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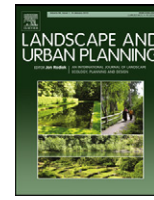

Responses of carabid beetles to urbanization in Transylvania (Romania)

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ABSTRACT

To investigate the impact of urbanization on carabid beetles samples were taken over two years using pitfall traps along a rural–urban forest gradient representing increasing human disturbance in and nearby the city of Sfântu Gheorghe (Romania). We predicted that total number of species should decrease, whereas number of opportunistic and matrix species should increase towards the urban end of the gradient. Both the overall species richness and the number of individuals were significantly the highest in the suburban area followed by the rural area and the lowest in the urban area. These findings contradicted the increasing disturbance hypothesis; the number of species did not decrease by the increasing disturbance. The proportion of the forest specialist individuals and species significantly decreased from the rural towards the urban area, supporting the habitat specialist hypothesis. An opposite pattern was observed in species richness of the generalist carabids, supporting the opportunistic species hypothesis. Both the proportion of matrix species and their density were significantly higher in the urban area, supporting the matrix species hypothesis. Our findings also highlighted that overall diversity is not an appropriate indicator; species with different habitat affinities should be analysed separately to evaluate the real effect of urbanization.

1. Introduction

Urbanization is a conversion of lands to urban or other built-up areas (Pickett, Cadenasso, & Grove, 2001; Xu et al., 2007). These areas account only for a few percentage of the earth's land surface. However, their influence on the functioning and services of ecosystems are rather large (Alberti, 2005; Berling-Wolff & Wu, 2004; Grimm, Grove, Pickett, & Redman, 2000). Urbanization is an increasingly important force shaping the landscape via habitat fragmentation and loss (Gibb & Hochuli, 2002; Miyashita, Shinkai, & Chida, 1998) and the alteration of habitat structure (Antrop, 2000; Fernandez-Juricic, 2004; Shochat, Stefanov, & Whitehouse, 2004). All these modifications affect species richness and community structure in urban areas. They create opportunities for generalist species favouring urban environments, and facilitate the invasion of alien and/or invasive species (Godefroid & Koedam, 2007; Honnay, Piessens, Van Landuyt, Hermy, & Gulinck, 2003). Understanding the relationship between urbanization and ecological processes is a major objective of urban ecology (Breuste, Feldmann, & Uhlmann, 1998; Wu & David, 2002), and in itself is a key research topic in landscape ecology (Wu & Hobbs, 2002).

A way to estimate the effects of urbanization on nature is to study the structure and function of ecological systems along rural–urban gradients (McDonnell & Pickett, 1990; Niemelä, Kotze, & Ashworth, 2000). Along these gradients, the original, native habitat (rural area and/or wildland) is first broken up by non-continuous development and habitation with moderate disturbance (suburban area). The remaining habitat fragments in urban areas are influenced by the densely populated, built-up and often highly disturbed city centres and they are more affected, managed, and fragmented than their suburban and rural complements. In 1998, an international research project called Globenet (Global Network for Monitoring Landscape Change) was initiated to assess and compare the impact of urbanization on biodiversity (Niemelä et al., 2000). This project applies the rural–suburban–urban gradient approach (Pickett et al., 2001) in forested habitats using a common, standardized methodology (pitfall trapping) and evaluating the responses of common invertebrates to urbanization. Until now, the majority of the published papers in the frame of the Globenet project investigated carabid beetles (Elek & Lövei, 2007; Ishitani, Kotze, & Niemelä, 2003; Magura, Tóthmérész, & Molnár, 2004; Magura, Lövei, & Tóthmérész, 2008; Niemelä et al., 2002; Sadler, Small, Fiszpan, Telfer, & Niemelä, 2006; Venn, Kotze,

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& Niemelä, 2003). Studies analysing other target invertebrates are rather limited (for spiders: Alaruikka, Kotze, Matveinen, & Niemelä, 2002; Magura, Tóthmérész, Hornung, & Horváth, 2008; for isopods: Hornung, Tóthmérész, Magura, & Vilisics, 2007; Magura, Hornung, & Tóthmérész, 2008; Vilisics, Elek, & Lövei, 2007).

The aim of the present study was to investigate the effects of urbanization on carabid beetles along a rural–urban gradient representing increasing human disturbance. Several hypotheses were formulated to explain the effects of disturbance on biotic communities. We tested the following hypotheses: (i) According to the *increasing disturbance hypothesis* formulated by Gray (1989), an increase in disturbance would monotonously decrease diversity. Thus, diversity should decrease from a high value in rural area to a low one in the heavily disturbed urban area. (ii) Frequent and/or severe disturbance would affect sensitive species; it primarily affects the habitat specialist (here the forest specialist) species. Thus, the *habitat specialist hypothesis* predicts that diversity of forest specialist species should decrease from the less disturbed rural forest towards the more disturbed urban area (Magura et al., 2004). (iii) Species that are able to cope with disturbance may benefit from the disturbance caused by urbanization, and they should gain dominance in the disturbed suburban and heavily disturbed urban area; *opportunistic species hypothesis* (Gray, 1989). (iv) The studied forests are surrounded by a matrix (open habitats). Urbanization changes considerable the structure of forested habitats, and it makes them vulnerable to the invasion of the matrix species. Species penetrating from the surrounding matrix (here the open-habitat species) may benefit from the habitat alteration. We are mentioning this new hypothesis as *matrix species hypothesis*.

