



## Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural gradients: an international comparison

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### Abstract

We studied communities of carabid beetles in residual forest patches along urban-suburban-rural gradients in three cities (Helsinki, Finland; Sofia, Bulgaria and Edmonton, Canada) to examine their responses to urbanisation. Only Finnish carabids showed a marked division of community structure along the gradient. In Bulgaria and Canada, carabids did not separate into distinct urban, suburban and rural communities. Our results provide some support for the predictions that species richness will decrease, that opportunistic species will gain dominance, and that small-sized species will become more numerous under disturbance such as that provided by urbanisation. The rather weak and varied response of carabids to this disturbance suggests that local factors and their interaction are of primary importance for community composition. Occurrence of reasonably similar carabid communities across the gradient at each of the three levels of urbanisation suggests that habitat changes commonly associated with urbanisation have not affected the ecological integrity of carabid assemblages in residual urban forest patches.

### Introduction

Approximately 80% of the human population in industrialised countries lives in cities (Vandruff et al. 1995), and more than 60% of the world's population will be urban by the year 2005 (Douglas 1992). In order to ensure that urban areas are planned both for the well-being of city-dwellers and urban nature, 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 biodiversity, widely accepted as a prime indicator that natural systems are being maintained in a 'functionally integrated state' (Heliövaara and Väisänen 1984; Probst and Crow 1991; Berg et al. 1994; Naeem et al. 1994).

The effects of urbanisation may be illuminated through investigations of biotic and abiotic changes across urban-to-rural gradients (McDonnell et al. 1997; Niemelä (1999, 2000); Niemelä et al. 2000). Such gradients, from densely built city cores to increasingly rural surroundings, reflect diminishing intensities of human intervention on originally similar land bases. The gradient occurs all over the world and provides a useful framework for comparative work on a global scale because it reflects similar anthropogenic patterns and processes (Niemelä 2000). For example, urban forests share unique features in relation to suburban and rural forests, including air pollution, 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). Furthermore, floristic richness of

many urban habitats exceeds that of less developed areas (Tonteri and Haila 1990), reflecting the diverse, mosaic nature of urban habitat composition and the affection of urban residents for introduced ornamental plants.

We have developed the GLOBENET programme as a multi-national research framework that employs the urban-rural gradient approach to examine the extent to which globally recurring patterns and convergence of communities can be distinguished from more local phenomena (Niemelä et al. 2000). GLOBENET uses a common field method (standardised pitfall trapping; 10 pitfall traps per site, 4 sites per treatment, 3 treatments: urban, suburban, rural) to study how communities of the same taxonomic group (carabid beetles) vary across visually similar land-mosaics that include urban-rural gradients (treatments as discrete categories; urban, suburban, rural) in different parts of the world.

Carabids (Coleoptera, Carabidae) are sufficiently varied taxonomically and ecologically, abundant and sensitive to human-caused disturbances to be a reliable monitoring group, and they have been widely studied in relation to land use throughout the world (e.g., Stork (1990) and Desender et al. (1991, 1994), Desender (1996), Luff (1996), Niemelä (1996), Dufrière and Legendre (1997)). A recent study, spanning two countries on two continents, has shown that although species identities differed, the general patterns of community response to anthropogenic disturbance was surprisingly similar (Niemelä et al. 1994). Such results illustrate the significance of a multi-regional approach.

In this first report based on application of the GLOBENET protocols, we compare data from forest remnants in and surrounding Sofia (Bulgaria), Edmonton (Canada) and Helsinki (Finland). We examine whether carabid communities respond in a similar way to urbanisation in different parts of the world, and ask whether changes associated with urbanisation are sufficient to prompt concern about ecological integrity of urban forest habitats. In particular, we examine whether the following three predictions about how community structure responds to disturbance (Gray's 1989) hold for carabids in urban environments: (a) diversity should decrease from a high in rural areas to a low in urban areas, (b) opportunistic species should gain dominance in urban areas, and (c) mean body size of the dominating species should decrease from less disturbed to more disturbed habitat (Blake et al. 1994), here from rural to urban areas.

## Materials and methods

### *Study areas and sampling design*

Three positions were selected along the urbanisation gradient in each city, defined as representing urban, suburban and rural areas, hereafter referred to as 'treatments'. Within each treatment we selected a number of forested sites, aiming to have four replicates of each treatment in each city. Detailed descriptions of all sites are given in Appendix 1.

In Sofia (Bulgaria), the study gradient extended from the city centre (42°38'N 23°19'E) to a distance of 29 km north-west from the centre (42°56'N 23°11'E). Four urban, three suburban and four rural sites were selected. All sites were dominated by oak (*Quercus* spp.).

In Edmonton (Canada), the study gradient extended from the city centre (53°33'N 114°28'W) eastward c. 45 km to Elk Island National Park (53°37'N 114°45'W). All sites were situated in relatively continuous patches of forest dominated by trembling aspen (*Populus tremuloides*) and comprising at least an area of 10 ha.

In Helsinki (Finland), the gradient covered a distance of approximately 20 km, from the city centre (60°10'N, 24°56'E), through the suburbs of Espoo to Nuuksio forest NW of Helsinki (60°17'N, 24°38'E). The Finnish study area lies within the hemiboreal vegetation zone (Ahti et al. 1968) and the forest canopy is dominated by spruce (*Picea abies*) and pine (*Pinus sylvestris*) trees.

### *Collecting technique*

Throughout the summer of 1998, ground beetles were collected at each site using pitfall traps. Ten traps (12 in Bulgaria) were placed at least 10 m apart at each site. This resulted in a total of 120 (132 in Bulgaria) traps distributed across each urban-rural gradient.

In both Canada and Finland, plastic cups with an opening diameter of 65 mm and a volume of 250 ml were used as pitfall traps. A propylene glycol-water mixture (50:50) was used as a preservative. Brown plastic roofs were placed above the traps to prevent dilution of the preservative. In Bulgaria, white polystyrene cups with an upper diameter of 90 mm and a volume of 500 ml were used because the smaller cups used elsewhere were not available. A 4% solution of formaldehyde in commercial vinegar was used as col-

lecting fluid, because of the high cost of propylene glycol. No roofs were placed on these traps.

The sampling period in Bulgaria was May 7 – October 22, in Canada June 7 - August 21, and in Finland May 1 – September 30, 1998. Because of trap damage and trap loss, we standardised the abundance of each carabid species at each trap to 100 trap days.

### Statistical analyses

Changes in composition of the carabid assemblages across the gradients were examined using cluster analysis based on presence-absence data for species and the group-average linking algorithm with the Czekanovski-Dice-Sørensen association index (Baev and Penev 1995). Cluster analysis aims to find natural groupings of sites such that sites within a group are more similar to each other than to sites in different groups (Clarke and Warwick 1994).

Furthermore, to examine distinctness we calculated complementarity between pairs of sites using the formula:

$$C_{jk} = 100 \left( \frac{\sum_{i=1}^{S_{jk}} |X_{ij} - X_{ik}|}{\sum_{i=1}^{S_{jk}} \max(X_{ij}, X_{ik})} \right)$$

where  $X_{ij}$  and  $X_{ik}$  are the presence/absence values for the  $i^{\text{th}}$  species in patch-classes  $j$  and  $k$ . Complementarity values range between 100% (no species shared) and 0% (identical species lists) (Colwell and Codrington 1994).

