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RESEARCH ARTICLE

Effects of urbanization on ground-dwelling spiders in forest patches, in Hungary

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Abstract Effects of urbanization on ground-dwelling spiders (Araneae) were studied using pitfall traps along an urban-suburban–rural forest gradient in Debrecen (Hungary). We found that overall spider species richness was significantly higher in the urban sites compared to the suburban and rural ones. The increased diversity was due to the significantly more open-habitat species in the assemblages at the urban sites. This suggests that species from the surrounding matrix (grasslands and arable lands) penetrated the disturbed urban sites. The ratio of forest species was significantly higher in the rural sites than in the suburban and urban ones, suggesting that forest species are indeed sensitive to the disturbance caused by urbanization. Canonical correspondence analysis revealed that the species composition changed remarkably along the urbanization gradient. Open-habitat spiders were associated with the urban sites of higher ground and air temperature. Forest spiders were characteristic of the rural sites with higher amount of decaying woods. Our findings suggest that the overall diversity was not the most appropriate indicator of disturbance; species with different habitat affinity should be analyzed separately to get an ecologically relevant picture of the effect of urbanization.

Keywords Araneae · Disturbance · Diversity · Forest species · Fragmentation · Habitat affinity

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Introduction

The worldwide increase in anthropogenic activities is causing significant changes to the environment and is creating patchworks of modified land-cover types that exhibit considerably similar patterns throughout the world (Gilbert 1989). A major force of this process is the urbanization (Magura et al. 2010). Urbanization is accelerating, as 45% of the human population around the world lives in cities. In the industrialized countries approximately 80% of people live in and around cities (United Nations 2004).

Global urbanization caused the loss of natural habitats (Miyashita et al. 1998; Gibbs and Stanton 2001) as well as alteration and modifications of the environment (Rebele 1994). Fragmentation also contributes to the effect of urbanization (Miyashita et al. 1998; Gibbs and Stanton 2001). In urban habitats, the numbers of exotic, invasive and generalist floral and faunal species are increasing (McDonnell and Pickett 1990; Godefroid and Koedam 2003; Honnay et al. 2003). There are generalist species that benefit from the changes caused by urbanization, and these species are colonizing and/or invading urban habitats (McIntyre et al. 2001; Gibb and Hochuli 2002; Fernandez-Juricic 2004; Shochat et al. 2004). Thus, urbanization is a rather complex process from the point of view of the biota, which needs a detailed, standardized and comparable study worldwide to explore the ecological consequences of urban development.

In 1998, an international research project called Globenet (Global Network for Monitoring Landscape Change) was initiated to assess and compare the influence of urbanization on biodiversity (Niemelä et al. 2000). The project examines urban-suburban–rural gradients, using a common standardized sampling methodology (pitfall trapping) and a target of ground-dwelling invertebrates. Up to now, majority of the published papers in the frame of the Globenet project investigated ground beetle assemblages (Niemelä et al. 2002; Ishitani et al. 2003; Magura et al. 2004, 2008b, c; Desender et al. 2005; Sadler et al. 2006; Elek and Lövei 2007). Studies analyzing other arthropod assemblages are very limited (for spiders: Alaruikka et al. 2002; for isopods: Hornung et al. 2005; Vilisics et al. 2007; Magura et al. 2008a). Without additional studies investigating other reliable indicator taxa (like spiders; e.g. Horváth et al. 2001; Willett 2001; Lawes et al. 2005) along the disturbance gradient, we can not determine properly whether urbanization influences invertebrates in a similar manner.

There are several hypotheses to explain the effects of urbanization on biotic communities; urbanization is usually considered as a kind of environmental disturbance (Rebele 1994; Niemelä et al. 2000). The increasing disturbance hypothesis suggests that species richness monotonously decreases as the disturbance increasing (Gray 1989). Species with different habitat affinity show idiosyncratic responses to disturbance. The habitat alteration hypothesis predicts that altered habitat structure accompanied by urbanization causes a decreased presence/dominance of forest species and an increased ratio of generalist and open-habitat species penetrating from the surrounding matrix (Magura et al. 2004). The aim of the study was to test these predictions: (1) diversity should increase from a low value in the urban area to a high one in the rural area (increasing disturbance hypothesis); (2) urbanization decreases the abundance of forest species and increases the generalist and the open-habitat species from the rural area to the urban one (habitat alteration hypothesis). We also investigated the relationships between the abundance of spiders and certain environmental variables along the urbanization gradient. Moreover, we tested the ratio of large, hunting spiders (Gnaphosidae, Lycosidae) along the urbanization gradient, as it was shown that they benefited from the disturbance (Pajunen et al. 1995; Pearce et al. 2004).

