carabids to urbanisation among the countries could reflect differences between boreal and temperate forests. Overall species richness changes along the disturbance gradient (urban-rural gradient) can be complex, because in a group of taxa,

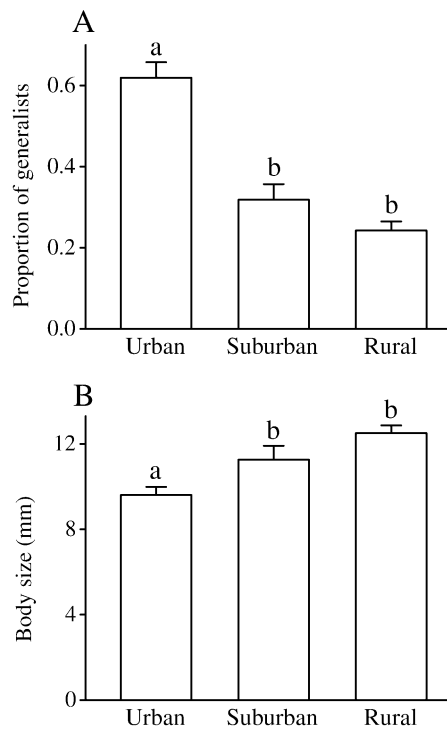


Figure 3. Average value (\pm SE) of (A) the ratio of generalist carabids to overall abundance, and (B) the mean carabid body size along the urban-suburban-rural gradient calculated for the traps. Different letters indicate significant ($p < 0.05$) differences based on the LSD (least significant difference) multiple comparison.

species richness may increase or decrease with disturbance depending on their habitat preference.

The initial hypothesis regarding forest specialists was supported: the number of forest species significantly increased from the urban to the rural area. The number of open-habitat species was significantly higher in the urban area than in the suburban and rural areas. These results indicate that human impacts caused a pronounced change in the carabid assemblages. Forest species require microsites with a particular kind of environmental heterogeneity, such as favourable microclimate, the presence of dead and decaying trees, significant cover of leaf litter, shrubs and herbs, together forming the undisturbed forest habitat (Desender et al. 1999; Magura 2002). Changes caused by urbanisation appear to eliminate favourable microsites for forest species, altering the original habitats. The degree of disturbance is higher in the urban (paved paths, thinned shrub layer), than in the suburban area (fallen trees removed), and is lowest in the rural area. This was also expressed by the differ-

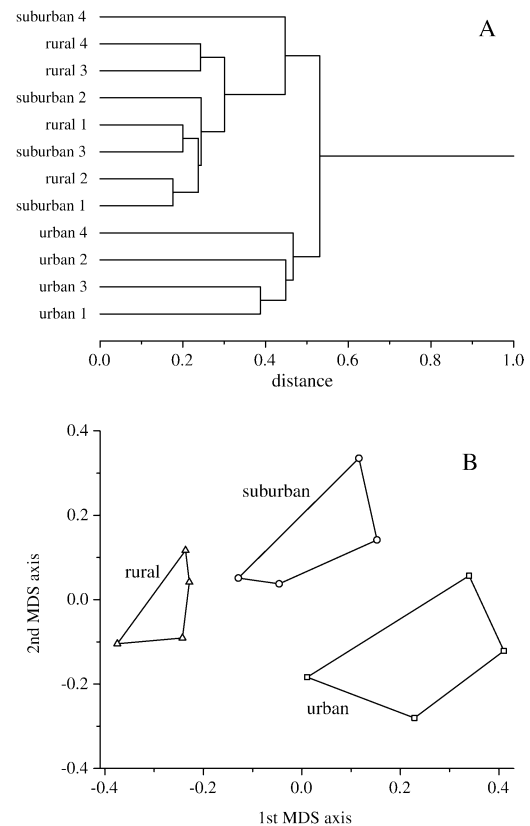


Figure 4. Cluster analysis of the carabid assemblages along the studied urban-rural gradient at site level using (A) the Sørensen index of similarity and the group average fusion algorithm and (B) MDS ordination of the abundances using the Bray-Curtis index of dissimilarity; stress of the two-dimensional configuration was 0.0528.

ence in the species richness of forest carabids. Results of Niemelä et al. (2002) also show that strictly forest species, like *Agonum mannerheimi* in Finland and *Molops* spp. in Bulgaria, are restricted to the rural areas. The remarkable alteration of the original habitats in the urban area was also reflected by the higher number of open-habitat species. Urban parks contain several microhabitats that open-habitat species can colonise. Previous studies (Thiele 1977; Magura et al. 2000b, 2001b) also emphasise that the number of open-habitat species increases as the closure of the forest stand decreases. Changes of carabid abundance along the urban-rural gradient showed a similar pattern.

