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## Original article

# Time-consistent rearrangement of carabid beetle assemblages by an urbanisation gradient in Hungary

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## ABSTRACT

To examine the impact of urbanisation on arthropod biodiversity, carabid (Coleoptera: Carabidae) assemblages were studied over 2 years along a rural–urban gradient representing increasing levels of human disturbance. Carabids were collected by pitfall trapping during their whole activity period in lowland oak forest patches in and near the city of Debrecen, Eastern Hungary, over two seasons (2001–2002). Carabid activity density was significantly higher in the rural than in the two other areas, but there was no significant difference in species richness (measured as mean number of species caught/trap). The proportion of forest specialists significantly decreased from the rural towards the urban area, and the proportion of forest specialist species was significantly higher in the rural and suburban areas than in the urban one. In contrast, the relative activity density of generalist species significantly increased along the rural–urban gradient. Both the relative number of open-habitat species and their activity density were significantly higher in the urban forest fragments than in the suburban and rural ones. The patterns found were consistent between the 2 years. Multidimensional scaling indicated pronounced changes in species composition along the gradient; the assemblages in urban forest fragments were more variable than in the other areas. A large proportion of the variation in overall activity density, species richness and the proportion of carabids with different habitat affinities could be explained by structural habitat variables (percentage cover by canopy, leaf litter, herbs and decaying wood), and prey availability.

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## 1. Introduction

An increase of human population causes increased resource use by humans, larger impact on non-urban habitats, and the conversion of original, rural habitats to urban ones. Urbanisation is increasing worldwide, and half or more of

the global human population lives in cities (United Nations, 2004). The obvious impact of urbanisation on the original habitats is the fragmentation and loss of the original habitat. There are also changes in temperature, soil acidity, pollution, decomposition, carbon and nitrogen cycling (Niemi, 1999; Rebele, 1994). Urbanisation causes changes in community

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structure and species richness via the alteration of habitat structure (Gibb and Hochuli, 2002), habitat fragmentation and loss (Gibbs and Stanton, 2001), creating opportunities for invasion of alien species (Honnay et al., 2003), climate warming (Hegelbach, 2001) and increased pollution (Steiner, 1995).

The phases of urbanisation seem to be similar all over the globe, but it is unknown whether these will cause similar changes in biodiversity (McDonnell and Pickett, 1990). Comparative ecological studies, done in different locations but using the same treatments are important for ecological understanding, but are very few and sorely needed (Lawton, 2000). Effects of urbanisation on arthropods are also understudied, even if urbanisation is one of the primary causes for declines in arthropod populations (McIntyre, 2000). The Globenet project (Niemelä et al., 2000; Niemelä and Kotze, 2000) aims to examine how urbanisation affects arthropod biodiversity in an originally forested area undergoing urbanisation, using a gradient approach (McDonnell and Pickett, 1990). Carabids (Coleoptera: Carabidae) were selected for study because they are diverse, abundant, their relatively short generation times allow them to respond quickly to anthropogenic effects, and are easy to sample (Lövei and Sunderland, 1996). Studies published so far analyse trends in the total number of carabid individuals and species, and the number of individuals and species with different habitat affinities (forest specialist species, generalist and open-habitat species; see Alaruiikka et al., 2002; Niemelä et al., 2002; Ishitani et al., 2003; Venn et al., 2003; Magura et al., 2004; Elek and Lövei, 2005, 2007; Gaublomme et al., 2005; Sadler et al., 2006).

The published papers, however, have several shortcomings. Most of them rely on a single year of study and assume that the trends found in the year of study provide a “real” picture. This can be questioned. Further, the gradient is not well characterised – the suburban stage is assumed to be “in-between” the other two phases, the original forest habitat and the urban forest fragment (Niemelä et al., 2000). Several studies analysed the total, or the mean number of species captured, which could be distorted by impacts of geography, climate and evolutionary history on the actual fauna (Huston, 1994).

In our earlier work (Magura et al., 2004), we tested several hypotheses using a single year of data. From these, the intermediate disturbance hypothesis (Connell, 1978) has rarely got support, and it is also difficult to quantify what constitutes an “intermediate” level of disturbance. Therefore, this hypothesis was not tested further. We tested several formal hypotheses that could explain the trends of biodiversity affected by urbanisation. These hypotheses would produce different patterns but would not be necessarily mutually exclusive. A hypothesis proposed by Gray (1989) states that increasing disturbance would monotonously decrease both components of diversity (species richness and evenness). More frequent and more severe disruptions would eliminate sensitive species, causing a decrease in species richness. Species that are able to cope with disturbance would increase their dominance, resulting in decreasing evenness of the assemblages. We also tested a further developed version of the “habitat alteration hypothesis” (Magura et al., 2004) which assumes that increasing levels of urbanisation will alter the structure of the original, rural habitat, causing a decreased presence/

dominance of the forest specialist species. However, as the original habitat patches become smaller, species from the surrounding matrix will have the opportunity to penetrate the remaining habitat islands (Lövei et al., 2006) and this could cause an increase in diversity. Therefore, habitat alteration can cause an overall decrease or increase of carabid diversity. In a region with few available generalist and open-habitat species, the overall diversity change can be determined by the reaction of forest-associated species to urbanisation. In areas with many generalist and open-habitat species, there can be an increase in total species richness.

