

Dear Author,

Here are the proofs of your article.

- You can submit your corrections **online**, via **e-mail** or by **fax**.
- For **online** submission please insert your corrections in the online correction form. Always indicate the line number to which the correction refers.
- You can also insert your corrections in the proof PDF and **email** the annotated PDF.
- For fax submission, please ensure that your corrections are clearly legible. Use a fine black pen and write the correction in the margin, not too close to the edge of the page.
- Remember to note the **journal title**, **article number**, and **your name** when sending your response via e-mail or fax.
- **Check** the metadata sheet to make sure that the header information, especially author names and the corresponding affiliations are correctly shown.
- **Check** the questions that may have arisen during copy editing and insert your answers/ corrections.
- **Check** that the text is complete and that all figures, tables and their legends are included. Also check the accuracy of special characters, equations, and electronic supplementary material if applicable. If necessary refer to the *Edited manuscript*.
- The publication of inaccurate data such as dosages and units can have serious consequences. Please take particular care that all such details are correct.
- Please **do not** make changes that involve only matters of style. We have generally introduced forms that follow the journal's style. Substantial changes in content, e.g., new results, corrected values, title and authorship are not allowed without the approval of the responsible editor. In such a case, please contact the Editorial Office and return his/her consent together with the proof.
- If we do not receive your corrections **within 48 hours**, we will send you a reminder.
- Your article will be published **Online First** approximately one week after receipt of your corrected proofs. This is the **official first publication** citable with the DOI. **Further changes are, therefore, not possible.**
- The **printed version** will follow in a forthcoming issue.

#### **Please note**

After online publication, subscribers (personal/institutional) to this journal will have access to the complete article via the DOI using the URL: [http://dx.doi.org/\[DOI\]](http://dx.doi.org/[DOI]).

If you would like to know when your article has been published online, take advantage of our free alert service. For registration and further information go to: <http://www.springerlink.com>.

Due to the electronic nature of the procedure, the manuscript and the original figures will only be returned to you on special request. When you return your corrections, please inform us if you would like to have these documents returned.

# Metadata of the article that will be visualized in OnlineFirst

---

**Please note: Images will appear in color online but will be printed in black and white.**

---

ArticleTitle	Effect of urbanization on ground dwelling spiders in forest patches, in Hungary	
Article Sub-Title		
Article CopyRight	Springer Science+Business Media B.V. (This will be the copyright line in the final PDF)	
Journal Name	Landscape Ecology	
Corresponding Author	Family Name	<b>Horváth</b>
	Particle	
	Given Name	<b>Roland</b>
	Suffix	
	Division	Department of Ecology
	Organization	Debrecen University
	Address	POB. 71, 4010, Debrecen, Hungary
	Email	horvathr@tigris.unideb.hu
Author	Family Name	<b>Magura</b>
	Particle	
	Given Name	<b>Tibor</b>
	Suffix	
	Division	
	Organization	Hortobágy National Park Directorate
	Address	POB. 216, 4002, Debrecen, Hungary
	Email	
Author	Family Name	<b>Tóthmérész</b>
	Particle	
	Given Name	<b>Béla</b>
	Suffix	
	Division	Department of Ecology
	Organization	Debrecen University
	Address	POB. 71, 4010, Debrecen, Hungary
	Email	
Schedule	Received	26 August 2009
	Revised	
	Accepted	22 December 2009
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 (separated by '-') Araneae - Disturbance - Diversity - Forest species - Fragmentation - Habitat affinity

---

Footnote Information

---

2 **Effect of urbanization on ground dwelling spiders in forest**  
3 **patches, in Hungary**

4 **Tibor Magura · Roland Horváth ·**  
5 **Béla Tóthmérés**

6 Received: 26 August 2009 / Accepted: 22 December 2009  
7 © Springer Science+Business Media B.V. 2009

8 **Abstract** Effects of urbanization on ground dwell-  
9 ing spiders (Araneae) were studied using pitfall traps  
10 along an urban-suburban–rural forest gradient in  
11 Debrecen (Hungary). We found that overall spider  
12 species richness was significantly higher in the urban  
13 sites compared to the suburban and rural ones. The  
14 increased diversity was due to the significantly more  
15 open-habitat species in the assemblages at the urban  
16 sites. This suggests that species from the surrounding  
17 matrix (grasslands and arable lands) penetrated the  
18 disturbed urban sites. The ratio of forest species was  
19 significantly higher in the rural sites than in the  
20 suburban and urban ones, suggesting that forest  
21 species are indeed sensitive to the disturbance caused  
22 by urbanization. Canonical correspondence analysis  
23 revealed that the species composition changed  
24 remarkably along the urbanization gradient. Open-  
25 habitat spiders were associated with the urban sites of  
26 higher ground and air temperature. Forest spiders  
27 were characteristic of the rural sites with higher  
28 amount of decaying woods. Our findings suggest that  
29 the overall diversity was not the most appropriate  
30 indicator of disturbance; species with different

habitat affinity should be analyzed separately to get 31  
an ecologically relevant picture of the effect of 32  
urbanization. 33