Using data from the individual traps we performed a nested analysis of variance to test for differences in overall carabid abundance and species richness among the treatments, and among the 12 sites selected in each country (sites nested within treatments). Data were transformed to approximate normality (see Table A1) to comply with parametric test assumptions (Sokal and Rohlf 1995). A Scheffé's test for multiple comparisons among means was performed to assess significance of differences revealed by the data.

Changes in carabid body size across the gradients were investigated using general linear regression. Regression analyses were blocked for carabid wing form to determine whether body size differences depend on beetle flight capability. Beetles were divided into those species in which at least some individuals can

fly (macropterous, i.e., long-winged species, and dimorphic, i.e., species with both long-winged and short-winged individuals) and those in which individuals cannot fly (apterous, i.e., wingless, and brachypterous, i.e., short-winged species). Data on body size and flight ability were obtained from the literature (Lindroth (1961, 1963, 1966, 1968, 1969, 1985, 1986); Freude et al. 1976; Hurka 1996) or by inspection of museum collections when wing condition was not reported in the literature. The full regression model included body size as the response variable, and gradient (urban-suburban-rural), sites (nested within gradient), and flight ability as factors.

Finally, we investigated carabid dominance structure by constructing rank-abundance plots for each disturbance treatment in each country.

## Results

### *Carabid assemblage-structure along the gradient*

Seventy-one carabid species (7 035 individuals) were captured in Bulgaria, 41 (15 543 individuals) in Canada, and 25 (2 203 individuals) in Finland (Appendix 2). In the Canadian study, four species comprising 76.7% of total catch were introductions from Europe (see Appendix 2) and when these were excluded, the catch was reduced to 3 628 individuals of 37 native species. In particular, the exotic *Pterostichus melanarius* was extremely abundant with 10 299 individuals (66.3% of the Canadian catch).

Structure of carabid assemblages changed considerably across the gradients in each country. In Bulgaria, the sites showed little pattern in terms of their position along the urban-rural gradient in the cluster analysis (Figure 1A). In terms of complementarity, 17 carabid species were shared between urban and suburban sites ( $C_{jk}=73.0\%$ ), and 22 between urban and rural sites (67.2%). Suburban and rural sites shared 28 species (47.2%), thus appearing to be more similar to each other than to the urban sites. Sites at each position on the gradient shared 14 species.

The native Canadian fauna, in general, was more similar across the gradient than the Bulgarian fauna (compare Canadian and Bulgarian association index values of the first branching). Again, however, little pattern existed in terms of an urban-rural separation (Figure 1B). The Canadian suburban sites shared many species with both urban (17 species,  $C_{jk}=39.3\%$ ) and rural sites (19 species,  $C_{jk}=42.4\%$ ),

Table A1. Nested ANOVA showing differences in carabid abundance and species richness across the urban-suburban-rural gradient and between the 12 sites (11 in Bulgaria) selected.

Country	Source of variation	df	MS	F	p
<b>Individuals</b>					
Bulgaria*	Gradient	2	0.944	0.968	0.420ns
	Sites	8	0.975	11.683	< 0.001
	Error	121	0.083		
Canada (-)	Gradient	2	0.755	12.529	< 0.001
	Sites	9	0.102	1.691	0.189ns
	Error	108	0.060		
Canada (+)	Gradient	2	0.744	13.918	< 0.001
	Sites	9	7.331	137.074	< 0.001
	Error	108	0.053		
Finland	Gradient	2	0.552	8.793	< 0.001
	Sites	9	2.221	35.409	< 0.001
	Error	108	0.063		
<b>Species</b>					
Bulgaria*	Gradient	2	0.081	0.276	0.766ns
	Sites	8	0.294	14.347	< 0.001
	Error	121	0.020		
Canada (-)	Gradient	2	17.108	5.336	< 0.001
	Sites	9	25.158	7.846	< 0.001
	Error	108	3.206		
Canada (+)	Gradient	2	2.808	0.821	0.443ns
	Sites	9	35.231	10.303	< 0.001
	Error	108	3.419		
Finland	Gradient	2	14.742	7.047	< 0.001
	Sites	9	84.175	40.243	< 0.001
	Error	108	2.092		

\* An unbalanced nested analysis of variance was performed on the Bulgarian data, as there were only three suburban sites.; Abundance data for all four data sets were log-transformed to apply with parametric test assumptions. Only the Bulgarian species data needed to be log-transformed to approximate normality.

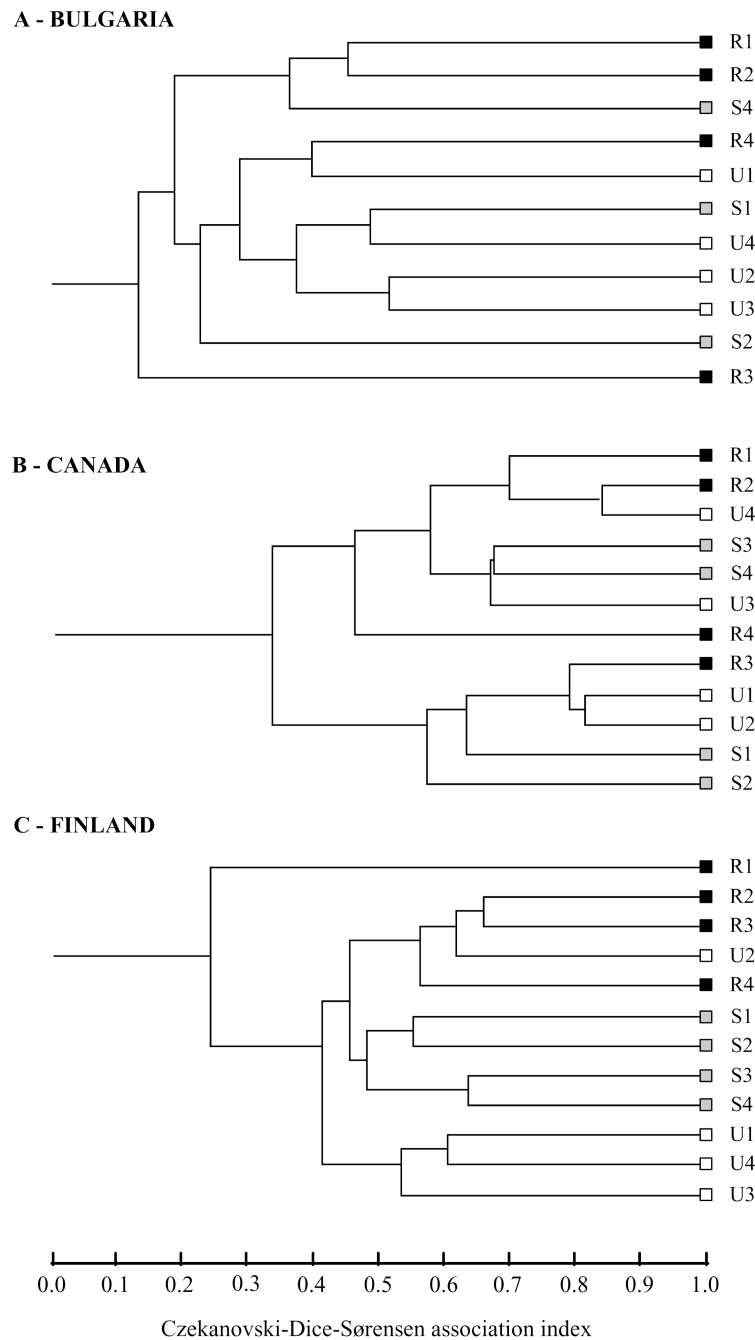


Figure 1. Carabid assemblage structure changes across the urban (U), suburban (S), rural (R) gradients in Bulgaria, Canada (native fauna) and Finland. Dendrograms were constructed using group-average linking algorithm with Czekanovski-Dice-Sørensen association index.

but urban sites shared fewer species with rural sites (14 species,  $C_{jk}=60.0\%$ ). Thus, in Canada suburban sites appear to be intermediate in terms of species composition. Overall, 14 species were shared across the Canadian gradient.