In this paper, we used data from 2 consecutive years that ease the problem of trying to generalise on the basis of a single year study. We precisely positioned the suburban stage between the two extremes (rural and urban), on the basis of percentage built-in area, using aerial photographs. Instead of the total number of species and individuals, as done by most published studies, we considered the proportions of species in different classes (specialists, generalists, etc.) in the assemblage. More precisely, the following hypotheses were tested: (i) diversity should decrease from a high value in the rural area to a low one in the urban area (increasing disturbance hypothesis, Gray, 1989); and (ii) urbanisation decreases the dominance of forest specialist species and increases generalist and open-habitat species from the rural area to the urban one (habitat alteration hypothesis; Magura et al., 2004). Our analysis indicated that urbanisation causes a decline of forest-dwelling carabids but not an overall species richness decrease in Hungary. The trends we found were consistent between the 2 years.

## 2. Materials and methods

### 2.1. Study area and sampling design

The study areas were in and around the city of Debrecen (Eastern Hungary, 47° 32' N; 21° 38' E), the second largest city of the country. Three forested areas were selected along a rural-urban gradient within the boundaries of the city, and in the surrounding forest (Nagyerdő Forest Reserve), as required by the Globenet protocol (Niemelä et al., 2000). All areas belong to a once-continuous old forest stand (>100 years) dominated by English oak (*Quercus robur*). All fragments were ≥6 ha. We characterised the level of urbanisation by the relative built-up area, measured by the ArcView GIS program using an aerial photograph. In the rural area, there were no buildings (built-up area 0%) and the forest was continuous. In the suburban area, approximately 30% of the surface was built-in or paved, while in the urban area, surface occupied by patches of the original habitat was reduced to 40% (60% of the area was built-up or drastically different from the original forest habitat). The distance between the sampling areas (rural, suburban, urban) was 1–3 km. According to Digweed et al. (1995), this arrangement fulfils the conditions for patch independence. Additional (not quantified) types of disturbance were the presence of people and the intensity of forestry/habitat maintenance operations. In the rural forest there was not regular forestry intervention. In the suburban area, the fallen trees and branches were regularly removed, but the

understory was not thinned. Most paths were not covered with tarmac. In the urban area, in addition to the routine forestry operations as in the suburban area, the shrub layer was strongly thinned. Grass between the forest patches was regularly moved, and the mowed grass was taken away. There were several asphalt-covered paths, increasing the isolation between the forested patches.

The sampling regime followed the Globenet protocol (Niemelä et al., 2002). At four sites per urbanisation stage, at least 50 m from each other, 10 pitfall traps (65 mm diameter, 75% ethylene glycol as preservative, with covers) were deployed randomly. Trapped beetles were collected fortnightly from the end of March to the end of November in 2001 and 2002. Traps were placed at the same locations in both years. Carabids were identified to species using keys in Hürka (1996). Voucher specimens are held in the Department of Zoology, Debrecen University.

Six environmental factors were measured that were assumed to affect the distribution of carabids. Within a circle of 2 m diameter around every trap, we estimated the percentage cover by leaf litter, decaying wood, herbs, shrubs and tree canopy. We also counted the number of other invertebrates (other Coleoptera, Chilopoda, Diplopoda, Gastropoda, and Isopoda) captured in the traps, which is a measure of the amount of potential prey (Sergeeva, 1994).

## 2.2. Data analyses

Nested analyses of variance with repeated measures were performed to test differences in the overall carabid activity density, species richness, the proportions of forest specialist, generalist and open-habitat species in the assemblages among the three sampling areas (rural, suburban, urban), the 12 sites, and between the 2 years (2001 and 2002). Data from the individual traps (sites nested within the sampling areas) were used. Ground beetles were categorised into forest specialist, generalist and open-habitat species according to information in Hürka (1996). Data were tested for normality (Kolmogorov–Smirnov test, Sokal and Rohlf, 1995) and all of them proved to be normally distributed (results not shown). Tukey test for multiple comparisons among means was performed when ANOVA results revealed significant differences among means.

The composition of carabid assemblages along the rural–urban gradient was compared at site level by non-metric multidimensional scaling (MDS), using the Hellinger distance (Legendre and Legendre, 1998). The relationships between the measured habitat variables and the overall carabid activity density, species richness and the proportion of carabids with different habitat affinities were examined by multiple linear regression analyses (Kutner et al., 1996).

## 3. Results

### 3.1. Carabid diversity along the rural–urban gradient

Altogether, we captured 4421 individuals representing 59 species (2140 individuals of 50 species in 2001, and 2281 individuals of 46 species in 2002; Table 1). In the rural area,

35 species and 2451 individuals were caught (1206 individuals, 25 species in 2001, 1245 individuals, 28 species in 2002); 34 species and 1026 individuals were captured in the suburban area (457 individuals, 26 species in 2001, 569 individuals, 27 species in 2002), and 944 individuals belonging to 51 species were captured in the urban area (477 individuals, 43 species in 2001, 467 individuals, 38 species in 2002). The most numerous species was *Pterostichus oblongopunctatus* in all habitats and both years (except in the urban area in 2002), and in total, made up 47% of the total catch. In the rural forest, *Carabus violaceus* (in both years), *Synuchus vivalis* (in 2002 only) and *Carabus convexus* (both years) were also numerous. In the suburban area, *Harpalus tardus*, *C. convexus* and *C. violaceus*, while in the urban habitats, *Amara convexior*, *Platyderus rufus*, and *H. tardus* were common (Table 1).