Methods

Spiders were studied along an urbanization gradient in Debrecen (Hungary), the second largest city of the country (47°32'N; 21°38'E). Three forested areas (in urban, suburban and rural contexts) were selected along the gradient within the boundaries of the city and in the surrounding forest (Nagyerdő Forest Reserve). All areas belong to a once-continuous old forest stand (>100 years) dominated by English oak (*Quercus robur*). All forest fragments were larger than 6 ha (urban: 6–10 ha, suburban: 6–8 ha, rural: 6–12 ha). We characterized the level of urbanization by the amount of built-up area (buildings, roads and asphalt covered paths), measured by the ArcView GIS program (version 3.2) from an aerial photograph in a square of 1 km^2 size centered around the sampling area. 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-up or paved. In the urban area, the amount of land comprised of the original forest 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. In addition to differences in land cover there also were differences in the intensity of forestry/habitat maintenance operations among the areas. In the urban area the fallen trees and branches were regularly removed and the shrub layer was strongly thinned. Grass between the forest patches was regularly moved, and the grass clippings were removed. Here, in the urban area, there were several asphalt-covered paths, increasing the isolation between the forested patches. In the suburban area, the fallen trees and branches were also regularly removed, but the understory was not thinned. Most paths were not covered with asphalt. In the rural forest there was not regular forestry intervention.

The sampling regime followed the Globenet protocol (Niemelä et al. 2000). Four sites, at least 50 m from each other, were selected within each of the tree sampling areas (urban, suburban, rural). Spiders were collected at each of the 4 sites in the 3 sampling areas using pitfall traps. Ten traps were placed randomly at least 10 m apart at each site. This resulted in a total of 120 traps (3 areas × 4 sites × 10 traps). Each pitfall trap was at least 50 m from the nearest forest edge in order to avoid edge effects (Horváth et al. 2002). The pitfall traps were unbated, consisting of plastic cups (diameter 65 mm) containing about 100 ml of 75% ethylene glycol as a killing-preserving solution. The traps were covered with bark to protect them from litter and rain. Trapped spiders were collected every 2 weeks from the end of March to the end of November, 2001. For the numerical analyses, data for each of the 12 sites were pooled for the whole activity period (from March to November).

Eight environmental factors were measured that can affect the distribution of spiders (Pearce et al. 2004; Oxbrough et al. 2005). They were measured nearby the traps and averaged for the sites. Ground temperature at 2 cm depth, air temperature on the soil surface and relative humidity on the soil surface were measured at each site monthly on the morning of a typical sunny day. The statistical analyses were based on averages. We also estimated the percentage cover of leaf litter, decaying wood material, herbs, shrubs and canopy cover in each site within a 10 × 10 m plot.

Habitat affinity (forest, generalist and open-habitat species) of the collected species were designated from the literature (Buchar 1992; Buchar and Ruzicka 2002; Table 1).

Dominance of the forest, generalist and open-habitat species in the given assemblage was expressed as the ratio of species in different classes (forest, generalist and open-habitat species). Using the ratios (vs. total numbers) of species in different affinity categories in an assemblage avoided one of the major limitations of pitfall trapping (Luff 1975).

To test for differences in total species richness and in the ratio of species with different habitat affinity (forest, generalist and open-habitat species) among the urban, suburban and rural areas, one-way analyses of variance (ANOVA) were performed using data from the individual sites. Normal distribution of the data was achieved by log $(x + 1)$ transformation. When ANOVA revealed a significant difference between the means, a Tukey-test was performed for multiple comparisons among means (Sokal and Rohlf 1995).