The Finnish fauna showed the most marked separation among sites along the gradient. Three urban and four suburban sites separated into distinct clusters (Figure 1C). One urban site clustered together with the rural sites, because large numbers of *Pteros-*

*tichus melanarius* and *P. oblongopunctatus* were collected in urban site 2 and the rural sites. In Finland, complementarity was generally lower, implying that many species were shared across the gradient. Thirteen species were shared between urban and suburban sites ( $C_{jk}=38.1\%$ ), 15 between urban and rural (37.5%), and 13 between suburban and rural (45.8%). Overall, 11 carabid species were common across the gradient.

#### *Carabid diversity across the gradients*

In order to study the effect of the introduced species on community changes along the Canadian urban-to-rural gradient the following analyses were performed both with and without these exotic species. Mean carabid abundance changed little across the Bulgarian gradient. In contrast, carabid abundance was significantly higher in suburban than rural sites in Canada and increased significantly from urban to rural sites in Finland (Figure 2A; Table 1). When the four introduced species were included in the Canadian study, significantly more individuals were collected from urban sites than from suburban or rural sites (Figure 2A; Table 1). In particular, *Pterostichus melanarius*, *Carabus granulatus* and *C. nemoralis* were captured abundantly in the city of Edmonton, but were less common in the rural surroundings (Appendix 2).

Gray (1987) and Gray's (1989) predicted that species richness should decrease with increasing disturbance. Our results provide some support for this prediction. There was little difference in species richness across the gradient in Sofia, but mean species richness did increase significantly from urban to rural sites in Edmonton and Helsinki (Figure 2B; Table 1). However, with the inclusion of introduced species in the Canadian study the difference became insignificant (Figure 2B).

#### *Dominance structure along the gradient*

Gray's (1989) proposed that opportunistic species should gain dominance with increasing disturbance (urbanisation in this case) on the community. In our study, the Canadian and Finnish samples supported this prediction, as both were characterised by a dominant species of the same genus in the urban samples (Canada: *Calathus ingratus*, 48% of urban catch; Finland: *Calathus micropterus*, 46%). However, the prediction is not supported by the Bulgarian data as none of the species gained clear dominance in the urban

sites. In Bulgaria *Aptinus bombardata* (48%) was dominant in suburban samples (Appendix 2). Interestingly, *Calathus* species are generalist forest species (Niemelä et al. 1994), while *Aptinus bombardata* is a forest specialist species (Magura et al. 2000), indicating that some specialist species can survive in the urban-suburban forest patches.

Dominance structure is illustrated by rank-abundance curves constructed for each country. In Canada and Finland, both suburban and rural sites were characterised by lower dominance than the urban sites (Figure 3B and 3D). Also, urban sites in Canada and Finland were characterised by a single dominant species and many rare species, while suburban and rural sites had at least a few relatively common species (Figure 3). However, this pattern was not detected in the Bulgarian data.

#### *Carabid body size differences along the gradients*

Gray's (1989) hypothesised that mean body size of the dominating species should decrease with increasing disturbance. This hypothesis was supported by the Bulgarian data in which carabid body size changed significantly from small beetles in urban Sofia to larger beetles in both suburban and rural sites (Table A2). There was a marginally significant change in the same direction across the Finnish gradient (Table A2). However, no significant changes in carabid body size were detected across the Canadian gradient.

Beetle flight ability changed significantly with body size in all three cities. In Bulgaria, flightless beetles were significantly larger than beetles with flight ability, whereas in both Canada and Finland beetles capable of flight were significantly larger than flightless ones (Table A2). This result appears surprising for Finland at first, as the larger *Carabus* species are flightless. However, not many *Carabus* individuals were captured.

## **Discussion**

### *Community changes along the urban-rural gradient*

Our results suggest that carabid communities have not responded similarly to urbanisation in the three cities studied. For example, in Bulgaria and Canada there was little discernible pattern in the cluster analyses of beetle communities representing different disturbance