The overall carabid activity density was significantly higher in the rural than in the urban and suburban areas. However, there were no statistically significant differences in the overall species richness (Table 2 and Fig. 1).

### 3.2. Patterns of species categorised by habitat affinity

The proportion of individuals belonging to forest specialist species decreased significantly from the rural area towards the urban one; the proportion of the forest specialist species was significantly higher in the suburban and rural areas than in the urban one (Table 2 and Fig. 2).

An opposite tendency was observed for generalists, whose relative activity density increased significantly along the rural–urban gradient (Table 2 and Fig. 2). There were no statistically significant differences in the proportion of generalist species among the studied areas, although this was highest in the urban area (Table 2 and Fig. 2).

Both the relative activity density of open-habitat species and their proportion in the total species richness were significantly higher in the urban area compared to the suburban or rural ones (Table 2 and Fig. 2).

### 3.3. Comparison of the carabid assemblages

The carabid assemblages of the rural, suburban and urban areas could be separated from each other by the ordination (Fig. 3). The carabid assemblages in the urban forest fragments were separated from the others along the first axis. The composition of the carabid assemblages of suburban and rural areas was more similar to each other than to the carabid assemblages of the urban forest fragments. The heterogeneity of the carabid composition among the sites of the given area, expressed by the size of the convex hull on the ordination graph, increased from the rural area towards the urban one (Fig. 3).

### 3.4. The influence of habitat factors on activity density and species occurrence

The urban sites had higher ground and air temperatures than the other two habitat types. The suburban sites had a higher relative humidity and leaf litter and shrub cover, while the rural sites had the highest percentage cover of decaying wood, herbs and prey availability. The overall activity density

**Table 1 – The numbers and habitat affinity of carabid species captured in pitfall traps in and around the city of Debrecen, Hungary, 2001–2002. Species sequence is according to the biannual total (most common first). F = forest specialist species, G = habitat generalist species, O = open-habitat species**

Species	Habitat affinity	2001			2002			Total
		Rural	Suburban	Urban	Rural	Suburban	Urban	
<i>Pterostichus oblongopunctatus</i>	F	795	197	60	710	263	57	2076
<i>Carabus violaceus</i>	G	124	30	51	113	48	24	390
<i>Harpalus tardus</i>	O	35	53	34	34	34	70	259
<i>Carabus convexus</i>	F	46	41	0	78	66	1	232
<i>Platyderus rufus</i>	G	40	18	45	39	23	31	196
<i>Amara convexior</i>	G	12	6	52	35	20	61	186
<i>Synuchus vivalis</i>	O	13	3	1	133	3	6	159
<i>Pterostichus strenuus</i>	G	7	25	10	4	27	17	90
<i>Amara saphyrea</i>	F	26	8	4	13	8	6	65
<i>Pterostichus melanarius</i>	G	0	1	33	1	2	25	62
<i>Pterostichus niger</i>	G	17	4	9	6	11	13	60
<i>Notiophilus rufipes</i>	G	3	11	28	4	3	10	59
<i>Pseudoophonus rufipes</i>	O	12	4	6	7	22	4	55
<i>Anisodactylus nemorivagus</i>	O	0	0	26	0	0	26	52
<i>Ophonus nitidulus</i>	G	32	1	1	10	1	0	45
<i>Stomis pumicatus</i>	G	19	14	1	8	1	0	43
<i>Bembidion lampros</i>	O	3	0	29	0	0	9	41
<i>Harpalus latus</i>	G	9	0	6	15	1	8	39
<i>Harpalus xanthopus winkleri</i>	G	0	0	0	3	10	21	34
<i>Calathus fuscipes</i>	O	0	0	11	3	0	15	29
<i>Harpalus luteicornis</i>	G	1	20	5	0	0	0	26
<i>Amara familiaris</i>	G	4	3	4	0	2	12	25
<i>Badister lacertosus</i>	G	1	9	2	0	6	3	21
<i>Carabus granulatus</i>	G	1	1	2	5	0	4	13
<i>Licinus depressus</i>	O	0	0	6	1	5	1	13
<i>Notiophilus palustris</i>	G	2	1	5	4	1	0	13
<i>Badister bullatus</i>	G	0	0	4	0	1	7	12
<i>Panagaeus bipustulatus</i>	G	0	0	4	0	5	3	12
<i>Amara anthobia</i>	G	0	0	5	0	0	5	10
<i>Amara ovata</i>	G	0	0	3	0	0	7	10
<i>Badister meridionalis</i>	G	0	2	7	0	0	1	10
<i>Calosoma inquisitor</i>	F	0	0	0	10	0	0	10
<i>Amara communis</i>	O	0	0	5	0	0	4	9
<i>Pterostichus anthracinus</i>	G	0	0	0	0	3	5	8
<i>Amara similata</i>	O	1	1	2	1	1	0	6
<i>Pterostichus melas</i>	G	0	0	1	3	0	1	5
<i>Amara consularis</i>	O	0	1	0	2	0	0	3
<i>Calathus erratus</i>	G	0	0	1	1	0	1	3
<i>Clivina fossor</i>	G	0	0	3	0	0	0	3
<i>Poecilus cupreus</i>	O	0	0	1	0	0	2	3
<i>Pseudoophonus griseus</i>	O	0	0	0	1	0	2	3
<i>Agonum lugens</i>	G	0	0	1	0	0	1	2
<i>Anisodactylus signatus</i>	O	0	0	0	0	1	1	2
<i>Asaphidion flavipes</i>	O	0	0	2	0	0	0	2
<i>Notiophilus biguttatus</i>	G	0	0	2	0	0	0	2
<i>Oxypselaphus obscurus</i>	G	1	1	0	0	0	0	2
<i>Trechus quadristriatus</i>	G	0	1	0	1	0	0	2
<i>Amara lucida</i>	G	0	0	0	0	0	1	1
<i>Anchomenus dorsalis</i>	O	0	0	1	0	0	0	1
<i>Calathus melanocephalus</i>	G	0	0	1	0	0	0	1
<i>Carabus ullrichi</i>	G	0	0	1	0	0	0	1
<i>Diachromus germanus</i>	O	0	0	1	0	0	0	1
<i>Harpalus distinguendus</i>	O	0	1	0	0	0	0	1
<i>Leistus ferrugineus</i>	G	1	0	0	0	0	0	1
<i>Ophonus schaubergerianus</i>	O	1	0	0	0	0	0	1
<i>Poecilus versicolor</i>	O	0	0	0	0	0	1	1
<i>Pterostichus macer</i>	O	0	0	1	0	0	0	1
<i>Pterostichus minor</i>	G	0	0	0	0	1	0	1
<i>Pterostichus ovoideus</i>	G	0	0	0	0	0	1	1
Number of individuals		1206	457	477	1245	569	467	4421
Number of species		25	26	43	28	27	38	59