The relationships between the environmental measurements and the overall abundance of the forest, generalist and open-habitat spiders were examined using the detrended canonical correspondence analysis by second order polynomials (DCCA) calculated by the CANOCO package (ter Braak and Šmilauer 1998). Triplot scaling in the ordination focused on the inter-species distances; the number of spider individuals was log $(x + 1)$ transformed.

Results

Spider assemblages along the gradient

The total spider catch consisted of 409 individuals representing 20 species (Table 1). In the urban area there were 176 individuals belonging to 15 species, whereas in the suburban area there were 88 individuals of 8 species, and in the rural area 145 individuals representing 6 species were captured. The most numerous species was *Pardosa alacris* (C. L. Koch, 1833), which made up 42% of the total catch. Regarding the habitat affinity of the spider species, there were 186 individuals of 7 forest species, whereas 131 individuals belonged to 4 generalist species, and 57 individuals represented 9 open-habitat species (Table 1).

The ratio of lycosid specimens did not differ significantly among sites ($F = 2.1727$; d.f. = 2,9; $P = 0.1699$). Moreover, the ratio of this species in the assemblage increased significantly from the urban area toward the rural one ($F = 6.5529$; d.f. = 2,9; $P = 0.0175$). Ratios of both the Gnaphosidae specimens and species in the assemblage was significantly higher at the urban sites ($F = 5.8040$; d.f. = 2,9; $p = 0.0240$ and $F = 6.8864$; d.f. = 2,9; $P = 0.0153$, respectively).

Changes of species richness along the gradient

Significantly more spider species were trapped in the urban area compared to the suburban and rural ones ($F = 14.4474$; d.f. = 2,9; $P = 0.0016$; Fig. 1).

Table 1 The catches of spider species and their habitat affinity along the urban–rural gradient

Species	Habitat affinity	Urban	Suburban	Rural
Dysderidae				
Harpactea rubicunda (C. L. Koch, 1838)	Generalist	3	2	0
Harpactea sp.	–	0	1	0
Theridiidae				
Enoplognatha thoracica (Hahn, 1833)	Open-habitat	1	0	0
Linyphiidae				
Ceratinella wideri (Thorell, 1871)	Forest	1	0	0
Diplostyla concolor (Wider, 1834)	Generalist	1	0	0
Lycosidae				
Alopecosa aculeata (Clerck, 1757)	Forest	1	0	0
Arctosa lutetiana (Simon, 1876)	Open-habitat	0	2	0
Lycosidae sp.	–	1	0	0
Pardosa agrestis (Westring, 1861)	Open-habitat	1	0	0
Pardosa alacris (C. L. Koch, 1833)	Forest	70	20	81
Pardosa sp.	–	3	6	10
Trochosa spinipalpis (F. O. P.-Cambridge, 1895)	Generalist	0	22	26
Trochosa terricola Thorell, 1856	Generalist	47	20	10
Trochosa sp.	–	4	5	3
Anyphaenidae				
Anyphaena accentuata (Walckenaer, 1802)	Forest	0	0	1
Liocranidae				
Agroeca brunnea (Blackwall, 1833)	Forest	0	1	9
Gnaphosidae				
Gnaphosa modestior Kulczynski, 1897	Open-habitat	1	0	0
Haplodrassus silvestris (Blackwall, 1833)	Forest	1	0	0
Trachyzelotes pedestris (C. L. Koch, 1837)	Open-habitat	17	5	0
Thomisidae				
Ozyptila praticola (C. L. Koch, 1837)	Open-habitat	16	4	0
Xysticus audax (Shrank, 1803)	Open-habitat	3	0	0
Xysticus kochi Thorell, 1872	Open-habitat	3	0	0
Xysticus luctator L. Koch, 1870z	Open-habitat	0	0	4
Xysticus sp.	–	1	0	1
Xysticus ulmi (Hahn, 1831)	Forest	1	0	0

The ratio of spider species associated with forest was significantly higher in the rural area than in the suburban and urban ones ($F = 9.0588$; d.f. = 2,9; $P = 0.0070$; Fig. 2a). An opposite tendency was observed for the open-habitat spider species, whose ratio decreased along the urban–rural gradient and was significantly lower in the rural area compared to the urban and suburban ones ($F = 11.4168$; d.f. = 2,9; $P = 0.0034$; Fig. 2c). There were no statistically significant differences in the ratio of generalist species among the studied areas ($F = 0.7975$; d.f. = 2,9; $P = 0.4799$; Fig. 2b).