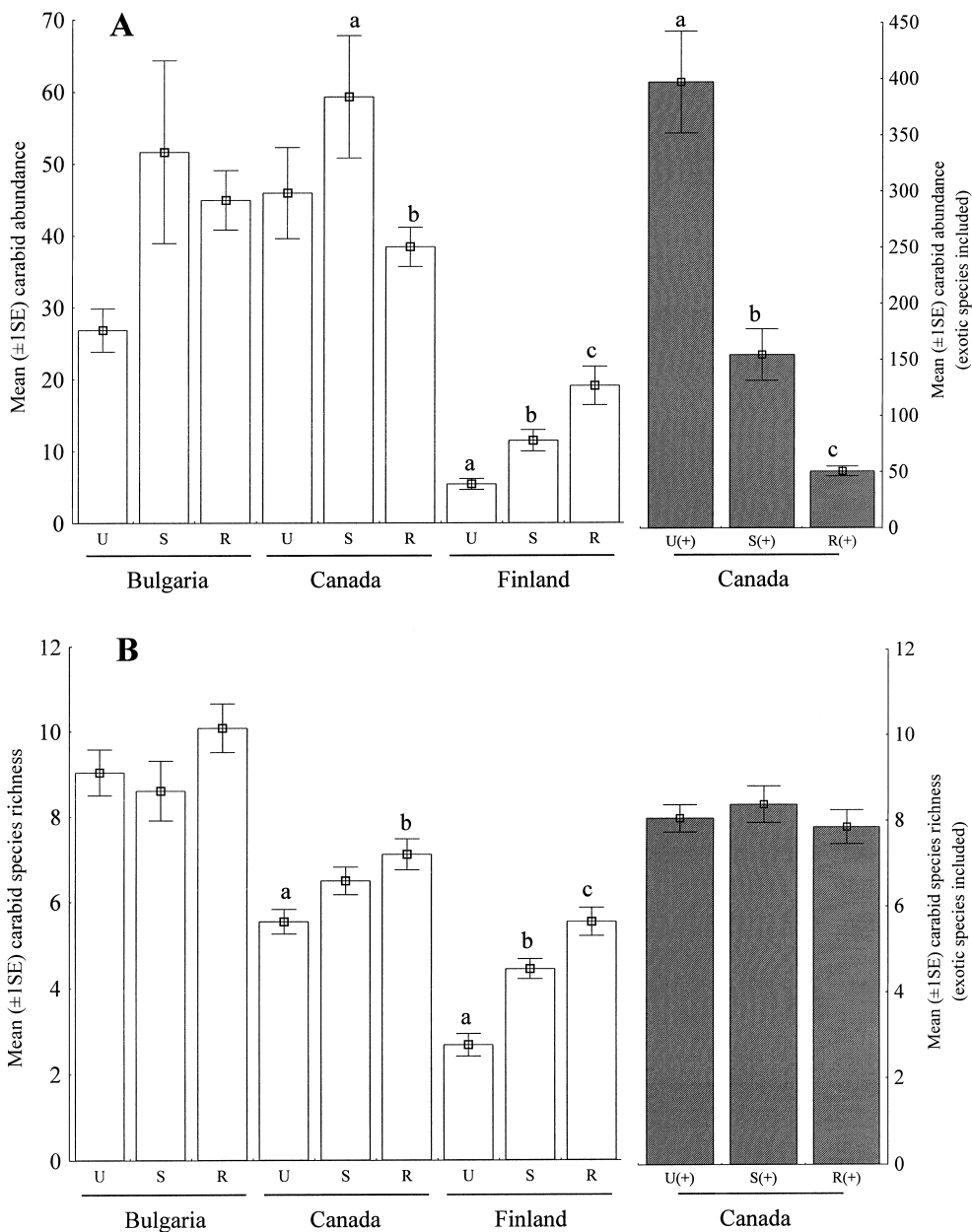


Figure 2. A - carabid standardised abundance across the urban (U), suburban (S), rural (R) gradients in Bulgaria, Canada and Finland. B – carabid species richness across the Bulgarian, Canadian and Finnish urban-rural gradient. Different letters above bars denote significant differences among sites within a country at the 5% level. Hatched bars are the Canadian gradient with introduced species included in the analysis.

intensities. In Finland, on the other hand, clearly distinct communities were identified along the urbanisation gradient. Interestingly, the Canadian and Finnish communities clustered across the gradient at generally higher levels of similarity than the Bulgarian communities (compare complementarity values and see Figure 1), perhaps reflecting broad differences be-

tween boreal and temperate forests. These data suggest that climatic or other factors may be more important in driving similar responses in these communities than are the possible differences between deciduous (Bulgaria and Canada) and coniferous (Finland) forests.

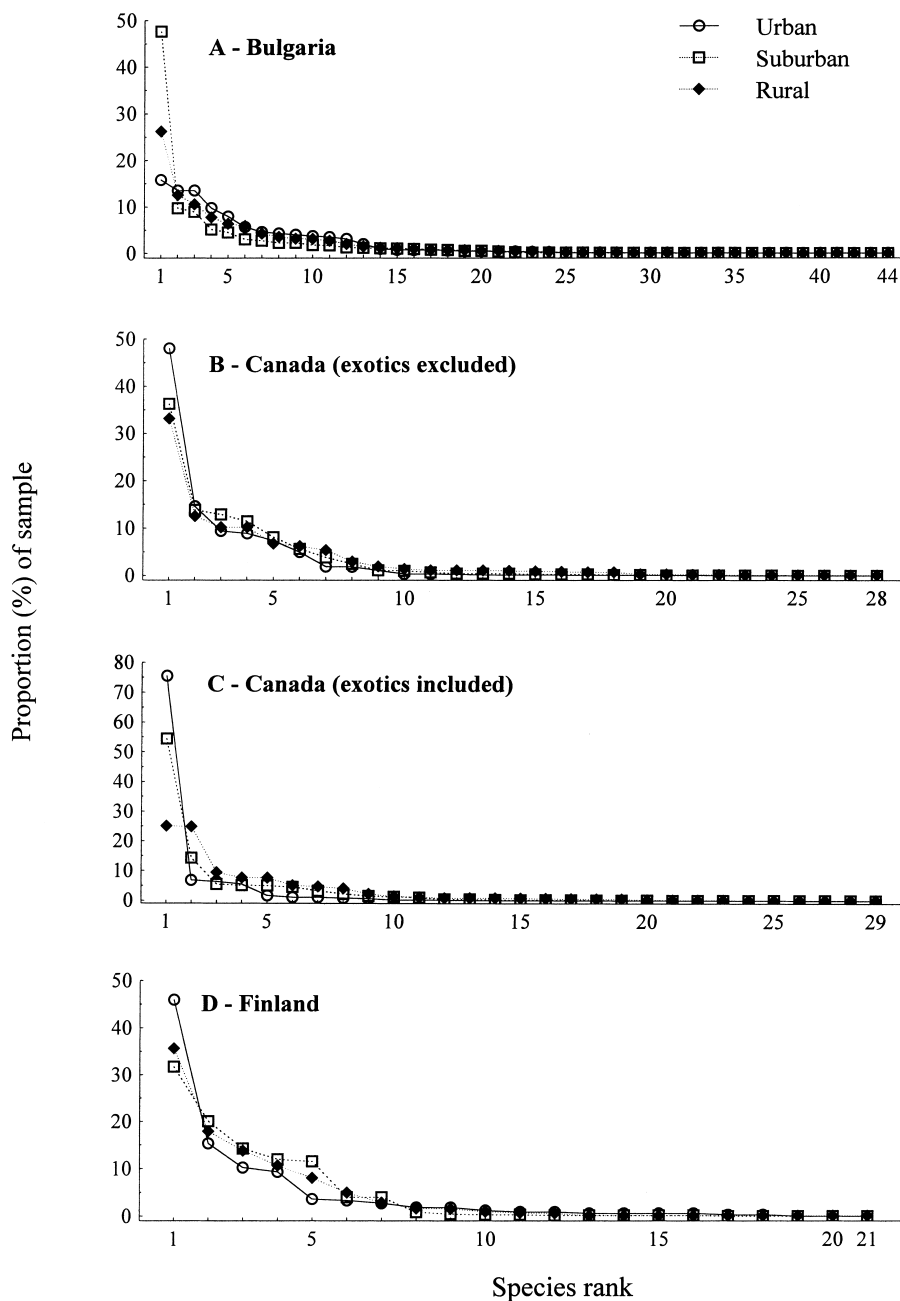


Figure 3. Rank abundance curves for Bulgaria (A), Canada without introduced species (B), Canada with introduced species (C) and Finland (D). Note the differences in axis values.

A possible explanation for the generally weak distinction of beetle communities along the gradients is that carabids are not influenced much by the moderate habitat disturbance that characterises suburban and urban forest habitats. For these insects, residual forest patches in urban areas may be large and undisturbed enough to retain most native species despite

habitat fragmentation, as is suggested by the dominance of typical forest species in urban sites in Canada and Finland. Another reason may be that the location for sampling points on the gradient could have a strong effect on patterns observed. According to McDonnell et al. (1993), two types of gradients have been described in nature: simple gradients and com-



Table A2. General linear regression results. Carabid body size (square root transformed) was regressed against flight ability (see text) across the gradient (urban-suburban-rural) and across the 12 sites selected (sites were nested within the gradient factor).

Country and variables	df	SS	MS	F	p
<b>Bulgaria</b>					
Gradient	2	31.333	15.667	20.46	< 0.001
Wings	1	34.575	34.575	45.14	< 0.001
Gradient × Sites	8	3.088	0.386	0.50	0.853
Gradient × Wings	2	0.183	0.092	0.12	0.887
Gradient × Sites × Wings	8	1.195	0.149	0.20	0.991
Residual	220	168.491	0.766		
Total	241	238.865	0.991		
<b>Canada</b>					
Gradient	2	0.121	0.060	0.33	0.722
Wings	1	1.350	1.350	7.31	0.008
Gradient × Sites	9	0.763	0.085	0.46	0.900
Gradient × Wings	2	0.318	0.159	0.86	0.425
Gradient × Sites × Wings	9	1.058	0.118	0.64	0.764
Residual	159	29.364	0.185		
Total	182	32.973	0.181		
<b>Finland</b>					
Gradient	2	5.342	2.671	2.59	0.080
Wings	1	7.352	7.352	7.14	0.009
Gradient × Sites	9	3.311	0.368	0.36	0.952
Gradient × Wings	2	0.346	0.173	0.17	0.846
Gradient × Sites × Wings	9	1.128	0.125	0.12	0.999
Residual	95	97.805	1.030		
Total	118	115.285	0.977		

plex ones. For example, it is easy to show that there is a simple, unimodal gradient in human population numbers from low in rural to high in urban environments. It is, however, more difficult to interpret the complex gradients of several possibly interacting factors (temperature, moisture, edaphic factors, pollution gradients) associated with the human population gradient but which are the actual drivers for beetle responses (McDonnell et al. 1993). Such factors interacting with specific combinations of species along the gradient will likely influence the carabid community in a more complex way than indicated by the simple human population gradient.