**Table 2 – Nested ANOVA with repeated measures showing differences in overall carabid activity density, species richness and in the proportion of forest specialist species, generalist and open-habitat species along the rural–urban gradient and among the 12 sites. Year = the effect of study year (2001 and 2002). Results of the Tukey test indicate which area(s) differs significantly ( $p < 0.05$ ) from the others; for example “Urban > Suburban = Rural” indicates that the variable was significantly higher in the urban area than in the suburban and rural areas (these two areas are not different from that point of view)**

Variable	Source	df	MS	F	p	Tukey test
Overall carabid activity density	<i>Between-Subjects Effects</i>					
	Gradient	2	9015.2040	6.0905	<0.05	Urban = Suburban < Rural
	Sites	9	1480.1970	7.7209	<0.001	
	Error	108	191.7130			
	<i>Within-Subjects Effects</i>					
	Year	1	91.2670	1.0968	ns	
	Year × Gradient	2	53.0040	0.6370	ns	
	Year × Sites	9	160.1690	1.9248	ns	
	Error	108	83.2148			
	Overall carabid species richness	<i>Between-Subjects Effects</i>				
Gradient		2	51.9875	2.2853	ns	
Sites		9	22.7486	4.4642	<0.001	
Error		108	5.0958			
<i>Within-Subjects Effects</i>						
Year		1	8.4375	1.7553	ns	
Year × Gradient		2	0.1625	0.0338	ns	
Year × Sites		9	11.9541	2.4868	<0.02	
Error		108	4.8069			
Proportion of forest specialist individuals		<i>Between-Subjects Effects</i>				
	Gradient	2	6.2697	29.6362	<0.001	Urban < Suburban < Rural
	Sites	9	0.2116	5.3790	<0.001	
	Error	108	0.0393			
	<i>Within-Subjects Effects</i>					
	Year	1	0.0216	0.6503	ns	
	Year × Gradient	2	0.0819	2.4616	ns	
	Year × Sites	9	0.0719	2.1594	<0.05	
	Error	108				
	Proportion of forest specialist species	<i>Between-Subjects Effects</i>				
Gradient		2	1.5360	17.0754	<0.001	Urban < Suburban = Rural
Sites		9	0.0900	3.7112	<0.001	
Error		108	0.0242			
<i>Within-Subjects Effects</i>						
Year		1	0.0021	0.0903	ns	
Year × Gradient		2	0.0132	0.5813	ns	
Year × Sites		9	0.0424	1.8652	ns	
Error		108	0.0227			
Proportion of generalist individuals		<i>Between-Subjects Effects</i>				
	Gradient	2	2.8950	19.5546	<0.001	Urban > Suburban > Rural
	Sites	9	0.1480	4.2750	<0.001	
	Error	108	0.0346			
	<i>Within-Subjects Effects</i>					
	Year	1	0.0064	0.1601	ns	
	Year × Gradient	2	0.0104	0.2618	ns	
	Year × Sites	9	0.0445	1.1183	ns	
	Error	108	0.0398			
	Proportion of generalist species	<i>Between-Subjects Effects</i>				
Gradient		2	0.4979	3.7210	ns	
Sites		9	0.1338	3.6711	<0.001	
Error		108	0.0365			
<i>Within-Subjects Effects</i>						
Year		1	0.0005	0.0128	ns	
Year × Gradient		2	0.0119	0.3114	ns	
Year × Sites		9	0.0436	1.1428	ns	
Error		108	0.0381			