Spiders and environmental factors

The DCCA triplot showed that there was a marked separation among the sites along the urban-rural gradient based on the abundance of species with

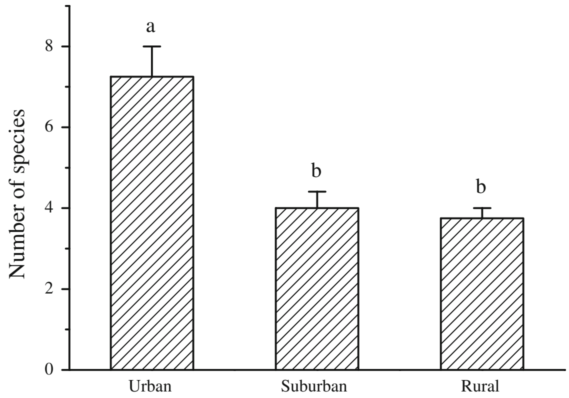

Fig. 1 Mean spider species richness per site (±SE) along the studied urban-rural gradient. *Different letters* indicate significant differences based on Tukey multiple comparisons ($P < 0.05$)

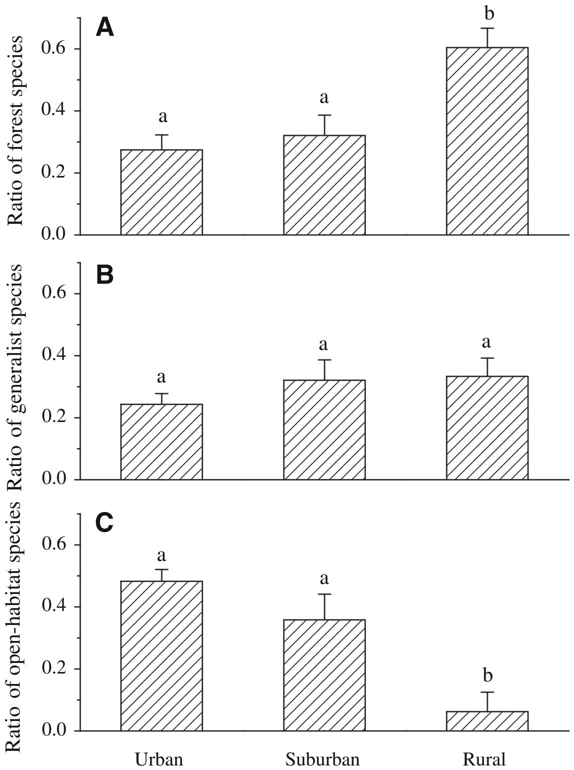

Fig. 2 Ratio of forest species (**A**), generalist species (**B**), and open-habitat spider species (**C**) per site (±SE) along the studied urban–rural gradient. *Different letters* indicate significant differences based on Tukey multiple comparisons ($P < 0.05$)

different habitat affinity. The four urban sites are located on the left lower part, whereas the suburban sites on the left upper region and the rural sites are on the right lower part of the ordination plot (Fig. 3).

The urban sites were characterized by higher ground and air temperature. The suburban sites disposed of higher relative humidity and cover of leaf litter and shrubs, but of lower cover of herbs and canopy. The rural sites had higher amount of decaying wood material, herbs and higher canopy cover. The triplot graph also showed that the forest spiders were characteristic of the rural sites with higher amount of decaying woods. Open-habitat spiders were associated with the urban sites of higher ground and air temperature, whereas the generalist spiders seemed to not be influenced by the changes of the studied environmental factors, as indicated by their position near the origin (Fig. 3). A total of 92.1% of the species and 99.8% of the species-environment variation were accounted for by the four axes of the DCCA using all of the studied variables.