**Keywords** Araneae · Disturbance · 34  
Diversity · Forest species · Fragmentation · 35  
Habitat affinity 36

**Introduction** 37  
39

The worldwide increase in anthropogenic activities is 40  
causing significant changes to the environment and is 41  
creating patchworks of modified land-cover types that 42  
exhibit considerably similar patterns throughout the 43  
world (Gilbert 1989). A major force of this process is 44  
the urbanization (Magura et al. 2010). Urbanization is 45  
accelerating, as 45% of the human population around 46  
the world lives in cities. In the industrialized 47  
countries approximately 80% of people live in and 48  
around cities (United Nations 2004). 49

Global urbanization caused the loss of natural 50  
habitats (Miyashita et al. 1998; Gibbs and Stanton 51  
2001) as well as alteration and modifications of the 52  
environment (Rebele 1994). Fragmentation also con- 53  
tributes to the effect of urbanization (Miyashita et al. 54  
1998; Gibbs and Stanton 2001). In urban habitats, the 55  
numbers of exotic, invasive and generalist floral and 56  
faunal species are increasing (McDonnell and Pickett 57  
1990; Godefroid and Koedam 2003; Honnay et al. 58  
2003). There are generalist species that benefit from 59

A1 T. Magura  
A2 Hortobágy National Park Directorate, POB. 216, 4002  
A3 Debrecen, Hungary

A4 R. Horváth (✉) · B. Tóthmérés  
A5 Department of Ecology, Debrecen University, POB. 71,  
A6 4010 Debrecen, Hungary  
A7 e-mail: horvathr@tigris.unideb.hu

60 the changes caused by urbanization, and these species  
61 are colonizing and/or invading urban habitats (McIn-  
62 tyre et al. 2001; Gibb and Hochuli 2002; Fernandez-  
63 Juricic 2004; Shochat et al. 2004). Thus, urbanization  
64 is a rather complex process from the point of view of  
65 the biota, which needs a detailed, standardized and  
66 comparable study worldwide to explore the ecological  
67 consequences of urban development.

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

90 There are several hypotheses to explain the effects  
91 of urbanization on biotic communities; urbanization  
92 is usually considered as a kind of environmental  
93 disturbance (Rebele 1994; Niemelä et al. 2000). The  
94 increasing disturbance hypothesis suggests that spe-  
95 cies richness monotonously decreases the increasing  
96 disturbance (Gray 1989). Species with different  
97 habitat affinity show idiosyncratic responses to  
98 disturbance. The habitat alteration hypothesis pre-  
99 dicted that altered habitat structure accompanied by  
100 urbanization causes a decreased presence/dominance  
101 of forest species and an increased ratio of generalist  
102 and open-habitat species penetrating from the sur-  
103 rounding matrix (Magura et al. 2004). The aim of the  
104 study was to test these predictions: (1) diversity  
105 should increase from a low value in the urban area to  
106 a high one in the rural area (increasing disturbance  
107 hypothesis); (2) urbanization decreases the abun-  
108 dance of forest species and increases the generalist

109 and the open-habitat species from the rural area to the  
110 urban one (habitat alteration hypothesis). We also  
111 investigated the relationships between the abundance  
112 of spiders and certain environmental variables along  
113 the urbanization gradient. Moreover, we tested the  
114 ratio of large, hunting spiders (Gnaphosidae, Lycos-  
115 idae) along the urbanization gradient, as it was shown  
116 that they benefited from the disturbance (Pajunen  
117 et al. 1995; Pearce et al. 2004).