(continued on next page)

Table 2 (continued)

Variable	Source	df	MS	F	p	Tukey test
Proportion of open-habitat individuals	<i>Between-Subjects Effects</i>					
	Gradient	2	0.6739	6.1562	<0.05	Urban > Suburban = Rural
	Sites	9	0.1095	3.4740	<0.001	
	Error	108	0.0315			
	<i>Within-Subjects Effects</i>					
	Year	1	0.0849	2.5231	ns	
	Year × Gradient	2	0.0614	1.8233	ns	
	Year × Sites	9	0.0267	0.7930	ns	
Error	108	0.0337				
Proportion of open-habitat species	<i>Between-Subjects Effects</i>					
	Gradient	2	0.3171	9.3649	<0.01	Urban > Suburban = Rural
	Sites	9	0.0339	1.3403	ns	
	Error	108	0.0253			
	<i>Within-Subjects Effects</i>					
	Year	1	0.0017	0.0545	ns	
	Year × Gradient	2	0.0376	1.1967	ns	
	Year × Sites	9	0.0299	0.9520	ns	
Error	108	0.0314				

was only influenced by herb cover (positively, in both years) and canopy cover (negatively, in 1 year). The overall species richness was only affected (positively) in 1 year by the number of potential prey items. The proportion of individuals belonging to forest specialist species was positively influenced (in both years) by the cover of leaf litter, decaying wood and herbs, and in 1 year, the number of potential prey items. The proportion of forest specialist species was similarly influenced by the same factors, but only in 1 year – except leaf litter cover, which had a positive influence on this parameter in both years of study (Table 3).

The proportion of individuals belonging to generalist species was negatively influenced by decaying wood (both years), leaf litter, and herb cover (in 1 year only). None of the measured habitat variables had a significant influence on the number of generalist species (Table 3).

The relative activity density of open-habitat species was negatively influenced by several habitat characteristics: the extent of herb cover (both years), leaf litter and the presence of decaying wood (one -but not the same- year). The proportion of open-habitat species had a negative relationship with leaf litter, canopy cover and the presence of decaying wood (Table 3).

## 4. Discussion

### 4.1. Diversity changes along the gradient

We found that the overall carabid activity density was significantly higher in the rural than in the urban and suburban areas, but the overall differences in species richness were statistically not significant. Similar diversity patterns were detected in Belgium (Gaublomme et al., 2005), and Bulgaria (Niemelä et al., 2002). In Denmark, the urban area had the highest species richness (Elek and Lövei, 2007).

Given that most of the profound changes in habitat quality during urbanisation is intuitively interpreted as making the habitat less favourable to arthropods, it is surprising that

our results did not support the "increasing disturbance" hypothesis (Gray, 1989). The overall species richness of carabids was almost as high in the heavily disturbed urban forest fragments as in the less disturbed rural area. This is in contrast with findings in Canada (Niemelä et al., 2002), England (Sadler et al., 2006), Finland (Niemelä et al., 2002; Venn et al., 2003) and