2. Materials and methods

2.1. Study area

The study areas were in and around the city of Sfântu Gheorghe (Sepsiszentgyörgy, Western-Transylvania, Romania; 45°51′N; 25°47′E). The distance between sampling areas (rural, suburban, urban) was 3–10 km and all studied sites covered an area of greater than 10 ha. It has been stressed recently that a forest patch needs to have a minimum size to maintain an intact, habitat-specific carabid assemblage; it is estimated to be at least tens of hectares (Niemelä, 2001). Therefore, our site selection fulfilled this criterion.

Rural sites were in a 90-year-old oak-hornbeam-beech forest on north-western slope at 630–719 m elevation. Percentage cover of the canopy layer was 70–80%; frequent species in the canopy: *Fagus sylvatica*, *Quercus petraea*, and *Carpinus betulus*. There were dense shrub layer (cover was 20%) and a relatively sparse herb layer (cover was 5–10%). Suburban sites were selected in a 60-year-old oak-hornbeam-beech forest on western slope at 600–700 m elevation. The same species were frequent in the canopy as in the rural forest. Percentage cover of the canopy layer was 80–90% with moderate shrub layer (percentage cover was 10%). Cover of herb layer was 10–15%. These suburban sites were popular for recreation by the local population. There were numerous pathways and trampling intensity was high. Dead trees were harvested, and fallen trees were also removed. Urban sites were in a castle park with moderately closed canopy (70–80% percentage cover) with sparse shrub layer (percentage cover was 5%) and dense herb layer (percentage cover was 30–40%). Besides the native species (*C. betulus*, *Fraxinus exelsior*, *Quercus robur*, *Acer campestre*, *F. sylvatica*, *Picea abies*, *Abies alba*, *Pinus nigra*, *Pinus strobus*, *Tilia cordata*, *Tilia platyphyllos*, *Aesculus hippocastanum*), several non-native, exotic species were also present: *Liriodendron tulipifera*, *Magnolia acuminata*, *Tsuga canadensis*, *Caragana arborescens*, *F. sylvatica* subsp. *atropurpurea*, and *Thuja plicata*. In the park fallen trees and branches were removed. Shrub layer was strongly thinned. Grass was regularly moved, and the mowed grass and leaf litter were taken away. There were several paved and asphalt-covered paths in the park.

2.2. Sampling design

Sampling design followed the Globenet protocol (Niemelä et al., 2002). Forested sampling areas were selected along a rural–urban gradient within the city, and in the surrounding forest, as required by the Globenet protocol. Four sites, at least 100 m apart were selected within each sampling area. Carabid beetles were collected by randomly placing ten pitfall traps at least 10 m apart at each site. This resulted in a total of 120 traps along the rural–urban gradient (3 areas × 4 sites × 10 traps). Pitfall traps consisted 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. Trapped beetles were collected fortnightly from the end of April to the end of September in both 2004 and 2005. Traps were placed at the same locations in both years. Carabids were identified to species using keys in Hůrka (1996).

2.3. Data analyses

The carabid assemblages along the rural–urban gradient was displayed by multidimensional scaling (MDS) using the Manhattan distance of the relative abundance of carabid species (Legendre & Legendre, 1998). Nested analyses of variance with repeated measures (using General Linear Models) were performed to test differences in the overall carabid density, species richness, standardized species richness, the ratio of forest, generalist and open-habitat species in the assemblages among the three sampling areas (rural, suburban, urban), among the 12 sites, and between the two years (2004 and 2005). Data from the individual traps were used. Sites were nested within the sampling areas and years were concerned as repeating (Sokal & Rohlf, 1995). To eliminate the effect of sample size, species richness was standardized for every trap using species rarefaction or expected species richness (Heck, van Belle, & Simberloff, 1975; Niemelä & Kotze, 2009). The minimum variance, unbiased estimates of the expected number of species was used (Smith & Grassle, 1977):

$$ES(m) = ST - \sum_{i=1}^{ST} \frac{\binom{N-n_i}{m}}{\binom{N}{n}},$$

where $ES(m)$ is the expected number of species in a subsample containing m individuals; ST is the total number of species, n_i is the abundance of the ith species and N is the total number of individuals. We choose $m = 10$ individuals (the lowest catch in a trap). Calculations were performed by the DivOrd package (Tóthmérész, 1993).

Carabid beetles were categorised into forest, generalist and open-habitat species according to the information in Hůrka (1996). The distribution of data used in the ANOVA model was normal (tested by the Kolmogorov–Smirnov test, Sokal & Rohlf, 1995). When ANOVA revealed a significant difference between the means, a Tukey test was performed for multiple comparisons among means.

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3. Results

3.1. Carabid assemblages along the gradient

The total carabid catch consisted of 6971 individuals representing 50 species (3651 individuals of 39 species in 2004, and 3320 individuals of 41 species in 2005; Table 1). In the rural area 20 species and 2076 individuals were caught (999 individuals 19 species in 2004, 1077 individuals 15 species in 2005); 26 species and 4194 individuals were captured in the suburban area (2352 individuals 22 species in 2004, 1842 individuals 21 species in 2005), and 701 individuals belonging to 36 species were captured in the urban area (300 individuals 26 species in 2004, 401 individuals 29 species in 2005). The most numerous species was *Pterostichus oblongopunctatus* in both years, and in total, made up 26.7% of the total catch. However, it occurred rarely in the urban area. In the rural forest, *P. oblongopunctatus*, *Carabus glabratus*, *Abax parallelus* and *Molops piceus* were the most abundant in both years. In the suburban area, *P. oblongopunctatus*, *Pterostichus hungaricus*, *C. glabratus* and *Carabus violaceus* were the most numerous. In the urban area *A. parallelus*, *Pseudoophonus rufipes*, *Abax carinatus* and *Harpalus latus* were the most common (Table 1).