Discussion

Disturbance and overall diversity

In their study of ground-dwelling spiders, Alaruikka et al. (2002) failed to uncover any significant differences in overall species richness along an urban-rural gradient in Finland. Thus, similarly to our results, the increasing disturbance hypothesis was not supported. Although, we found significantly higher number of species in the urban area. A possible reason for the lack of support of the increasing disturbance hypothesis may be that the gradient is a complex system where many factors (temperature, moisture, edaphic conditions, acidity, pollution, decomposition) interact (McDonnell et al. 1997; Niemelä 1999). In the case of urban and suburban forests paths appear, increasing edges or edge-like habitats, which modify species patterns (Lövei et al. 2006). A more obvious reason for the lack of support for the increasing disturbance hypothesis is the variability of responses of spider species with differing habitat affinities to disturbance. Forest species may have narrower tolerance limits and consequently suffer, whereas generalist and open-habitat species may benefit from the disturbance and habitat alteration caused by urbanization. It is likely that diversity itself, as measured by overall species richness, is not the most appropriate indicator of disturbance. Therefore, species with different habitat

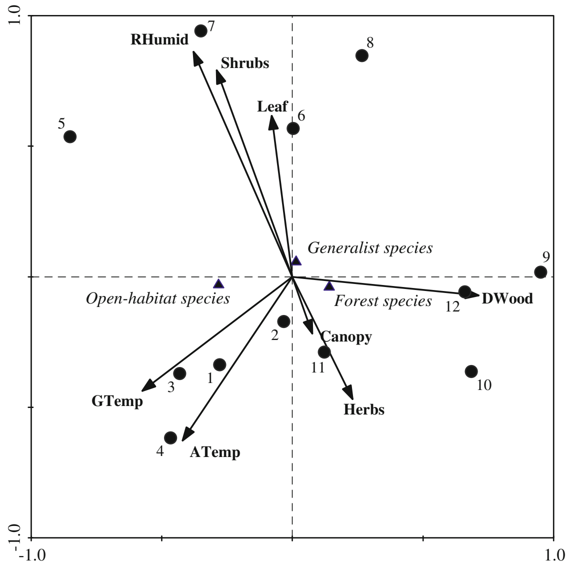

Fig. 3 Result of the DCCA ordination for the spiders. *Filled circles* represent the studied sites (1–4: urban sites, 5–8: suburban sites, and 9–12: rural sites). The *arrows* denote the increase of the value of the studied environmental factors (GTemp: ground temperature at 2 cm depth; ATemp: air temperature on the surface; RHumid: relative humidity on the surface; Leaf: cover of leaf litter; DWood: cover of decaying wood material; Herbs: cover of herbs; Shrubs: cover of shrubs, and Canopy: canopy cover). *Filled triangles* indicate the spiders with different habitat affinity

affinities should be analyzed separately to evaluate the real effect of urbanization.

Several studies examining forest patches with different level of human disturbance found that overall diversity (overall species richness or value of a particular diversity index) did not differ among these patches, although the composition of spider assemblages differed considerably among the patches (Alaruikka et al. 2002; Hsieh et al. 2003; Chen and Tso 2004). These findings highlight that species with different habitat affinity respond differently to the human-generated disturbance. Our results also showed that the overall diversity was not the most appropriate indicator of disturbance. To evaluate the effect of urbanization on ground-dwelling spiders based on overall species richness, the conclusion would be that urbanization has no harmful consequence on the spiders. Moreover, it causes a significant increase in diversity. However, the increase in diversity was mostly due to species penetrating from the neighboring grassland and arable land matrix (open-habitat species). Simultaneously, the ratio of the forest species significantly decreased in the disturbed urban sites.

Disturbance and the ratio of species penetrating from the matrix

Considering the habitat affinity of spiders, we have shown that the open-habitat spiders occurred most frequently in the urban sites. These open-habitat spiders were not characteristic of forests, because they can survive and reproduce in the surrounding matrix (grasslands and arable lands, Buchar and Ruzicka 2002). Alaruikka et al. (2002) did not find any significant difference in the richness of species with different habitat affinity along the urbanization gradient in Finland. This could be either because we used species ratios while Alaruikka et al. (2002) used absolute species numbers. Another possible reason is that in Hungary the open habitat matrix, a source of open habitat immigrant is more extensible than in Finland.