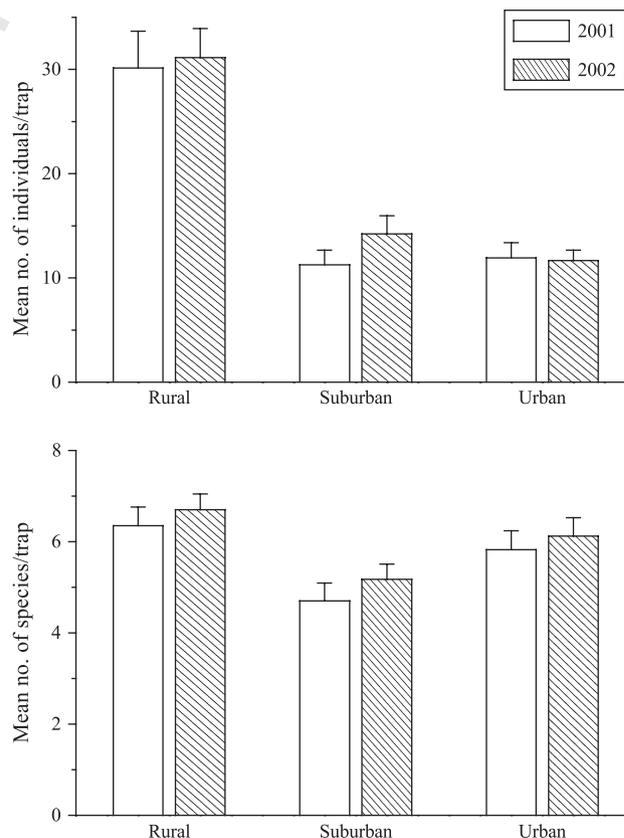
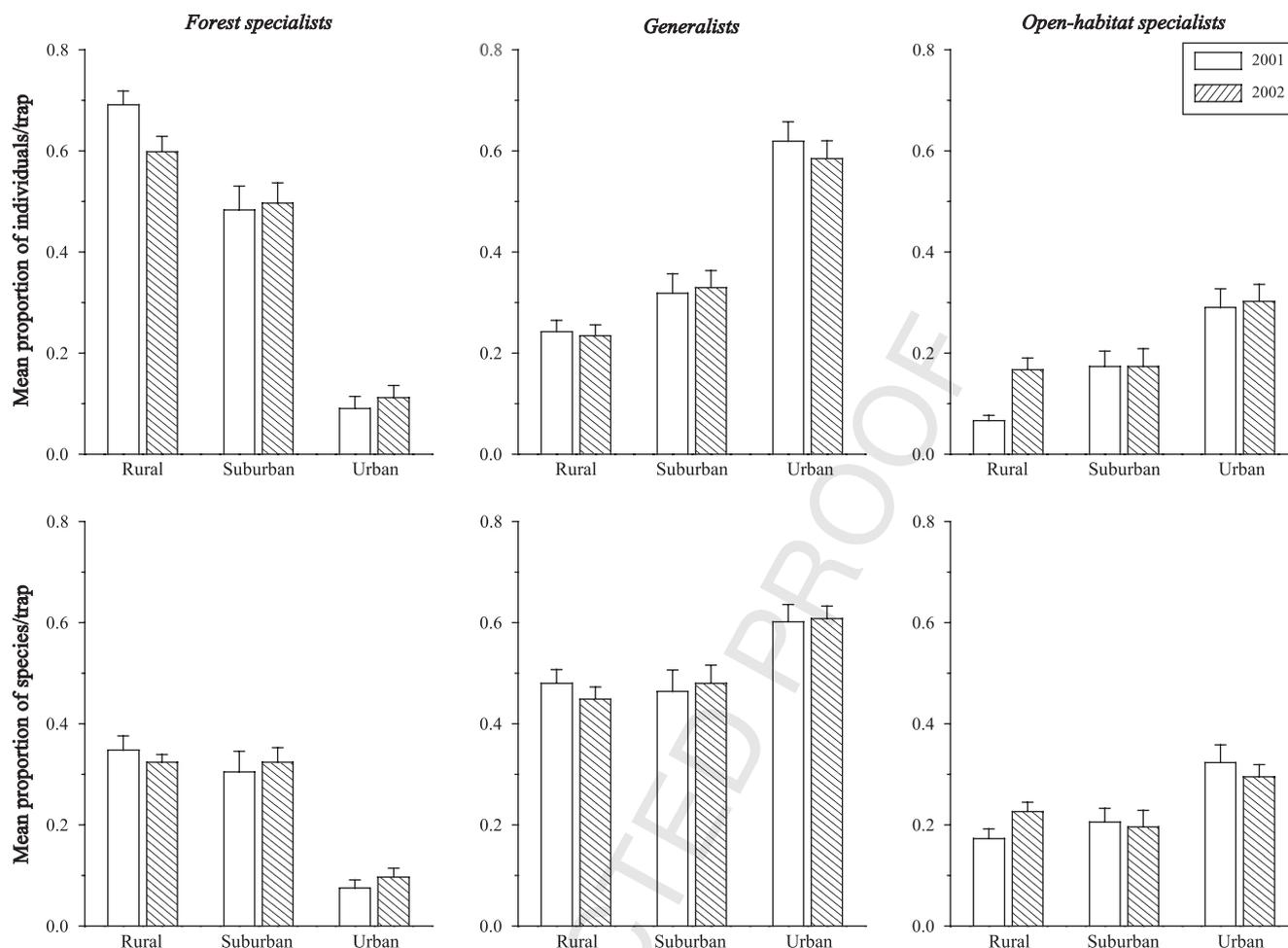


Fig. 1 – Mean values (±SE) of the overall carabid activity density (top) and species richness (bottom) along the rural-urban gradient at Debrecen, Hungary, in 2001–2002.



**Fig. 2 – Mean values ( $\pm$ SE) of the relative activity density (top row) and species richness (bottom row) of forest specialist, generalist and open-habitat ground beetle species along the rural-urban gradient at Debrecen, Hungary, in 2001-2002.**

Japan (Ishitani et al., 2003). A possible reason is the differences in the size of the available species pool of the different habitat affinity categories. In Hungary, open-habitat species could have a larger species pool, and thus could contribute more species than countries with extensive forests, such as Finland. As a consequence, open-habitat-favouring species can increase the species richness in urban forest fragments in Hungary more than in Finland.