Urban carabid assemblages differed from suburban and rural assemblages; MDS ordination revealed a clear separation between them (Fig. 1). The assemblages of suburban and rural areas were very similar to each other. The carabid assemblages in the urban sites were separated from the others along the first axis. The size of the convex hull on the ordination scatterplot was the highest in the case of urban area, indicating a high heterogeneity, that is the composition of the trapped carabids changed considerably from trap to trap (Fig. 1).

Table 1
The numbers and habitat preference of carabid beetle species captured in pitfall traps in and around the city of Sfântu Gheorghe, Transylvania (Romania), in 2004 and 2005. 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	2004			2005			Total
		Rural	Sub-urban	Urban	Rural	Sub-urban	Urban	
Pterostichus oblongopunctatus	F	361	797	6	281	412	2	1859
Carabus glabratus	F	266	396	0	227	369	0	1258
Abax parallelus	F	117	112	119	219	144	255	966
Pterostichus hungaricus	G	9	492	0	2	305	0	808
Carabus violaceus	G	30	236	6	49	313	9	643
Molops piceus	F	94	78	0	91	43	0	306
Carabus coriaceus	F	28	80	1	16	34	1	160
Pterostichus niger	G	26	8	0	77	41	0	152
Abax parallelepipedus	F	2	41	0	20	81	0	144
Cychrus semigranosus	F	23	35	0	19	15	0	92
Pseudoophonus rufipes	G	0	10	45	0	1	25	81
Platyderus rufus	G	0	41	6	0	31	1	79
Carabus auronitens	F	18	4	0	26	10	0	58
Abax carinatus	G	0	0	25	6	2	21	54
Abax schueppeli	F	4	8	0	23	18	0	53
Leistus rufomarginatus	F	5	2	8	8	14	6	43
Harpalus latus	G	0	0	13	0	0	19	32
Carabus intricatus	F	11	0	0	13	0	0	24
Leistus piceus	G	1	0	11	0	0	9	21
Harpalus quadripunctatus	F	0	0	8	0	0	9	17
Licinus depressus	O	0	0	12	0	0	4	16
Laemostenus terricola	G	1	0	9	0	0	5	15
Harpalus progrediens	O	0	0	6	0	0	6	12
Trechus quadristriatus	G	1	0	3	0	0	7	11
Notiophilus rufipes	G	0	2	4	0	2	2	10
Carabus arvensis	G	1	5	0	0	2	0	8
Badister bullatus	O	0	0	2	0	0	5	7
Panagaeus bipustulatus	G	0	0	5	0	0	1	6
Amara convexior	G	0	0	2	0	0	1	3
Notiophilus biguttatus	G	0	1	0	0	0	2	3
Platynus assimilis	G	0	1	2	0	0	0	3
Synuchus vivalis	G	0	0	0	0	2	1	3
Amara familiaris	G	0	0	2	0	0	0	2
Carabus convexus	G	1	1	0	0	0	0	2
Cymindis humeralis	O	0	0	0	0	2	0	2
Leistus ferrugineus	G	0	0	0	0	0	2	2
Poecilus cupreus	O	0	1	1	0	0	0	2
Stomis pumicatus	G	0	0	0	0	0	2	2
Amara montivaga	O	0	0	1	0	0	0	1
Amara similata	O	0	0	1	0	0	0	1
Anchomenus dorsalis	O	0	0	0	0	0	1	1
Anysodactylus binotatus	O	0	0	0	0	0	1	1
Calathus melanocephalus	O	0	0	0	0	0	1	1
Harpalus distinguendus	O	0	1	0	0	0	0	1
Loricera pilicornis	G	0	0	0	0	1	0	1
Notiophilus palustris	G	0	0	0	0	0	1	1
Ophonus affinis	O	0	0	0	0	0	1	1
Ophonus cordatus	O	0	0	0	0	0	1	1
Pterostichus macer	O	0	0	1	0	0	0	1
Pterostichus melanarius	G	0	0	1	0	0	0	1
Number of individuals		999	2352	300	1077	1842	401	6971
Number of species		19	22	26	15	21	29	50

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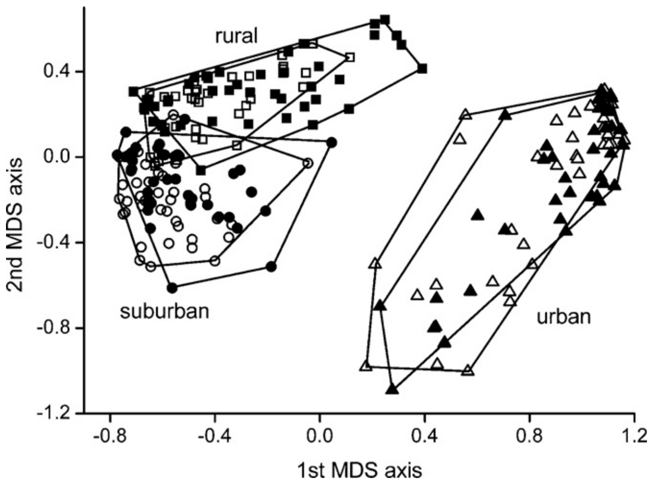


Fig. 1. Ordination (non-metric multidimensional scaling using the Manhattan distance of the relative frequency of the species) of the carabid assemblages along the studied Romanian urbanization gradient based on the catches of pitfall traps in 2004 and 2005. Stress of the two-dimensional configuration was 22.86%. Open symbols denote data from 2004, while filled ones data from 2005.