Urbanization causes several forms of disturbance which all contribute to the alteration of indigenous habitats (Gilbert 1989; Niemelä 1999). In the present study, this habitat alteration was the most pronounced in the urban sites, where the forest patches were significantly fragmented by asphalt-covered paths, and the habitat structure was heavily modified by removal of dead wood and thinning of the shrub layer. All these modifications also caused significant changes in environmental conditions. Alteration of habitat structure with accompanying changes in environmental conditions may alter spider community structure (Shochat et al. 2004; Schowalter and Zhang 2005). For example, Pajunen et al. (1995) and Pearce et al. (2004) studying community structure of spiders in forests showed that the abundance and species richness of large, hunting-spider species (Gnaphosidae, Lycosidae) increased by disturbance. Jocqué and Alderweireldt (2005) showed that the abundance of Lycosidae is higher in open habitats with low vegetation, than in dense forests. However, our results contradicted these findings, as the ratio of lycosid specimens did not differ significantly among sites, moreover the ratio of this species in the assemblage increased significantly from the urban area toward the rural one. Ratios of both the Gnaphosidae specimens and species in the assemblage were significantly higher at the urban sites, probably due to the high numbers of *Trachyzelotes pedestris* (C. L. Koch, 1837, Table 1). Disturbed forest patches could be invaded by generalist species and by species from the surrounding matrix (Buddle et al. 2000; Gurdebeke et al. 2003). The matrix surrounded the studied forest patches were grasslands and arable lands. The open-habitat species can be regarded as a species characteristic of the matrix habitats. The disturbed, thinned urban park with increased ground and air temperature contained several favorable microhabitats for open-habitat species.

Disturbance and the ratio of forest species

Several studies emphasized that alteration of habitat structure alters spider community structure (Hurd and Fagan 1992; Schowalter et al. 2003; Shochat et al. 2004; Schowalter and Zhang 2005). Forest species are associated with rural sites and their abundance increased with the increasing of the amount of decaying wood. Oxbrough et al. (2005) similarly showed that forest spider species were positively correlated with twig materials; perhaps these spiders prey on invertebrates in and on decaying wood. Urbanization causes an extensive alteration of habitat structure (e.g. by strong thinning and removing decaying wood material, creating asphalt-covered paths). These alterations generally cause unfavorable changes in the microclimatic, abiotic and biotic conditions of the area. All these changes affected directly the forest species. Lawes et al. (2005), in studying forests that spanned a gradient from relatively undisturbed to highly disturbed forest patches, also showed that the abundance of a spider species characteristic to the undisturbed forests decreased with increasing disturbance. Langellotto and Denno (2004) argued that habitat simplification affects spiders' ability to capture prey eliminating enough refuge from intraguild predation, and providing no alternative resources (e.g. alternative prey). All these may contribute to the decreased ratio of forest spiders at the disturbed urban sites. Habitat alteration caused by urbanization also has indirect effects on forest spiders. Creating sealed paths fragments the habitat into even smaller patches. The division of the original forested area into small, isolated patches causes also a loss of forest species through a reduction in the habitat area, an increase in remnant isolation and a decrease in habitat connectivity (Didham et al. 1996). Miyashita et al. (1998), studying continuous forest and fragmented forest patches, also showed that smaller fragments had fewer species and lower density of individuals. Forest patches divided by asphalt-covered paths are isolated from each other, as ground-dwelling spiders only rarely cross them (Mader et al. 1990). The population size of forest spider species in isolated patches could decrease because the patches are too small to maintain viable populations and there is too little dispersal between the patches. Small populations of forest spiders in isolated patches are at greater risk of local extinction and genetic isolation. Gurdebeke et al. (2000), in studying a forest-specific spider species (*Coelotes terrestris* (Wider, 1834)) in forest patches with different degrees of isolation and size, showed that there was a very high degree of genetic isolation between the spider populations inhabiting the patches.

Our results showed that the forest species were significantly affected by urbanization. The main reason for decreasing of their ratio was the alteration of the habitat structure. Therefore, we propose that during the management of the urban sites the extensive alteration of habitat structure should be avoided. Habitat management that does not modify considerably the habitat structure but rather mimics natural processes could serve both the demands of humans and the maintenance of the diversity of habitat-specific species.