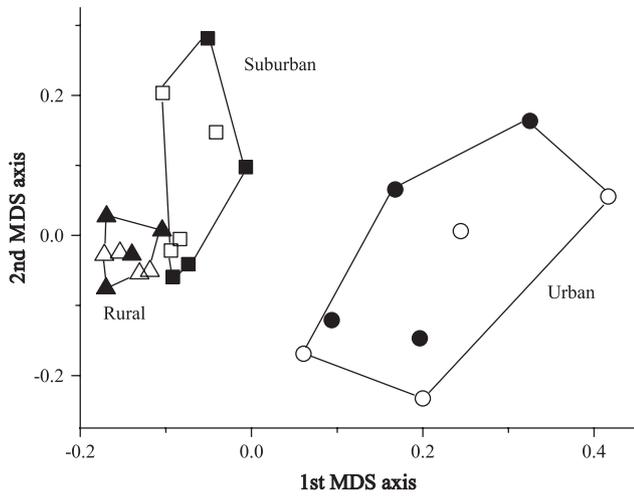
#### 4.2. Dominance changes along the gradient

Urbanisation causes several forms of disturbance, all of which contribute to the alteration of the original habitats (Gilbert, 1989; Niemelä, 1999). The habitat alteration hypothesis was supported, because the proportion of the individuals and species in forest specialists was significantly higher, while the proportion of individuals of generalist and open-habitat species as well as their number of species were significantly lower in the less disturbed rural area than in the more disturbed urban one. The proportion of generalist species also increased along the rural-urban gradient. Similar result were obtained in Belgium (Gaublomme et al., 2005), England (Sadler et al., 2006), Finland (Alarukka et al., 2002), and Japan (Ishitani et al., 2003), as forest specialist individuals were more

likely caught in suburban and rural areas than in the urban one.

The response by generalist carabids is more complicated, as there was no difference in the number of generalist individuals along the rural-urban gradient in Belgium (Gaublomme et al., 2005) or Japan (Ishitani et al., 2003) but they were more dominant in the urban area than in the suburban and rural ones in Canada, Finland (Niemelä et al., 2002), as well as Denmark (Elek and Lövei, 2007). An idiosyncratic response was found in another study in Finland where more generalist individuals were collected from rural areas than either urban or suburban ones (Alarukka et al., 2002).

Urbanisation caused the strongest effect on the forest specialist carabid species. These species require sites with a special microclimate, the presence of dead and decaying trees, significant cover of leaf litter, shrubs and herbs, together forming the undisturbed forest floor habitat (Desender et al., 1999). Habitat alteration caused by urbanisation appears to eliminate favourable microsites and contributes to the decline of forest specialists in the assemblage. Along the studied gradient, the disturbance was the lowest in the original forest (rural area), moderate in the suburban area (fallen trees regularly removed, medium number of human visitors), and highest in the urban forest fragments (thinned shrub layer,



**Fig. 3 – Ordination (non-metric multidimensional scaling using the Hellinger distance) of the carabid assemblages along the studied rural-urban gradient at Debrecen, Hungary, in 2001-2002. Analysis was made at site level; the stress of the two-dimensional configuration was 0.1033. Open symbols: data from 2001, closed symbols: data from 2002.**

highest number of visitors). This increasing disturbance was reflected by the decreasing proportion of forest specialist carabids. Further, habitat alteration accompanying urbanisation increased the proportion of both generalist and open-habitat carabids. This is in agreement with Gray's Increasing Disturbance Hypothesis (Gray, 1989), according to which the generalist (opportunistic) species should gain dominance within the assemblage as disturbance increases. Generalist species can invade disturbed forest habitats as they tolerate the altered conditions (Koivula, 2002; Koivula and Niemelä, 2003; Magura et al., 2000, 2003). The significant alteration of the original habitats in the urban area was also reflected by the dominance of open-habitat species in the assemblage. The urban park contains several microhabitats that open-habitat species can colonise. Previous studies (Koivula, 2002; Koivula and Niemelä, 2003; Magura et al., 2000, 2001) also emphasised that the number of open-habitat species increased as the closure of the forest stand decreased. Recent work (Hartley et al., 2007) indicated that open-habitat species could successfully colonise grassland patches in urban areas. Such "matrix species" can penetrate forest fragments in an agricultural landscape (Lövei et al., 2006), and probably also the generally small urban forest fragments.

**4.3. Compositional changes along the gradient**

The ordination analysis separated the urban sites from the suburban and rural ones, indicating that urbanisation caused a considerable change in the composition of carabid assemblages along the rural-urban gradient. The composition of carabid assemblages was similar at the suburban and rural sites. Forest specialist species preferred the moderately disturbed or lightly disturbed areas (suburban and rural), while generalist and open-habitat species preferred the urban area. The highest compositional heterogeneity was at the

**Table 3 – Relationship between the selected environmental variables and the overall carabid activity density, species richness and the proportion of forest specialist species, generalist and open-habitat species as determined by multiple linear regression analysis (df = 6, 113 in all cases). Positive and negative relationships are indicated. ns: not significant, \* p < 0.05, \*\* p < 0.01, \*\*\* p < 0.001**