#### *Beetle responses to habitat disturbance*

Gray's (1989) postulated that in habitats affected by increased disturbance, diversity should decrease, opportunistic species should gain dominance and mean size of the dominant species should decrease. Our results corroborate these hypotheses to some extent.

Carabid species richness increased significantly with decreasing urbanisation both in Canada and Finland. Species richness was also higher in the Bulgarian rural environment, but not significantly so. This general relationship could be driven by several processes that result in habitats becoming either more favourable or more predictable as disturbance level decreases (Putman 1996). For example, we observed that more frequent disturbance seemed to homogenise urban forests patches, perhaps eliminating microhabitats favoured by some species. Disturbances in urban and suburban areas are continuous, directed and long lasting, leading to decreased diversity. This contrasts with the increase in diversity at low to intermediate levels of disturbance as predicted by the intermediate disturbance hypothesis (Connell 1978; Giller 1996). Wootton (1998) showed that basal species of food webs are likely to follow the intermediate disturbance hypothesis, but top consumers like carabids (Lövei and Sunderland 1996) are not. Also, in urban areas potential carabid habitats are fragmented and isolated from each other by a matrix of built-up and

inhospitable habitat, making dispersal and recolonisation of potential habitat difficult and risky (McDonnell et al. 1993; Niemelä 2000). Finally, urban environments may be unfavourable to specialist species. Indeed, differences in species number were accounted for exclusively by rarely collected species in Canada and two strict stenotopic species, *Agonum mannerheimi* and *Trechus rubens* (Lindroth (1985, 1986)) were collected only from rural sites in Finland. The same is true for the rural surroundings of Sofia, where *Pterostichus brucki*, *Platynus scrobiculatus* and the forest specialist species of the genus *Molops* occur.

The Canadian results clearly supported the proposition that increased urbanisation is associated with increased dominance. In Edmonton, three of the four introduced species dominated the urban environment as is common for urban carabid communities in Canada (Spence and Spence 1988) and for exotic earthworms in New York City (McDonnell et al. 1997). This pattern probably reflects, at least to some extent, historical centres of introductions rather than a strict effect of the disturbance gradient. *Pterostichus melanarius*, an exotic species with good migratory ability and occurring in many habitat types (Lindroth (1985, 1986); Niemelä and Spence 1991), dominated the urban (76% of the catch) and suburban (54%) catches in Canada. Although this species was also most abundant at the rural sites, it comprised only 25% of the catch. This dominance pattern is not simply a reflection of the spread and dominance of an exotic species, however, because even when exotic species are excluded, carabid communities in urban Edmonton were less even than at suburban or rural sites. Furthermore, the most dominant native species, *Calathus ingratus*, represented 48, 36 and 33% of urban, suburban and rural catch respectively, when exotics were excluded. Similarly, in Helsinki *Calathus micropterus* represented 46 and 32% of urban and suburban catch. As an interesting contrast to the Canadian study, *Pterostichus melanarius* was most common at the rural Finnish sites representing 36% of the catch. In Bulgaria, however, the dominance pattern did not hold, as suburbia was most highly dominated by *Aptinus bombardaria* representing 48% of catch; rural (*A. bombardaria*, 26%) and urban (*Nebria brevicollis*, 16%) sites showed less single species dominance.

Gray's (1989) hypothesis that mean size of the dominant species should decrease was supported by a British study in disturbed habitats (Blake et al. 1994). Both the Bulgarian and Finnish results follow this pattern. As with carabid diversity, changes in body

size distributions across the gradient may reflect differences in resource availability or alternatively habitat capacity. Blake et al. (1994) argued that in woodland, for example, increased organic matter was linked to increased carabid biomass, and this may better promote persistence of larger-bodied species. The chief source of organic matter in forest soils is decaying plant material and it is likely that less disturbed forest habitats, like our rural sites, have more organic matter than the more disturbed, urban and suburban sites, providing a larger area for invertebrate life (Giller 1996).

#### *Nature conservation in the city*

Cities and their surroundings provide a good experimental design in which the urban-suburban-rural gradient can be used to study impacts of humans on their environment (McDonnell and Pickett 1990; McDonnell et al. 1997). The GLOBENET programme spanning several countries (Niemelä et al. 2000) sets out an example of how this can be done to improve understanding of the urban environment.

Our results showed that urbanisation indeed has an effect on carabid communities of urban environments. The intensity of effects varied, however, and overall the effects of the gradient per se seem not particularly strong. With respect to ground beetles, city centres are still quite species-rich. For example, only one more species was captured in the rural surroundings than in urban Sofia, four more in rural Edmonton, and three more in rural Helsinki. This is perhaps attributed to the fact that urban habitats retain significant heterogeneity by having usually more plant species, more pest species and individuals, and more anthropogenically modified habitats which serve as habitat for carabids (Frankie and Ehler 1978; Spence and Spence 1988; Eversham et al. 1996). Niemelä (1999) attributed the high total species richness in urban landscapes both to high alpha-diversity and variation in species communities between patches (beta-diversity). In our study, variation in carabid communities between sites was quite high (Figure 1).

Urban green areas, including forest patches of the sort studied here, contribute to the quality of urban life and thus should be conserved. Apart from their recreational value, which is widely appreciated and enjoyed by human inhabitants, such green urban spaces provide seemingly adequate habitat for most species of carabid beetles found in less developed rural areas some distance from the city core. Thus, in

the three cities studied the carabid data suggest that ecological integrity of residual habitat patches is presently secure. However, corroboration of Gray's (1989) hypotheses about the effects of disturbance on biological communities by our data suggest that urbanisation is affecting carabid communities in the three urban centres investigated. Furthermore, it is clear that large scale urbanisation can take its toll on carabid diversity if sufficient area of suitable habitat is not protected (Davis (1978a, 1978b); Halme and Niemelä 1993). Research programmes like GLOBENET provides a framework for similar studies in other parts of the world to test the generality of our results. Furthermore, these results can help city

planners to protect urban biodiversity through habitat management and lead us away from devolution of urban areas into 'concrete jungles'.

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Table A1. Study site characteristics. There were 12 study sites per country except for Bulgaria where there were 11 sites (3 suburban sites only).