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References

Alaruikka DM, Kotze DJ, Matveinen K, Niemelä J (2002) Carabid and spider assemblages along an urban to rural gradient in Southern Finland. J Insect Conserv 6:195–206

Buchar J (1992) Komentierte Artenliste der Spinnen Böhmens (Araneida). Acta Univ Carol Biol 36:383–428

Buchar J, Ruzicka V (2002) Catalogue of spiders of the Czech Republic. Peres Publishers, Praha

Buddle CM, Spence JR, Langor DW (2000) Succession of boreal forest spider assemblages following wildfire and harvesting. Ecography 23:424–436

Chen KC, Tso IM (2004) Spider diversity on Orchid Island, Taiwan: A comparison between habitats receiving different degrees of human disturbance. Zool Stud 43:598–611

Desender K, Small E, Gaublomme E, Verdyck P (2005) Rural-urban gradients and the population genetic structure of woodland ground beetles. Conserv Genet 6:51–62

Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in fragmented forests: a functional approach. Trends Ecol Evol 11:255–260

Elek Z, Lövei GL (2007) Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. Acta Oecol 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. Landsc Urban Plan 69:17–32

Gibb H, Hochuli DF (2002) Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. Biol Conserv 106:91–100

Gibbs JP, Stanton EJ (2001) Habitat fragmentation and arthropod community change: carrion beetles, phoretic mites, and flies. Ecol Appl 11:79–85

Gilbert OL (1989) The ecology of urban habitats. Chapman and Hall, London

Godefroid S, Koedam N (2003) Distribution pattern of the flora in a peri-urban forest: an effect of the city-forest ecotone. Landsc Urban Plan 65:169–185

Gray JS (1989) Effects of environmental stress on species rich assemblages. Biol J Linn Soc 37:19–32

Gurdebeke S, Neirynck B, Maelfait JP (2000) Population genetic effects of forest fragmentation in Flanders (Belgium) on Coelotes terrestris (Wider) (Araneae: Agelenidae) as revealed by allozymes and RAPD. Ekol-Bratisl 19:87–96

Gurdebeke S, De Bakker D, Vanlanduyt N, Maelfait JP (2003) Plans for a large regional forest in eastern Flanders (Belgium): assessment of spider diversity and community structure in the current forest remnants. Biodivers Conserv 12:1883–1900

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. Landsc Urban Plan 63:241–250

Hornung E, Tóthmérész B, Magura T, Vilisics F (2005) Changes of isopod assemblages along an urban-suburban-rural gradient in Hungary. Eur J Soil Biol 43:158–165

Horváth R, Magura T, Cs Szinetár (2001) Effects of immission load on spiders living on black pine. Biodivers Conserv 10:1531–1542

Horváth R, Magura T, Péter G, Tóthmérész B (2002) Edge effect on weevils and spiders. Web Ecol 3:43–47

Hsieh YL, Lin YS, Tso IM (2003) Ground spider diversity in the Kenting uplifted coral reef forest, Taiwan: a comparison between habitats receiving various disturbances. Biodivers Conserv 12:2173–2194

Hurd LE, Fagan WF (1992) Cursorial spiders and succession—age or habitat structure. Oecologia 92:215–221

Ishitani M, Kotze DJ, Niemelä J (2003) Changes in carabid beetle assemblages across an urban–rural gradient in Japan. Ecography 26:481–489

Jocqué R, Alderweireldt M (2005) Lycosidae: the grassland spiders. Acta zool bulg 1:125–130

Langellotto GA, Denno RF (2004) Responses of invertebrate natural enemies to complex-structured habitats: a meta-analytical synthesis. Oecologia 139:1–10

Lawes MJ, Kotze DJ, Bourquin SL, Morris C (2005) Epigaeic invertebrates as potential ecological indicators of afromontane forest condition in South Africa. Biotropica 37:109–118

Lövei GL, 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 Ecol Biogeogr 15:283–289

Luff ML (1975) Some features influencing the efficiency of pitfall traps. Oecologia 19:345–357

Mader HJ, Schell C, Kornacker P (1990) Linear barriers to arthropod movements in the landscape. Biol Conserv 54:209–222

Magura T, Tóthmérész B, Molnár T (2004) Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. Landscape Ecol 19:747–759