	Overall activity density		Overall species richness		Proportion of forest specialist species		Proportion of generalist species		Proportion of open-habitat species	
	2001	2002	2001	2002	2001	2002	2001	2002	2001	2002
F	9.5839	5.6831	5.7969	3.6355	2.4285	2.6044	1.1471	1.5259	2.7737	2.8575
Significance	0.0001	0.0001	0.0001	0.005	0.05	0.01	0.40	0.20	0.05	0.05
R	0.5807	0.4815	0.4851	0.4022	0.3380	0.3795	0.2396	0.2738	0.3583	0.3630
Leaf litter cover	+	ns	-	ns	+	+	-	ns	-	*
Decaying wood	+	ns	+	ns	+	+	+	ns	-	ns
Herb cover	+	ns	+	ns	+	+	-	ns	-	*
Shrub cover	-	ns	-	ns	-	-	+	ns	+	ns
Canopy cover	*	ns	-	ns	+	+	+	ns	-	ns
Prey activity density	+	ns	+	ns	-	+	+	ns	+	ns

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urban sites (expressed by the size of the convex hull on the ordination graph). In the urban area, the forest patches had forest specialist, as well as generalist and open-habitat species. Because of the high level of fragmentation, disturbance, and isolation, forest specialists did not appear consistently in all urban forest fragments. Moreover, the colonisation success of generalist and open-habitat species at the urban sites seems to be variable, and thus the composition of invading species varied. Contrary to this, in the less disturbed forest area, forest specialist species and the dominant and subdominant generalist species were present at most sites leading to lower compositional heterogeneity. The moderately disturbed suburban area lies between the other two. Niemelä (1999) also noticed that compositional heterogeneity among sites ( $\beta$ -diversity) is high in urban areas.

#### 4.4. The impact of habitat characteristics on carabids

Regression analyses showed that a significant proportion of the variation in overall activity density, species richness and in the proportion of carabids with different habitat affinity was associated with selected habitat factors. The overall carabid activity density (number of beetles/trap) increased with increasing herb cover and decreasing canopy cover. The decreased canopy cover may provide a favourable habitat for the invading open-habitat and generalist species, which may increase the overall activity density.

The proportion of both individuals and species belonging to forest specialist species increased as the cover by leaf litter cover, decaying wood, and herbs as well as prey availability increased. Leaf litter greatly influences the spatial occurrence pattern of carabids (Koivula et al., 1999; Magura et al., 2000, 2004, 2005; Taboada et al., 2004). A high cover of leaf litter and decaying wood material indicate an undisturbed forest habitat which is preferred by forest specialists and provides shelter against predators, suitable sites for aestivation, hibernation, egg and larval development. The increasing herb cover may also influence microclimate (e.g. temperature and air moisture), which is an important factor controlling ground beetle distribution (Niemelä et al., 1992; Magura et al., 2000). Moreover, there may be a positive correlation between the cover of herbs and the amount of herbivorous invertebrates. Herbivorous invertebrates could be prey for predatory carabids and can provide a more uniform resource distribution in time (Niemelä and Spence, 1994; Niemelä et al., 1996) resulting in aggregation of carabids at microsites with abundant prey (Bryan and Wratten, 1984; Guillemain et al., 1997; Fournier and Loreau, 1999).

The proportion of individuals belonging to generalist species and that of both individuals and species of open-habitat-associated ones decreased as the leaf litter and decaying wood cover increased. Guillemain et al. (1997) showed that the abundance of habitat generalist species decreases with increasing leaf litter thickness. The negative relationship between herb cover and the proportion of individuals of both generalist and open-habitat species could indicate habitat “resistance” hampering ground beetle movement. The proportion of open-habitat species increased as the canopy cover decreased – such species may be attracted to light and avoid shaded areas.

#### 4.5. Implications for the management of urban forest fragments

Urban green areas have recreational importance and increase the quality of urban life (Niemelä, 1999). Current urban habitat management, however, is one of the leading causes of alteration in indigenous arthropod assemblages (Davis, 1978). Therefore, there is a growing need for management strategies, which simultaneously consider recreational, economic and conservation criteria (Gilbert, 1989).

The available information from the Globenet project (Alarukka et al., 2002; Niemelä et al., 2002; Ishitani et al., 2003; Venn et al., 2003; Magura et al., 2004; Elek and Lövei, 2005, 2007; Gaubloimme et al., 2005; Sadler et al., 2006), as well as other research (Grandchamp et al., 2000; Weller and Ganzhorn, 2004) indicates that urban forest fragments can still be relatively species-rich, but the assemblages are dominated by generalist and open-habitat species. The dominance of forest specialist species in the assemblages significantly decreased along the disturbance gradient. We note that the importance of selected habitat factors was mostly consistent in time, but the same factors were not always significant. This underlines that single year studies, including the majority of published Globenet studies, does not necessarily indicate the important factors determining the structure of arthropod assemblages. Our 2-year study is an improvement over the usual single year Globenet studies (e.g. Niemelä et al., 2002; Ishitani et al., 2003; Elek and Lövei, 2007; Sadler et al., 2006) but longer-term studies are necessary to gain valid insights into the impact of urbanisation on ground beetles and on arthropod biodiversity in general.

Unfavourable impacts of park management on biodiversity can be lessened by habitat management which minimises the modification of habitat structure, thereby allowing the maintenance of natural processes of decomposition and nutrient cycling. Recent research indicates that urban dwellers notice and appreciate diversity in urban parks (Fuller et al., 2007). Consequently, adopting management regimes that try to maximise diversity could also increase the value of urban parks for people.

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