Sites	Location	Dominant tree species	Field layer characteristics
<b>Bulgaria</b>			
Urban 1-4	U1 – Knyaz Borissova Gradina Park, 4km SE from the centre of Sofia, U2 – 5km WSW from city, U3 – Severen Park, 6km NW from city and U4 – Loven Park, 4km from city.	Dominated by <i>Quercus rubra</i> . Other species include <i>Fraxinus</i> , <i>Acer</i> , <i>Carpinus</i>	Shrub layer mainly <i>Crataegus</i> , but also <i>Quercus</i> , <i>Tilia</i> , <i>Fraxinus</i> and <i>Acer</i> saplings. Herb layer poorly developed.
Suburban 1-4	S1 – 12km SE from city centre. Close to a German village, S2 – 11km WSW from city, close to Lyulin mountains, S4 – 13km SW from city, close to Vladoya village.	Mainly <i>Querceto-Carpinetum</i> stands and <i>Quercus rubra</i> , <i>Tilia</i> , <i>Carpinus</i> and <i>Acer</i> trees.	Shrub layer consisted of saplings of the major tree species. Herb layer poorly developed
Rural 1-4	R1 – 15km SE from city centre. Close to a German Monastery, R2 – 12km WSW from city, R3 – 29km NW from city, R4 – 12km SW from city in Vitosha mountains.	<i>Querceto-Carpinetum</i> stands and <i>Fagus</i> , <i>Quercus cerris</i> and <i>Q. dalechampii</i> trees.	Well developed shrub layer, except for R2. Species include <i>Quercus</i> saplings, <i>Rosa</i> spp., <i>Crataegus</i> , <i>Cornus</i> , <i>Prunus spinosa</i> , <i>Corylus avellana</i> . Poorly developed herb layer for R1-2, well developed herb layer for R3-4 (species include <i>Calamagrostis arundinacea</i> , <i>Luzula luzoloides</i> and <i>Galium sylvaticum</i> ).
<b>Canada</b>			
Urban 1-4	In Edmonton in the North Saskatchewan River valley. U1 – Mill Creek ravine, U2 – MacKinnon ravine, U3 – McKenzie ravine, U4 – Laurier Park.	Trembling aspen ( <i>Populus tremuloides</i> )	Well-developed trails, a high level of maintenance activity (e.g. grass cut periodically).
Suburban 1-4	Periphery of Edmonton. S1 – Rabbit Hill Road, S2 – Whitemud creek, S3 – Sherwood Park, S4 – between Edmonton and St. Albert.	Trembling aspen ( <i>Populus tremuloides</i> )	All sites were relatively flat. S1 and S2 had a few small trails and well-used hiking trails in the surrounding area. S3 and S4 had human activity similar to that of the rural sites described below.
Rural 1-4	R1 and R2 – Elk Island National Park, R3 – Blackfoot Provincial Park, R4 – 10–15km S of the Blackfoot Park.	Continuous, more even-aged aspen ( <i>Populus tremuloides</i> ) stands	Hiking trails adjacent to most sites.
<b>Finland</b>			
Urban 1-4	In Helsinki, 1-4.5km from city centre. U1 and U4 are near hospitals. U2 and U3 are in a large forest corridor.	<i>Picea abies</i> , <i>Pinus sylvestris</i>	Well developed trails and heavy trampling outside the trails. <i>Vaccinium myrtillus</i> and <i>Oxalis acetosella</i> in field layer.
Suburban 1-4	In the suburban area of Espoo, NW of Helsinki. S1 – 9km from city, S2 – 11km from city, S3 – 14.5km from city, S4 – 12.5km from city.	<i>Picea abies</i> , <i>Pinus sylvestris</i>	Well developed trails with less trampling outside the trails. Relatively untouched undergrowth. <i>Vaccinium myrtillus</i> and <i>Oxalis acetosella</i> in field layer.
Rural 1-4	Nuukio National Park, NW from city centre. R1 – 16km from city, R2 – 17km from city, R3 and R4 – 18km from Helsinki.	<i>Picea abies</i> , <i>Pinus sylvestris</i>	Large recreational area, but with little disturbance. The field layer vegetation was basically intact. <i>Vaccinium myrtillus</i> and <i>Oxalis acetosella</i> in field layer.

Table A2. Carabid species captured across an urban-suburban-rural gradient in Canada, Finland, and Bulgaria.

	U	S	R
<b>Canada</b>			
<i>Agonum corvus</i> (Leconte 1860)	3	6	1
<i>A. cupreum</i> (Dejean 1831)	1	0	0
<i>A. gratiosum</i> (Mannerheim 1853)	1	4	29
<i>A. piceolum</i> (Leconte 1879)	23	16	0
<i>A. placidum</i> (Say 1823)	4	10	1
<i>A. propinquum</i> (Gemminge & Harold 1868)	0	0	1
<i>A. retractum</i> (Leconte 1848)	89	199	53
<i>A. sordens</i> (Kirby 1837)	0	4	61
<i>A. superior</i> (Lth?)	0	0	9
<i>A. thoreyi</i> (Dejean 1828)	0	1	1
<i>Amara cupreolata</i> (Putzeys 1866)	1	0	0
<i>A. hyperborea</i> (Dejean 1831)	0	0	2
<i>A. quenseli</i> (Schönherr 1806)	1	0	0
<i>Bembidion fortetrium</i> (Motschulsky 1845)	0	0	1
<i>Bradycellus lugubris</i> (Leconte 1848)	0	0	3
<i>Calathus ingratus</i> (Dejean 1828)	579	523	325
<i>Calosoma frigidum</i> (Kirby 1837)	0	2	11
<i>Carabus chamissonis</i> (Fischer 1822)	0	1	7
<i>C. granulatus</i> (L. 1758)*	716	184	0
<i>C. nemoralis</i> (Müller 1764)*	666	48	0
<i>Chlaenius alternatus</i> (Horn 1871)	0	0	1
<i>Clivina fossor</i> (L. 1758)*	1	1	0
<i>Cymindis cribricollis</i> (Dejean 1831)	2	4	3
<i>Harpalus fulvilabris</i> (Mannerheim 1853)	13	15	7
<i>H. ventralis</i> (Leconte 1848)	0	1	0
<i>Loricera pilicornis</i> (F. 1775)	2	2	2
<i>Nebria gyllenhalii</i> (Schönherr 1806)	22	6	0
<i>Patrobus foveocollis</i> (Eschscholtz 1823)	2	6	11
<i>P. lecontei</i> (Chaudoir 1871)	0	0	11
<i>P. septentrionalis</i> (Dejean 1828)	0	1	19
<i>Platynus decentis</i> (Say 1823)	176	165	123
<i>P. mannerhiemi</i> (Dejean 1828)	0	0	14
<i>Pterostichus adstrictus</i> (Eschscholtz 1823)	114	117	100
<i>P. lucublandus</i> (Say 1823)	1	0	0
<i>P. melanarius</i> (Illiger 1798)*	7970	2001	328
<i>P. pensylvanicus</i> (Leconte 1873)	107	81	66
<i>P. riparius</i> (Dejean 1829)	4	55	0
<i>P. stygicus</i> (Say 1823)	0	0	10
<i>Scaphinotus marginatus</i> (Fischer 1822)	0	36	0
<i>Synuchus impunctatus</i> (Say 1823)	60	186	100
<i>Trechus apicalis</i> (Motschulsky 1845)	1	1	8
Total number of individuals	10559	3676	1308
Total number of species	25	28	29
Total number of individuals (- introductions)	1206	1442	980
Total number of species (- introductions)	21	24	28
<b>Finland</b>			
<i>Agonum fuliginosum</i> (Panzer 1809)	0	0	1
<i>A. mannerheimi</i> (Dejean 1828)	0	0	1
<i>A. obscurum</i> (Herbst 1784)	2	0	7
<i>A. thoreyi</i> (Dejean 1828)	0	0	1
<i>Amara brunnea</i> (Gyllenhal 1810)	9	141	19
<i>A. eurynota</i> (Panzer 1797)	0	1	0
<i>Calathus micropterus</i> (Duftschmid 1812)	153	223	209
<i>Carabus glabratus</i> (Paykull 1790)	0	2	8
<i>C. hortensis</i> (L. 1758)	4	81	58
<i>C. nemoralis</i> (Müller 1764)	3	28	18
<i>Cychrus caraboides</i> (L. 1758)	0	1	1
<i>Dromius fenestratus</i> (F. 1794)	2	1	0
<i>Leistus ferrugineus</i> (L. 1758)	3	1	0
<i>L. terminatus</i> (Hellwig 1793)	1	0	1
<i>Notiophilus biguttatus</i> (F. 1779)	6	6	11
<i>Patrobus assimilis</i> (Chaudoir 1844)	6	0	1
<i>P. atrorufus</i> (Ström 1768)	2	0	94
<i>Pterostichus diligens</i> (Sturm 1824)	2	1	1
<i>P. melanarius</i> (Illiger 1798)	34	84	416
<i>P. niger</i> (Schaller 1793)	12	28	161
<i>P. oblongopunctatus</i> (F. 1787)	51	100	124
<i>P. strenuus</i> (Panzer 1797)	11	2	1
<i>Synuchus vivalis</i> (Illiger 1798)	1	0	0
<i>Trechus rubens</i> (F. 1792)	0	0	1
<i>T. secalis</i> (Paykull 1790)	31	3	33
Total number of individuals	333	703	1167
Total number of species	18	16	21
<b>Bulgaria</b>			
<i>Abax carinatus</i> (Duftschmid 1812)	230	215	185
<i>Agonum viduum</i> (Panzer 1797)	1	0	0
<i>Amara aenea</i> (DeGeer 1774)	0	1	0
<i>A. eurynota</i> (Panzer 1797)	0	2	0
<i>A. familiaris</i> (Duftschmid 1812)	2	0	0
<i>A. ovata</i> (F. 1792)	5	0	5
<i>A. saphyrea</i> (Dejean 1828)	0	0	1
<i>Anchomenus dorsalis</i> (Pontoppidan 1763)	73	0	1
<i>Aptinus bombardus</i> (Illiger 1800)	0	1053	820
<i>Asaphidion flavipes</i> (L. 1761)	63	0	0
<i>Badister bullatus</i> (Schrank 1798)	1	0	0
<i>Bembidion lampros</i> (Herbst 1784)	68	0	3
<i>B. tetracolum</i> (Say 1823)	0	0	14
<i>Calathus fuscipes</i> (Goeze 1777)	7	60	0
<i>C. melanocephalus</i> (L. 1758)	1	1	0
<i>C. inquisitor</i> (L. 1758)	0	3	6
<i>Carabus convexus</i> (F. 1775)	0	12	64
<i>C. coriaceus</i> (L. 1758)	97	114	199
<i>C. hortensis</i> (L. 1758)	0	17	86
<i>C. intricatus</i> (L. 1761)	0	3	32
<i>C. montivagus</i> (Pallardi 1825)	0	2	17