3.2. Carabid diversity along the gradient

The total number of individuals was significantly the highest in the suburban area followed by the rural area and it was the lowest in the urban area (Fig. 2a and Table 2). The total number of carabid species was also significantly the highest in the suburban area followed by the rural area and was the lowest in the urban area (Fig. 2b and Table 2). After standardizing the sample size by species rarefaction, the species richness was significantly higher

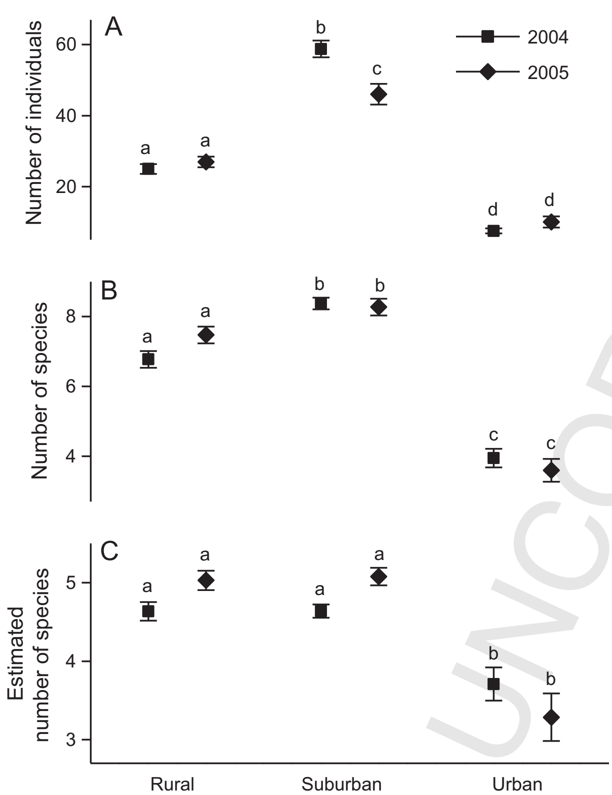


Fig. 2. Mean (±SE) values of the total number of carabid individuals (A), the total number of carabid species (B) and the estimated number of species for 10 individuals (C) along the studied urbanization gradient calculated for the pitfall traps. Different letters indicate significant differences by Tukey test.

in the rural and suburban areas than in the urban one. There was no statistically significant difference between the rural and suburban areas (Fig. 2c and Table 2). These findings contradicted the increasing disturbance hypothesis.

Both the ratio of forest specialist carabid species and the ratio of their abundance decreased significantly from the rural area towards the urban one (Fig. 3 and Table 2) supporting the habitat specialist hypothesis. An opposite tendency was observed for generalists. The share of both the generalist species and individuals increased significantly from rural to urban area, albeit difference in the ratio of generalist individuals were not statistically significant between the suburban and urban areas (Fig. 4 and Table 2). Our findings partially supported the opportunistic species hypothesis. Both the ratio of the open-habitat individuals and species were significantly higher in the urban area compared to the rural or suburban ones (Fig. 5 and Table 2), supporting the matrix species hypothesis.

4. Discussion

The disturbance gradient from rural to urban is a gradient of a number of disturbance events, such as trampling, management, and perhaps pollution. We found that both the species richness and the number of individuals were the highest in the suburban area followed by the rural area and the lowest in the urban area, contradicting the increasing disturbance hypothesis. Proportion of the forest specialists decreased from the rural towards the urban area, supporting the habitat specialist hypothesis. Generalist carabids showed the opposite pattern, supporting the opportunistic species hypothesis. Both the proportion of matrix species and their density were significantly higher in the urban area, supporting the matrix species hypothesis.

4.1. Ratios vs. totals

Analysing total number of individuals and species richness as an indicator of the impacts of urbanization on invertebrates was not an entirely suitable parameter because given groups of species may suffer (e.g. habitat specialists), while other groups may benefit (e.g. generalists and/or matrix species) from the disturbance and habitat alteration caused by urbanization. Species with different habitat affinities (forest specialists, generalists, matrix species) should be considered separately to detect accurately the diversity pattern along the urbanization gradient (McIntyre, 2000; Magura et al., 2004; Magura, Tóthmérész, & Molnár, 2008). The overall impact of urbanization is different on different species, so a more articulated interpretations is not possible using the summary diversity descriptors. These limitations could be resolved by considering the ratios (vs. total numbers) of species with different habitat affinities in an assemblage.

4.2. Increasing disturbance hypothesis

Increasing disturbance hypothesis predicts that increasing disturbance would monotonously decrease diversity (Gray, 1989). Our results, however, did not support this prediction as the total number of carabid species was significantly the highest in the suburban area followed by the rural area and was the lowest in the urban area. Some papers published in the frame of the Globenet project also contradicted this hypothesis (Alaruikka et al., 2002; results from Bulgaria in Elek & Lövei, 2007; Magura et al., 2004; Niemelä et al., 2002), whereas others supported it (results from Canada and Finland in Gaublomme, Hendrickx, Dhuyvetter, & Desender, 2008; Ishitani et al., 2003; Niemelä et al., 2002; Sadler et al., 2006; Venn et al., 2003). As there is a significant relationship between the trapped number of individuals and the collected number of

Table 2
Nested ANOVA with repeated measures showing differences in total number of individuals and species, in estimated species richness and in proportion of forest specialist, generalist and open-habitat individuals and species along the rural–urban gradient and among the 12 sites. Year = the effect of study year (2004 and 2005).