Table 2. Species character power for the studied areas, and the habitat preference of the species which were present by five or more individuals. The IndVal column shows the species character value for the corresponding clustering level. Notations: G = Generalist species, F = Forest species, and O = Open-habitat species, ns – not significant; * – $p < 0.05$. In the cells of the table, the first number indicates the number of specimens present and the second one corresponds to the number of traps where the species is present, in this sample group.

Species	Habitat	IndVal	p	Urban area	Suburban area	Rural area
All areas						
<i>Harpalus tardus</i>	O	56.67	ns	34/18	53/31	35/20
<i>Carabus violaceus</i>	G	52.5	ns	51/17	30/17	124/29
<i>Platyderus rufus</i>	G	50	ns	45/24	18/14	40/22
<i>Pterostichus strenuus</i>	G	20.83	ns	10/7	25/13	7/5
<i>Pseudoophonus rufipes</i>	O	16.67	ns	6/4	4/4	12/12
<i>Amara familiaris</i>	G	8.33	ns	4/4	3/3	4/3
Suburban and Rural areas						
<i>Carabus convexus</i>	F	51.25	*	0/0	41/16	46/25
<i>Stomis pumicatus</i>	G	30.64	*	1/1	14/11	19/15
Urban area						
<i>Amara convexior</i>	G	38.36	*	52/18	6/5	12/10
<i>Notiophilus rufipes</i>	G	30	*	28/15	11/7	3/3
<i>Anisodactylus nemorivagus</i>	O	25	*	26/10	0/0	0/0
<i>Calathus fuscipes</i>	O	25	*	11/10	0/0	0/0
<i>Pterostichus melanarius</i>	G	24.63	*	33/10	1/1	0/0
<i>Bembidion lampros</i>	O	23.77	*	29/10	0/0	3/3
<i>Licinus depressus</i>	O	12.5	*	6/5	0/0	0/0
<i>Badister meridionalis</i>	G	10.94	*	7/5	2/2	0/0
<i>Amara communis</i>	O	10	*	5/4	0/0	0/0
<i>Notiophilus palustris</i>	G	7.69	ns	5/4	1/1	2/2
<i>Amara anthobia</i>	G	5	ns	5/2	0/0	0/0
Suburban area						
<i>Harpalus luteicornis</i>	G	21.15	*	5/4	20/11	1/1
<i>Badister lacertosus</i>	G	15	*	2/2	9/8	1/1
Rural area						
<i>Pterostichus oblongopunctatus</i>	F	76	*	60/15	197/26	795/40
<i>Ophonus nitidulus</i>	G	37.65	*	1/1	1/1	32/16
<i>Amara saphyrea</i>	F	20.53	*	4/3	8/7	26/12
<i>Synuchus vivalis</i>	O	19.12	*	1/1	3/2	13/10
<i>Pterostichus niger</i>	G	18.42	*	9/5	4/4	17/13
<i>Harpalus latus</i>	G	10.5	ns	6/5	0/0	9/7

Intermediate Disturbance Hypothesis

Both our findings and those of Niemelä et al. (2002) contradict the IDH (Connell 1978). Species richness was not the highest in the moderately disturbed suburban areas as IDH predicts. This may be because basal species in food webs probably conform to this hypothesis (Wootton 1998), but carabids, considered as top consumers (Lövei and Sunderland 1996) do not.

According to the opportunistic species hypothesis (Gray 1989) the generalist (opportunistic) species should gain dominance with increasing disturbance within the assemblage. Our results supported this prediction, as the ratio of the individuals of the op-

portunistic carabid species to the total number of individuals was significantly higher in the urban area than in the other ones. Niemelä et al. (2002) reported similar findings concerning the dominance of opportunistic species in the urban area of Canada and Finland. Several previous studies (Magura et al. 2000a, 2003; Koivula 2002) emphasised that generalist species invaded disturbed forest habitats due to the alteration of abiotic factors and biotic interactions.

Mean body size hypothesis

Gray (1989) hypothesised that the mean size of the species should decrease in disturbed habitats. Disturbed habitats (Holliday 1991; Blake et al. 1994;

Table 3. Relationship between carabid abundance and species richness per trap and selected environmental variables as determined by forward stepwise multiple linear regression analysis. Significant positive and negative relationships are indicated. ns: not significant.