<i>C. ullrichi</i> (Germar 1824)	0	23	36
<i>C. violaceus</i> (L. 1758)	135	39	98
<i>Clivina fossor</i> (L. 1758)	3	0	0
<i>Cychnus semigranosus</i> (Pallairdi 1825)	0	51	46
<i>Diachromus germanus</i> (L. 1758)	0	0	1
<i>Gynandromorphus etruscus</i> (Quensel 1806)	0	4	2
<i>Harpalus affinis</i> (Schrank 1781)	1	0	0
<i>H. atratus</i> (Latreille 1804)	2	12	6
<i>H. cupreus fastuosus</i> (Faldermann 1836)	1	1	1
<i>H. luteicornis</i> (Duftschmid 1812)	11	0	0
<i>H. quadripunctatus</i> (Dejean 1829)	0	0	1
<i>H. rubripes</i> (Duftschmid 1812)	1	0	2
<i>H. rufipes</i> (DeGeer 1774)	14	6	13
<i>H. serripes</i> (Quensel 1806)	0	1	0
<i>Laemostenus terricola</i> (Herbst 1783)	53	100	133
<i>Lebia humeralis</i> (Dejean 1825)	2	0	0
<i>Leistus ferrugineus</i> (L. 1758)	13	0	0
<i>L. rufomarginatus</i> (Duftschmid 1812)	230	26	3
<i>Loricera pilicornis</i> (F. 1775)	2	0	0
<i>Molops dilatatus dilatatus</i> (Chaudoir 1868)	0	21	0
<i>M. piceus bulgaricus</i> (Maran 1938)	0	67	99
<i>M. robustus parallelus</i> (Mlynar 1976)	0	29	112
<i>M. rufipes golobardensis</i> (Mlynar 1976)	0	0	331
<i>Myas chalybaeus</i> (Palliard 1825)	0	198	25
<i>Nebria brevicollis</i> (F. 1792)	269	9	17
<i>Notiophilus palustris</i> (Duftschmid 1812)	3	0	0
<i>N. rufipes</i> (Curtis 1829)	60	40	22
<i>Ophonus nitidulus</i> (Stephens 1828)	9	1	0
<i>O. rufibarbis</i> (F. 1792)	7	0	0
<i>Panagaeus bipustulatus</i> (F. 1775)	1	0	0
<i>Patrobus atrorufus</i> (Stroem 1768)	2	0	0
<i>Platyderus rufus</i> (Duftschmid 1812)	0	0	2
<i>Platynus assimilie</i> (Paykull 1790)	166	2	242
<i>P. scrobiculatus</i> (F. 1801)	0	0	3
<i>Poecilus cupreus</i> (L. 1758)	1	0	0
<i>Pterostichus anthracinus</i> (Illiger 1798)	3	0	0
<i>P. brucki</i> (Schaum 1859)	0	0	5
<i>P. melanarius</i> (Illiger 1798)	78	50	38
<i>P. melas</i> (Creutzer 1799)	0	24	0
<i>P. niger</i> (Schaller 1783)	1	0	8
<i>P. nigrita</i> (Paykull 1790)	0	0	1
<i>P. oblongopunctatus</i> (F. 1787)	9	0	11
<i>P. ovoideus</i> (Sturm 1824)	13	0	0
<i>P. strenuus</i> (Panzer 1797)	17	0	4
<i>Stomis pumicatus</i> (Panzer 1796)	2	1	1
<i>Syntomus obscuroguttatus</i> (Duftschmid 1812)	4	0	0
<i>S. vivalis</i> (Illiger 1798)	3	1	5
<i>Tapinopterus kaufmanni</i> (Ganglbauer 1896)	0	3	24
<i>Trechus obtusus</i> (Erichson 1837)	2	0	7
<i>T. quadristriatus</i> (Schrank 1781)	34	0	0
<i>Xenion ignitum</i> (Kraatz 1875)	0	18	393

Total number of individuals	1700	2210	3125
Total number of species	44	36	45

\* In Canada these four species are European introductions. U – urban, S – suburban, R – rural.