Variable	Source	*df*	*MS*	*F*	*p*
Total number of individuals	*Between-subjects effects*				
	Gradient	2	38703.30	214.66	<0.001
	Sites	9	180.30	1.14	ns
	Error	108	158.70		
	Within-subjects effects				
	Year	1	456.50	4.68	<0.05
	Year × Gradient	2	1499.20	15.37	<0.001
	Year × Sites	9	403.70	4.14	<0.001
	Error	108	97.50		
Total number of species	*Between-subjects effects*				
	Gradient	2	444.87	85.27	<0.001
	Sites	9	5.22	2.35	<0.05
	Error	108	2.22		
	Within-subjects effects				
	Year	1	0.42	0.17	ns
	Year × Gradient	2	6.02	2.48	ns
	Year × Sites	9	4.87	2.01	<0.05
	Error	108	2.42		
Estimated number of species richness	*Between-subjects effects*				
	Gradient	2	48.37	8.96	<0.01
	Sites	9	5.40	6.11	<0.001
	Error	108	0.88		
	Within-subjects effects				
	Year	1	1.12	0.92	ns
	Year × Gradient	2	4.72	3.85	<0.05
	Year × Sites	9	1.39	1.14	ns
	Error	108	1.23		
Proportion of forest individuals	*Between-subjects effects*				
	Gradient	2	2.57	12.81	<0.01
	Sites	9	0.20	7.16	<0.001
	Error	108	0.03		
	Within-subjects effects				
	Year	1	0.05	2.74	ns
	Year × Gradient	2	0.31	17.10	<0.001
	Year × Sites	9	0.05	2.65	<0.01
	Error	108	0.02		
Proportion of forest species	*Between-subjects effects*				
	Gradient	2	3.50	45.98	<0.001
	Sites	9	0.08	2.97	<0.01
	Error	108	0.03		
	Within-subjects effects				
	Year	1	0.01	0.60	ns
	Year × Gradient	2	0.08	3.52	<0.05
	Year × Sites	9	0.06	2.78	<0.01
	Error	108	0.02		
Proportion of generalist individuals	*Between-subjects effects*				
	Gradient	2	1.95	15.80	<0.01
	Sites	9	0.12	4.31	<0.001
	Error	108	0.03		
	Within-subjects effects				
	Year	1	0.03	2.17	ns
	Year × Gradient	2	0.26	16.74	<0.001
	Year × Sites	9	0.05	3.36	<0.01
	Error	108	0.02		
Proportion of generalist species	*Between-subjects effects*				
	Gradient	2	2.06	38.28	<0.001
	Sites	9	0.05	2.12	<0.05
	Error	108	0.03		
	Within-subjects effects				
	Year	1	0.01	0.38	ns
	Year × Gradient	2	0.06	2.92	ns
	Year × Sites	9	0.06	2.71	<0.01
	Error	108	0.02		
Proportion of open-habitat individuals	*Between-subjects effects*				
	Gradient	2	0.11	6.37	<0.05
	Sites	9	0.02	6.37	<0.001
	Error	108	0.002		
	Within-subjects effects				
	Year	1	0.001	0.51	ns
	Year × Gradient	2	0.002	0.67	ns

Table 2 (*Continued*)

Variable	Source	*df*	*MS*	*F*	*p*
	Year × Sites	9	0.002	0.38	ns
	Error	108	0.003		
Proportion of open-habitat species	*Between-subjects effects*				
	Gradient	2	0.22	7.59	<0.05
	Sites	9	0.03	4.07	<0.01
	Error	108	0.01		
	Within-subjects effects				
	Year	1	0.001	0.15	ns
	Year × Gradient	2	0.001	0.21	ns
	Year × Sites	9	0.0002	0.06	ns
	Error	108	0.004		

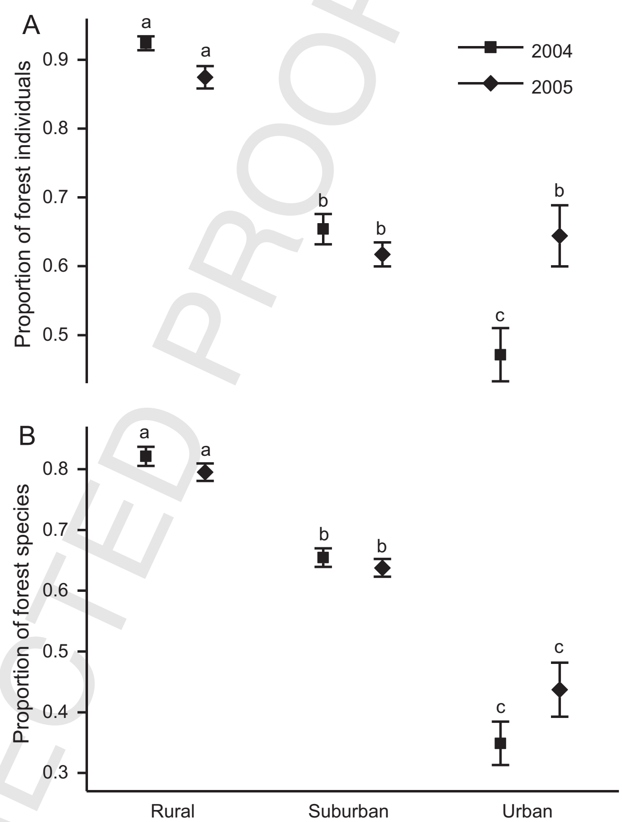
species, a possible reason for the inconsistent results is the difference in the number of carabid individuals captured by pitfall traps. Using rarefaction, the prediction from the decreasing diversity with increasing disturbance was not supported: the (rarified) number of species was significantly higher in the rural and suburban areas than in the urban one. One possible reason of this failure is that the rural–urban gradient is a complex system where many environmental factors (temperature, moisture, edaphic conditions, acidity, pollution, decomposition, etc.) interact (Niemelä, 1999). These factors are likely to be different in the studied countries, which could lead to variation in responses of carabids along the gradients (Ishitani et al., 2003). Moreover, in the modified suburban and/or urban areas with increasing edge or edge-like habitats the species pattern may be strongly modified (Lövei, Magura, Tóthmérész, & Ködöböcz, 2006). A more obvious reason is the diverse responses of carabids with different habitat affinities to disturbance. Forest specialists may suffer, while generalists and species penetrating from the surrounding matrix may benefit from the disturbance and habitat alteration caused by urbanization. For that reason, it is likely that the overall diversity is not the most appropriate indicator for disturbance. Therefore, species with different habitat affinities should be analysed separately to evaluate the real effect of urbanization (Magura et al., 2004; Magura, Hornung, et al., 2008).