	Overall abundance	Abundance of forest carabids	Abundance of open-habitat carabids	Overall species richness	Species richness of forest carabids	Species richness of open-habitat carabids
Ground temperature, °C	F = 14.16 d.f. = 5, 114 p < 0.0001 r = 0.62	F = 13.91 d.f. = 6, 113 p < 0.0001 r = 0.65	F = 5.97 d.f. = 4, 115 p < 0.0002 r = 0.41	F = 9.46 d.f. = 4, 115 p < 0.0001 r = 0.50	F = 17.58 d.f. = 5, 114 p < 0.0001 r = 0.66	F = 7.77 d.f. = 5, 114 p < 0.0001 r = 0.50
Surface temperature, °C	ns	ns	ns	+	not entered	not entered
Relative humidity, %	ns	-*	not entered	not entered	-***	not entered
Leaf litter cover, %	-**	-**	not entered	not entered	ns	not entered
Decaying wood material, %	not entered	not entered	not entered	not entered	not entered	ns
Herb cover, %	not entered	not entered	-**	ns	+	-*
Shrub cover, %	+	+	+	+	+	ns
Canopy cover, %	not entered	ns	not entered	not entered	not entered	not entered
Prey abundance, no individuals/trap	-***	-***	ns	not entered	not entered	-***
	not entered	not entered	not entered	+	+	not entered

*, p < 0.05, ***, p < 0.01, ***p < 0.001, and not entered: the given variable was not entered into the regression model.

Magura et al. 2002) support a carabid fauna with smaller average body size. Šustek (1987), analysing changes in body size structure of carabids along an urbanisation gradient, also found that disturbance caused by urbanisation produced smaller average carabid body size. Carabid body size changes from small in urban to larger one in both suburban and rural sites in Bulgaria and Finland (Niemelä et al. 2002).

Blake et al. (1994) argued that larger carabids were predominantly autumn breeders with overwintering larvae and a longer larval period required an availability and stability of resources that were missing in disturbed habitats. Several field studies confirmed that the abundance of carabids that overwinter as larvae was higher in less disturbed habitats compared to more disturbed ones (Butterfield 1997; Lövei 1984, Magura et al. 2002). In woodlands, increasing organic matter is linked to increased carabid biomass, and this may contributed to the persistence of larger-bodied carabids (Blake et al. 1994). In woodlands, the chief source of soil organic matter is from decaying plant material and it is possible that a high organic matter content is an indication of less disturbed forest habitats. At our sites, the rural area had significantly more herbs and decaying wood than the other areas and therefore probably more organic matter. This could contribute to the existence of larger carabids. The smaller mean body size in the urban area may also be explained with the flight ability, as species capable of flying are generally small-sized. The majority of open-habitat species collected in the urban area are able to fly which enables their rapid dispersal.

Changes in species structure

The result of the cluster analysis separated the urban sites indicating that urbanisation caused a pronounced change of carabid assemblages from the suburban and rural sites. Forest species preferred the moderately disturbed or undisturbed areas (suburban and rural), while open-habitat species occurred mainly in the urban area. These changes along the urban-rural gradient and the different patterns of occurrence were confirmed by the results of the IndVal procedure. High heterogeneity of species composition among sites in the urban area was likely caused by the patchy environment. In the urban area, habitat patches with closed canopy co-occur with patches of moderate closure because of the walking paths and thinned

shrubs. This patchiness facilitated the survival and persistence of forest species, generalist species as well as open-habitat species in the urban area. The rural area had a less diverse mosaic of habitat patches, therefore the dominant and subdominant generalist and forest species were relatively uniformly distributed leading to lower between-site heterogeneity. Niemelä (1999) also attributed the high overall species richness in urban areas both to high α -diversity and β -diversities. The species richness of forest carabids decreased from the rural towards the urban area, indicating the sensitivity of these species to disturbance.

The total number of individuals was much higher in the rural area compared to the suburban and urban ones, confirming a pattern found in Bulgaria and Finland (Appendix 2, Niemelä et al. 2002). A similar effect of disturbance on the total number of individuals was reported by Pócs and Tóthmérész (1997) in the case of foliicolous tropical mosses. The decrease of the total abundance is often a sensitive indicator of disturbance. The number of individuals can change quickly, reflecting important changes in a habitat. The loss of species richness is a much slower process.

Environmental factors and carabids

Regression analyses showed that a significant proportion of the variation in abundance and species richness was associated with environmental factors. The positive relationship between the ground temperature and the overall species richness can be attributed to the high number of generalist and open-habitat species in habitats with higher temperature. Open-habitat species prefer habitats with open or less closed canopy, where the sunlight can warm up the soil and they aggregate in these patches (Thiele 1977).