## References

- Ahti T., Hämet-Ahti L. and Jalas J. 1968. Vegetation zones and their sections in northwestern Europe. *Annales Botanici Fennici* 5: 169–211.
- Baev P.V. and Penev L.D. 1995. BIODIV: Program for calculating biological diversity parameters, similarity, niche overlap, and cluster analysis. Pensoft, Sofia, Bulgaria.
- Berg A., Ehnstrom B., Gustaffsson L., Hallingback T., Jonsell M. and Weslien J. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. *Conservation Biology* 8: 718–731.
- Blake S., Foster G.N., Eyre M.D. and Luff M.L. 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia* 38: 502–512.
- Clarke K.R. and Warwick R.M. 1994. Change in Marine Communities: An Approach to Statistical Analysis and Interpretation. Bowne Press Limited, UK.
- Colwell R.K. and Coddington J.A. 1994. Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London B* 345: 101–118.
- Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199: 1302–1310.
- Davis B.N.K. 1978a. The ground arthropods of London gardens. *The London Naturalist* 58: 15–24.
- Davis B.N.K. 1978b. Urbanisation and the diversity of insects. In: Mound L.A. and Waloff N. (eds), *Diversity of Insect Faunas*. Blackwell, London, pp. 126–138.
- Desender K. 1996. Diversity and dynamics of coastal dune carabids. *Annales Zoologici Fennici* 33: 65–76.
- Desender K., Dufrière M., Loreau M., Luff M.L. and Maelfait J.-P. 1994. Carabid Beetles: Ecology and Evolution. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Desender K., Maelfait J.-P. and Baert L. 1991. Carabid beetles as ecological indicators in dune management. *Elytron*: 239–247.
- Douglas I. 1992. The case for urban ecology. *Urban Nature Magazine* 1: 15–17.
- Dufrière M. and Legendre P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.
- Eversham B.C., Roy D.B. and Telfer M.G. 1996. Urban, industrial and other manmade sites as analogues of natural habitats for Carabidae. *Annales Zoologici Fennici* 33: 149–156.
- Frankie G.W. and Ehler L.E. 1978. Ecology of insects in urban environments. *Annual Review of Entomology* 23: 367–387.
- Freude H., Harde K.W. and Lohse G.A. 1976. Die Käfer Mitteleuropas (Bd. 2: Adephega 1: Fam. Carabidae). Goecke & Evers, Krefeld, Germany.
- Giller P.S. 1996. The diversity of soil communities, the 'poor man's tropical rainforest'. *Biodiversity and Conservation* 5: 135–168.

- Gray J.S. 1987. Species-abundance patterns. In: Gee J.H.R. and Giller P.S. (eds), *Organization of communities, past and present*. Blackwell Scientific Publications, Oxford, UK, pp. 53–67.
- Gray's J.S. 1989. Effects of environmental stress on species rich assemblages. *Biological Journal of the Linnean Society* 37: 19–32.
- Halme E. and Niemelä J. 1993. Carabid beetles in fragments of coniferous forest. *Annales Zoologici Fennici* 30: 17–30.
- Heliövaara K. and Väisänen R. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. *Acta Forestalia Fennica* 189: 1–32.
- Hurka K. 1996. Carabidae of the Czech and Slovak Republics. Ka-bourek, Zlin, Czech Republic.
- Lindroth C.H. 1961. The ground beetles of Canada and Alaska. *Opuscula Entomologica*: 1–200.
- Lindroth C.H. 1963. The ground beetles of Canada and Alaska. *Opuscula Entomologica*: 201–408.
- Lindroth C.H. 1966. The ground beetles of Canada and Alaska. *Opuscula Entomologica*: 409–648.
- Lindroth C.H. 1968. The ground beetles of Canada and Alaska. *Opuscula Entomologica*: 649–944.
- Lindroth C.H. 1969. The ground beetles of Canada and Alaska 1–6. *Opuscula Entomologica*: 945–1192.
- Lindroth C.H. 1985. The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 15, part 1. Scandinavian Science Press Ltd., Copenhagen, Denmark.
- Lindroth C.H. 1986. The Carabidae (Coleoptera) of Fennoscandia and Denmark. *Fauna Entomologica Scandinavica* 15, part 2. Scandinavian Science Press Ltd., Copenhagen, Denmark.
- Lövei G.L. and Sunderland K.D. 1996. Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology* 41: 231–256.
- Luff M. 1996. Use of carabids as environmental indicators in grasslands and cereals. *Annales Zoologici Fennici* 33: 185–195.
- Magura T., Tothmeresz B. and Molnar T. 2000. Spatial distribution of carabids along grass-forest transects. *Acta Zoologica Academiae Scientiarum Hungaricae* 46: 1–17.
- McDonnell M.J. and Pickett S.T.A. 1990. Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. *Ecology* 71: 1232–1237.
- McDonnell M.J., Pickett S.T.A., Groffman P., Bohlen P., Pouyat R.V., Zipperer W.C. et al. 1997. Ecosystem processes along an urban-to-rural gradient. *Urban Ecosystems* 1: 21–36.
- McDonnell M.J., Pickett S.T.A. and Pouyat R.V. 1993. The application of the ecological gradient paradigm to the study of urban effects. In: McDonnell M.J. and Pickett S.T.A. (eds), *Humans as Components of Ecosystems*. Springer-Verlag, New York, pp. 175–189.
- Naeem S., Thompson L.J., Lawler S.P., Lawton J.H. and Woodfin R.M. 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368: 734–736.
- Niemelä J. 1996. From systematics to conservation – carabidologists do it all. *Annales Zoologici Fennici* 33: 1–4.
- Niemelä J. 1999. Ecology and urban planning. *Biodiversity and Conservation* 8: 119–131.
- Niemelä J. 2000. Is there a need for a theory of urban ecology? *Urban Ecosystems* 3: 57–65.
- Niemelä J., Kotze J., Ashworth A., Brandmayr P., Desender K., New T. et al. 2000. The search for common anthropogenic impacts on biodiversity: a global network. *Journal of Insect Conservation* 4: 3–9.
- Niemelä J. and Spence J.R. 1991. Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. *Oikos* 62: 351–359.
- Niemelä J., Spence J.R., Langor D., Haila Y. and Tukia H. 1994. Logging and boreal ground-beetle assemblages on two continents: implications for conservation. In: Gaston K., Samways M. and New T. (eds), *Perspectives in insect conservation*. Intercept Publications, Andover, UK, pp. 29–50.
- Pouyat R.V., McDonnell M.J. and Pickett S.T.A. 1997. Litter decomposition and nitrogen mineralization in oak stands along an urban-rural land use gradient. *Urban Ecosystems* 1: 117–131.
- Probst J.R. and Crow T.R. 1991. Integrating biological diversity and resource management. *Journal of Forestry* 89: 12–17.
- Putman R.J. 1996. *Community Ecology*. Chapman & Hall, London, UK.
- Sokal R.R. and Rohlf F.J. 1995. *Biometry*. 3rd edn. Freeman, New York.
- Spence J.R. and Spence D.H. 1988. Of ground beetles and men: introduced species and the synanthropic fauna of western Canada. *Memoirs of the Entomological Society of Canada* 144: 151–168.
- Stork N. 1990. *The Role of Ground Beetles in Ecological and Environmental Studies*. Intercept, Andover, UK.
- Tonteri T. and Haila Y. 1990. Plants in a boreal city: ecological characteristics of vegetation in Helsinki and its surroundings, southern Finland. *Annales Botanici Fennici* 27: 337–352.
- Vandruff L.W., Leedy D.L. and Stearns F.W. 1995. Urban wildlife and human well-being. In: Sukopp H., Numata M. and Huber A. (eds), *Urban Ecology as the Basis for Urban Planning*. SPB Academic Publishing, The Hague, The Netherlands, pp. 203–211.
- Wootton J.T. 1998. Effects of disturbance on species diversity: a multitrophic perspective. *The American Naturalist* 152: 803–825.