4.3. Habitat specialist hypothesis

In accordance with the habitat specialist hypothesis, both the proportion of individuals and the species of forest specialist carabids decreased significantly from the rural area towards the urban one. All the Globenet papers, which studied forest species separately, demonstrated that urbanization caused a pronounced change in the assemblages with the strongest effect upon the forest specialist species (Magura, Lövei, & Tóthmérész, 2010; Niemelä & Kotze, 2009). Forest specialist species require microsites with a particular kind of environmental heterogeneity, such as favourable microclimate, presence of dead and decaying trees, significant cover of leaf litter, shrubs and herbs, together forming an undisturbed forest habitat (Desender, Ervynck, & Tack, 1999). Habitat alteration caused by urbanization appears to eliminate favourable microsites for forest specialists and contributes to the decline of forest specialists' proportion in the assemblage. Along the studied gradient, disturbance was the highest in the urban area (paved paths, thinned shrub layer), it was moderate in the suburban area (dead trees harvested, and fallen trees and branches removed), and lowest in the rural area. This decreasing disturbance was also expressed by the increased abundance and species richness of forest specialist carabid species.

4.4. Opportunistic species hypothesis

Opportunistic species hypothesis predicts that species that are able to cope with disturbance would increase their dominance (Gray, 1989). Our results did support this hypothesis, as the proportion of both the individuals and species in generalists were significantly the highest in the heavily disturbed urban area compared to the other moderately or lightly disturbed suburban and rural areas. Data from Canada (Niemelä et al., 2002), Denmark (Elek & Lövei, 2007), Finland (Niemelä et al., 2002; Venn et al., 2003) and Hungary (Magura et al., 2004) supported this prediction, as opportunistic species were dominant; the generalist species were frequent, or their proportion was the highest in the urban areas. There was no difference in the number of generalist individuals along the rural–urban gradient in Belgium (Gaublomme et al., 2008) or Japan (Ishitani et al., 2003), and none of the species gained clear dominance in the urban area in Bulgaria (Niemelä et al., 2002). A surprising pattern was found in Finland where more generalist individuals were collected from rural areas than either urban or suburban ones (Alaruikka et al., 2002).



Q2 **Fig. 3.** Mean (±SE) proportions of the forest specialist individuals (A) and the forest specialist species (B) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by Tukey test.

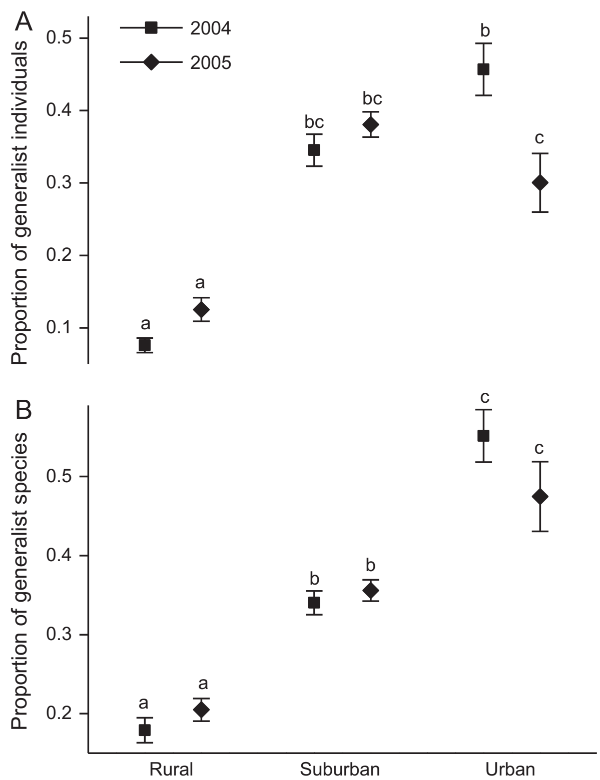


Fig. 4. Mean (±SE) proportions of the generalist individuals (A) and the generalist species (B) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by Tukey test.

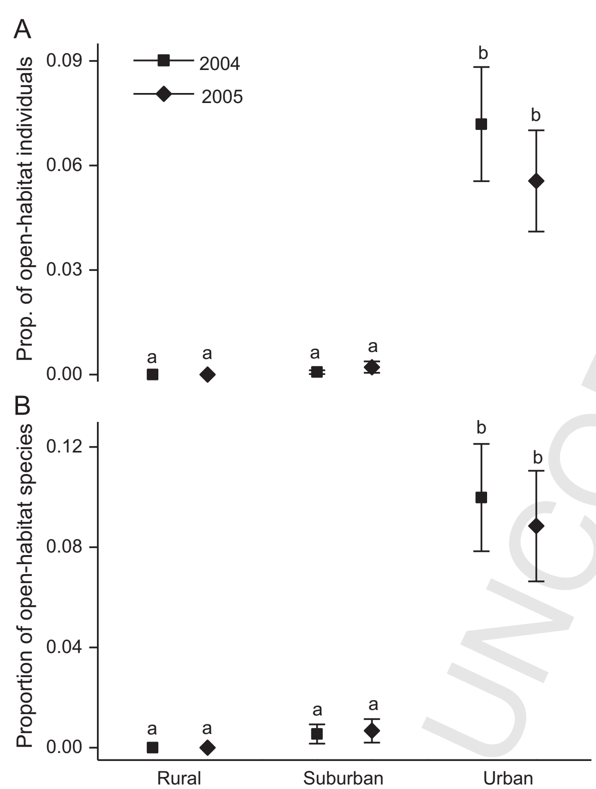


Fig. 5. Mean (±SE) ratios of the open-habitat individuals (A) and the open-habitat species (B) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by Tukey test.