The significant negative relationship between the humidity and the abundance of the forest species is unexpected, as the forest carabids generally favour habitats of higher humidity (Thiele 1977). However, more than 89% of the individuals of the collected forest carabids, and half of the overall carabids, were *Pterostichus oblongopunctatus*, a xerophilic species. The negative relationship between humidity and overall carabid abundance was probably caused by the dominance of this species.

Leaf litter cover was not a significant predictor for either the abundance or the species richness of carabids, even though several studies emphasised the importance of leaf litter in the occurrence of carabid beetles (Koivula et al. 1999; Magura et al. 2000a). In

the broad-leaved forests, temperature and humidity altered by the leaf litter might play a more important role in carabid occurrence than leaf litter cover alone. In this study, humidity increased, while ground and surface temperature decreased with increasing leaf litter coverage.

Both the abundance and species richness of open-habitat carabids decreased, while the number of forest carabid species increased as the amount of decaying wood material increased. Open-habitat carabids are not adapted to environment with dense decaying wood material. For forest carabids, decaying wood provides favourable microsites, shelter against predators, and sites for aestivation, hibernation, egg and larval development (Thiele 1977).

Except for the number of open-habitat species, both the abundance and species richness of carabids increased as herb cover increased. These can be interpreted as a habitat structure effect. Carabid beetles depend more on habitat structure than on specific plant species (Lövei and Sunderland 1996; Spence et al. 1996). Vegetation structure and the resulting changes in microclimate (e.g., temperature and air moisture) are likely to be among the most important factors controlling the distribution of carabids (Niemelä et al. 1992; Magura et al. 1997, 2000b). An increased herb cover can also increase the amount of invertebrate prey available for predatory carabids and can provide a more uniform resource distribution in time (Niemelä and Spence 1994; Niemelä et al. 1994, 1996).

There was a significant positive relationship between the amount of potential prey items and both the overall species richness and the number of forest species. Thiele (1977) and Den Boer (1985) emphasised the importance of abiotic environmental factors in carabid ecology, but not the influence of biotic factors, such as the amount of potential prey. However, Bryan and Wratten (1984) reported that carabids may aggregate in microsites with plentiful prey, and Guillemain et al. (1997) and Fournier and Loreau (1999) emphasised that prey density plays a crucial role in carabid distribution. Our results draw attention to the relevance of prey density in determining carabid species richness.

Preservation of biodiversity in the urban landscape

Both our results and those of Niemelä et al. (2002) showed that species richness as well as assemblage composition changed along the urban-suburban-rural

gradient. Forested urban areas were still relatively species-rich, but the majority of the observed species were generalists and open-habitat species invading from the surrounding habitats. In contrast, the number of native forest carabid species significantly decreased along the disturbance gradient.

Urban green areas contribute to the quality of urban life and thus should be conserved. Apart from the recreational importance of the urban green areas, they provide suitable habitats for many carabid species living in undisturbed or moderately disturbed areas (e.g., meadows, grasslands, pastures, agricultural areas) surrounding the city. Moreover, urban green areas could support rare species. We collected *Pterostichus melas* from the urban area. In Hungary, this species occurs mainly in the hills and mountains and only few lowland occurrences were known. However, as our results also demonstrated, that urbanisation could be one of the leading causes of decline in indigenous arthropod diversity and abundance (Davis 1978).

How can the biodiversity preservation function of urban parks be enhanced? We suggest that extensive alteration of habitat structure (e.g., by strong thinning and removing decaying wood material) and creating only asphalt-covered paths should be avoided. These alterations generally cause unfavourable changes in the microclimatic, abiotic and biotic conditions of the area. All these changes affect forest carabids directly. Creating sealed paths fragments the habitat into even smaller patches. The division of the original forests into smaller, isolated patches causes a loss of forest species through a reduction in the habitat area, an increase in remnant isolation and a decrease in habitat connectivity (Didham et al. 1996). Several studies found that the number of carabid species decreased with the decreasing area of the forest patch (Burke and Goulet 1998; Davies and Margules 1998; Fournier and Loreau 2001; Magura et al. 2001a). Forest patches divided by asphalt-covered paths are isolated from each other, as carabids only infrequently cross them (Mader 1984; Mader et al. 1990). The population size of forest carabid species in isolated patches could decrease because the patches are too small to maintain viable populations and there is too little dispersal between patches. Small populations of forest carabids in isolated patches are at greater risk of local extinction through stochastic population fluctuations than are the larger populations (Den Boer 1985; Niemelä et al. 1994). Judicious habitat management can ease these pressures on carabids as well as other components of urban biodiversity, and thus serve both the demands of city-dwellers and the maintenance of biodiversity.

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