Magura T, Hornung E, Tóthmérész B (2008a) Abundance patterns of terrestrial isopods along an urbanisation gradient. Community Ecol 9:115–120

Magura T, Lövei GL, Tóthmérész B (2008b) Time-consistent rearrangement of carabid beetle assemblages by an urbanisation gradient in Hungary. Acta Oecol 34:233–243

Magura T, Tóthmérész B, Molnár T (2008c) A species-level comparison of occurrence patterns in carabids along an urbanisation gradient. Landsc Urban Plan 86:134–140

Magura T, Lövei GL, Tóthmérész B (2010) Does urbanization decrease diversity in ground beetle (Carabidae) assemblages? Global Ecol Biogeogr 19:16–26

McDonnell MJ, Pickett STA (1990) Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology 71:1232–1237

McDonnell MJ, Pickett STA, Groffman P, Bohlen P, Pouyat RV, Zipperer WC, Parmelee RW, Carreiro MM, Medley K (1997) Ecosystem processes along an urban to-rural gradient. Urban Ecosyst 1:21–36

McIntyre NE, Rango J, Fagan WF, Faeth SH (2001) Ground arthropod community structure in a heterogeneous urban environment. Landsc Urban Plan 52:257–274

Miyashita T, Shinkai A, Chida T (1998) The effects of forest fragmentation on web spider communities in urban areas. Biol Conserv 86:357–364

Niemelä J (1999) Ecology and urban planning. Biodivers Conserv 8:119–131

Niemelä J, Kotze J, Ashworth A, Brandmayr P, Desender K, New T, Penev L, Samways M, Spence J (2000) The search for common anthropogenic impacts on biodiversity: a global network. J Insect Conserv 4:3–9

Niemelä J, Kotze JD, Venn S, Penev L, Stoyanov I, Spence J, Hartley D, Montes de Oca E (2002) Carabid beetle assemblages (Coleoptera, Carabidae) across urban-rural

gradients: an international comparison. Landscape Ecol 17:387–401
Oxbrough AG, Gittings T, O'Halloran J, Giller PS, Smith GF (2005) Structural indicators of spider communities across the forest plantation cycle. Forest Ecol Manag 212:171–183
Pajunen T, Haila Y, Halme E, Niemelä J, Punttila P (1995) Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. Ecography 18:62–72
Pearce JL, Venier LA, Eccles G, Pedlar J, McKenney D (2004) Influence of habitat and microhabitat on epigeal spider (Araneae) assemblages in four stand types. Biodivers Conserv 13:1305–1334
Rebele F (1994) Urban ecology and special features of urban ecosystems. Global Ecol Biogeogr Lett 4:173–187
Sadler JP, Small EC, Fiszpan H, Telfer MG, Niemelä J (2006) Investigating environmental variation and landscape characteristics of an urban-rural gradient using woodland carabid assemblages. J Biogeogr 33:1126–1138
Schowalter TD, Zhang YL (2005) Canopy arthropod assemblages in four overstory and three understory plant species in a mixed-conifer old-growth forest in California. For Sci 51:233–242
Schowalter TD, Zhang YL, Rykken JJ (2003) Litter invertebrate responses to variable density thinning in western Washington forest. Ecol Appl 13:1204–1211
Shochat E, Stefanov WL, Whitehouse MEA, Faeth SH (2004) Urbanization and spider diversity: Influences of human modification of habitat structure and productivity. Ecol Appl 14:268–280
Sokal RR, Rohlf FJ (1995) Biometry. Freeman, New York
ter Braak CJF, Šmilauer P (1998) CANOCO reference manual and user's guide to 8 Canoco for Windows. Software for Canonical Community Ordination (version 4). Centre for Biometry Wageningen and Microcomputer Power, Wageningen and Ithaca
United Nations (2004) World Urbanization Prospects: The 2003. Revision. United Nations Department of Economic and Social Affairs, Population Division, New York
Vilisics F, Elek Z, Lövei GL, Hornung E (2007) Composition of terrestrial isopod assemblages along an urbanisation gradient in Denmark. Pedobiologia 51:45–53
Willett TR (2001) Spiders and other arthropods as indicators in old-growth versus logged redwood stands. Restor Ecol 9:410–420