4.5. Matrix species hypothesis

Our results did support this hypothesis, as the proportion of both the individuals and species of open-habitat carabids were significantly the highest in the heavily disturbed urban area compared to the other moderately or lightly disturbed suburban and rural areas. The significant alteration of the original habitats in the urban area was reflected by the high number of matrix species in the species pool; still their proportion were low compared to generalist and forest species in case of traps. In the urban area, the forest patches with closed canopy and moderate closure because of the walking paths and thinned shrubs allows the colonisation and survival of open-habitat species. Results concerning the matrix species are reported from Finland and Hungary; open-habitat species were more abundant in the urban area in Finland (Venn et al., 2003) and in Hungary (Magura et al., 2004). Profound changes in habitat quality during urbanization (Gilbert, 1989; Niemelä, 1999) provide possibility to the matrix species to invade the altered urban habitats. Koivula and Niemelä (2003) also pointed out that matrix species can invade disturbed forest habitats because of the alteration of abiotic factors and biotic interactions.

4.6. Summary and recommendations

The modifications caused by urbanization changed considerably the structure of forested habitats. They affected species richness and community structure in urban areas. Diversity of forest specialist species adapted to the forest habitats decreased considerably by the increasing urbanization. Regarding the total number of species, this decrease was compensated by the invasion of generalist and open-habitat species. In the urban area there were open patches produced by walking paths, thinned shrubs and lawn; the open patches allowed the colonisation and survival of open-habitat species and supported generalist species. In the modified suburban and/or urban areas there was an increasing edge or edge-like habitats which also may have a contribution to the increased species richness of these areas. Forest specialist species require microsites with a particular kind of environmental heterogeneity. Thus, it is vital to increase the patchiness of the urban parks and create closed-canopy forest patches with fallen tree trunks, shrubs, herbs and thick litter layer. It is also important to minimize the open patches created by wide paths and/or roads; the asphalt-covered paths/roads are barriers for the carabids and many other components of the soil fauna, thus they are especially harmful and paved paths are preferred.

Uncited reference Q1

Lövei and Sunderland (1996).

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References

Alaruikka, D., Kotze, D. J., Matveinen, K., & Niemelä, J. (2002). Carabid beetle and spider assemblages along a forested urban–rural gradient in Southern Finland. *Journal of Insect Conservation*, *6*, 195–206.

Alberti, M. (2005). The effects of urban patterns on ecosystem function. *International Regional Science Review*, *28*, 168–192.
Antrop, M. (2000). Changing patterns in the urbanized countryside of Western Europe. *Landscape Ecology*, *15*, 257–270.
Berling-Wolff, S., & Wu, J. (2004). Modeling urban landscape dynamics: A review. *Ecological Research*, *19*, 119–129.
Breuste, J., Feldmann, H., & Uhlmann, O. (1998). *Urban ecology*. Berlin: Springer.
Desender, K., Ervynck, A., & Tack, G. (1999). Beetle diversity and historical ecology of woodlands in Flanders. *Belgian Journal of Zoology*, *129*, 139–156.
Elek, Z., & Lövei, G. L. (2007). Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. *Acta Oecologica*, *32*, 104–111.
Fernandez-Juricic, E. (2004). Spatial and temporal analysis of the distribution of forest specialists in an urban-fragmented landscape (Madrid, Spain) implications for local and regional bird conservation. *Landscape and Urban Planning*, *69*, 17–32.
Gaublomme, E., Hendrickx, F., Dhuyvetter, H., & Desender, K. (2008). The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. *Biological Conservation*, *141*, 2585–2596.
Gibb, H., & Hochuli, D. F. (2002). Habitat fragmentation in an urban environment large and small fragments support different arthropod assemblages. *Biological Conservation*, *106*, 91–100.
Gilbert, O. L. (1989). *The ecology of urban habitats*. London UK: Chapman and Hall.
Godefroid, S., & Koedam, N. (2007). Urban plant species patterns are highly driven by density and function of built-up areas. *Landscape Ecology*, *22*, 1227–1239.
Gray, J. S. (1989). Effects of environmental stress on species rich assemblages. *Biological Journal of the Linnean Society*, *37*, 19–32.
Grimm, N. B., Grove, J. M., Pickett, S. T. A., & Redman, C. L. (2000). Integrated approaches to long-term studies of urban ecological systems. *Bioscience*, *50*, 571–584.
Heck, K. L., van Belle, G., & Simberloff, D. (1975). Explicit calculation of the rarefaction diversity measurement and the determination of sufficient sample size. *Ecology*, *56*, 1459–1461.
Honnay, O., Piessens, K., Van Landuyt, W., Hermy, M., & Gulinck, H. (2003). Satellite based land use and landscape complexity indices as predictors for regional plant species diversity. *Landscape and Urban Planning*, *63*, 241–250.
Hornung, E., Tóthmérész, B., Magura, T., & Vilisics, F. (2007). Changes of isopod assemblages along an urban–suburban–rural gradient in Hungary. *European Journal of Soil Biology*, *43*, 158–165.
Hůrka, K. (1996). *Carabidae of the Czech and Slovak Republics*. Zlin: Kabourek.
Ishitani, M., Kotze, D. J., & Niemelä, J. (2003). Changes in carabid beetle assemblages across an urban–rural gradient in Japan. *Ecography*, *26*, 481–489.
Koivula, M., & Niemelä, J. (2003). Gap felling as a forest harvesting method in boreal forests: Responses of carabid beetles (Coleoptera, Carabidae). *Ecography*, *26*, 179–187.
Legendre, P., & Legendre, L. (1998). *Numerical ecology*. Amsterdam: Elsevier Science.
Lövei, G. L., Magura, T., Tóthmérész, B., & Ködöböcz, V. (2006). The influence of matrix and edges on species richness patterns of ground beetles (Coleoptera, Carabidae) in habitat islands. *Global Ecology and Biogeography*, *15*, 283–289.
Lövei, G. L., & Sunderland, K. D. (1996). Ecology and behavior of ground beetles (Coleoptera Carabidae). *Annual Review of Entomology*, *41*, 231–256.
Magura, T., Hornung, E., & Tóthmérész, B. (2008). Abundance patterns of terrestrial isopods along an urbanization gradient. *Community Ecology*, *9*, 115–120.
Magura, T., Lövei, G. L., & Tóthmérész, B. (2008). Time-consistent rearrangement of carabid beetle assemblages by an urbanisation gradient in Hungary. *Acta Oecologica*, *34*, 233–243.
Magura, T., Tóthmérész, B., Hornung, E., & Horváth, R. (2008). Urbanisation and ground-dwelling invertebrates. In L. N. Wagner (Ed.), *Urbanization 21st century issues and challenges* (pp. 213–225). Nova Science Publishers.
Magura, T., Tóthmérész, B., & Molnár, T. (2008). A species-level comparison of occurrence patterns in carabids along an urbanisation gradient. *Landscape and Urban Planning*, *86*, 134–140.
Magura, T., Lövei, G. L., & Tóthmérész, B. (2010). Does urbanisation decrease diversity in ground beetle (Carabidae) assemblages? *Global Ecology and Biogeography*, *19*, 16–26.
Magura, T., Tóthmérész, B., & Molnár, T. (2004). Changes in carabid assemblages along an urbanisation gradient. *Landscape Ecology*, *19*, 747–759.
McDonnell, M. J., & Pickett, S. T. A. (1990). Ecosystem structure and function along urban–rural gradients an unexploited opportunity for ecology. *Ecology*, *71*, 1232–1237.
McIntyre, N. E. (2000). Ecology of urban arthropods: A review and a call to action. *Annals of the Entomological Society of America*, *93*, 825–835.
Miyashita, T., Shinkai, A., & Chida, T. (1998). The effects of forest fragmentation on web spider communities in urban areas. *Biological Conservation*, *86*, 357–364.
Niemelä, J. (1999). Ecology and urban planning. *Biodiversity and Conservation*, *8*, 119–131.
Niemelä, J. (2001). Carabid beetles (Coleoptera: Carabidae) and habitat fragmentation: A review. *European Journal of Entomology*, *98*, 127–132.
Niemelä, J., Kotze, J., & Ashworth, A. (2000). The search for common anthropogenic impacts on biodiversity: A global network. *Journal of Insect Conservation*, *4*, 3–9.
Niemelä, J., & Kotze, J. D. (2009). Carabid beetle assemblages along urban to rural gradients: A review. *Landscape and Urban Planning*, *92*, 65–71.
Niemelä, J., Kotze, J. D., Venn, S., Penev, L., Stoyanov, I., Spence, J., et al. (2002). Carabid beetle assemblages (Coleoptera, Carabidae) across urban–rural gradients: An international comparison. *Landscape Ecology*, *17*, 387–401.
Pickett, S. T. A., Cadenasso, M. L., & Grove, J. M. (2001). Urban ecological systems: Linking terrestrial ecological, physical, and socioeconomic components of metropolitan areas. *Annual Review of Ecology, Evolution, and Systematics*, *32*, 127–157.
Sadler, J. P., Small, E. C., Fiszpan, H., Telfer, M. G., & Niemelä, J. (2006). Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. *Journal of Biogeography*, *33*, 1126–1138.
Shochat, E., Stefanov, W. L., & Whitehouse, M. E. A. (2004). Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. *Ecological Applications*, *14*, 268–280.
Smith, W., & Grassle, F. J. (1977). Sampling properties of a family of diversity measures. *Biometrics*, *33*, 283–292.
Sokal, R. R., & Rohlf, F. J. (1995). *Biometry*. New York: Freeman.
Tóthmérész, B. (1993). NuCoSA 1.0: Number cruncher for community studies and other ecological applications. *Abstracta Botanica*, *17*, 283–287.
Venn, S. J., Kotze, D. J., & Niemelä, J. (2003). Urbanization effects on carabid diversity in boreal forests. *European Journal of Entomology*, *100*, 73–80.
Vilisics, F., Elek, Z., & Lövei, G. L. (2007). Composition of terrestrial isopod assemblages along an urbanisation gradient in Denmark. *Pedobiologia*, *51*, 45–53.
Wu, J., & David, J. (2002). A spatially explicit hierarchical approach to modeling complex ecological systems: Theory and applications. *Ecological Modelling*, *153*, 7–26.
Wu, J., & Hobbs, R. (2002). Key issues and research priorities in landscape ecology: An idiosyncratic synthesis. *Landscape Ecology*, *17*, 355–365.
Xu, C., Liu, M., Zhang, C., An, S., Yu, W., & Chen, J. M. (2007). The spatiotemporal dynamics of rapid urban growth in the Nanjing metropolitan region of China. *Landscape Ecology*, *22*, 925–937.

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