## 118 Methods

119 Spiders were studied along an urbanization gradient  
120 in Debrecen (Hungary), the second largest city of  
121 the country (47°32'N; 21°38'E). Three forested  
122 areas (in urban, suburban and rural contexts) were  
123 selected along the gradient within the boundaries of  
124 the city and in the surrounding forest (Nagyerdő  
125 Forest Reserve). All areas belong to a once-contin-  
126 uous old forest stand (>100 years) dominated by  
127 English oak (*Quercus robur*). All forest fragments  
128 were larger than 6 ha (urban: 6–10 ha, suburban:  
129 6–8 ha, rural: 6–12 ha). We characterized the level  
130 of urbanization by the amount of built-up area  
131 (buildings, roads and asphalt covered paths), mea-  
132 sured by the ArcView GIS program (version 3.2)  
133 from an aerial photograph in a square of 1 km<sup>2</sup> size  
134 centered around the sampling area. In the rural area,  
135 there were no buildings (built-up area = 0%) and  
136 the forest was continuous. In the suburban area,  
137 approximately 30% of the surface was built-up or  
138 paved. In the urban area, the amount of land  
139 comprised of the original forest habitat was reduced  
140 to 40% (60% of the area was built up or drastically  
141 different from the original forest habitat). The  
142 distance between the sampling areas (rural, subur-  
143 ban, urban) was 1–3 km. In addition to differences  
144 in land cover there also were differences in the  
145 intensity of forestry/habitat maintenance operations  
146 among the areas. In the urban area the fallen trees  
147 and branches were regularly removed and the shrub  
148 layer was strongly thinned. Grass between the forest  
149 patches was regularly moved, and the grass clip-  
150 pings were removed. Here, there were several  
151 asphalt-covered paths, increasing the isolation  
152 between the forested patches. In the suburban area,  
153 the fallen trees and branches were also regularly  
154 removed, but the understory was not thinned. Most

155 paths were not covered with asphalt. In the rural  
156 forest there was not regular forestry intervention.

157 The sampling regime followed the Globenet  
158 protocol (Niemelä et al. 2000). Four sites, at least  
159 50 m from each other, were selected within each of  
160 the tree sampling areas (urban, suburban, rural).  
161 Spiders were collected at each of the 4 sites in the 3  
162 sampling areas using pitfall traps. Ten traps were  
163 placed randomly at least 10 m apart at each site. This  
164 resulted in a total of 120 traps (3 areas × 4  
165 sites × 10 traps). Each pitfall traps was at least  
166 50 m from the nearest forest edge in order to avoid  
167 edge effects (Horváth et al. 2002). The pitfall traps  
168 were unbated, consisting of plastic cups (diameter  
169 65 mm) containing about 100 ml of 75% ethylene  
170 glycol as a killing-preserving solution. The traps were  
171 covered with bark to protect them from litter and rain.  
172 Trapped spiders were collected every 2 weeks from  
173 the end of March to the end of November, 2001. For  
174 the numerical analyses, data for each of the 12 sites  
175 were pooled for the whole activity period (from  
176 March to November).

177 Eight environmental factors were measured that can  
178 affect the distribution of spiders (Pearce et al. 2004;  
179 Oxbrough et al. 2005). They were measured nearby the  
180 traps and averaged for the sites. Ground temperature at  
181 2 cm depth, air temperature on the soil surface and  
182 relative humidity on the soil surface were measured at  
183 each site monthly on the morning of a typical sunny  
184 day. The statistical analyses were based on averages.  
185 We also estimated the percentage cover of leaf litter,  
186 decaying wood material, herbs, shrubs and canopy  
187 cover in each site within a 10 × 10 m plot.

188 Habitat affinity (forest, generalist and open-habitat  
189 species) of the collected species were designated from  
190 the literature (Buchar 1992; Buchar and Ruzicka  
191 2002; Table 1).

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

199 To test for differences in total species richness and  
200 in the ratio of species with different habitat affinity  
201 (forest, generalist and open-habitat species) among the  
202 urban, suburban and rural areas, one-way analyses of  
203 variance (ANOVA) were performed using data from

the individual sites. Normal distribution of the data  
204 was achieved by log ( $x + 1$ ) transformation. When  
205 ANOVA revealed a significant difference between the  
206 means, a Tukey-test was performed for multiple  
207 comparisons among means (Sokal and Rohlf 1995).  
208

209 The relationships between the environmental  
210 measurements and the overall abundance of the  
211 forest, generalist and open-habitat spiders were  
212 examined using the detrended canonical correspon-  
213 dence analysis by second order polynomials (DCCA)  
214 calculated by the CANOCO package (ter Braak  
215 and Šmilauer 1998). Triplot scaling in the ordination  
216 focused on the inter-species distances, with the  
217 number of spider individuals was log ( $x + 1$ ) trans-  
218 formed.

## 219 Results

### 220 Spider assemblages along the gradient

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

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

### 243 Changes of species richness along the gradient

244 Significantly more spider species were trapped in the  
245 urban area compared to the suburban and rural ones  
246 ( $F = 14.4474$ ; 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

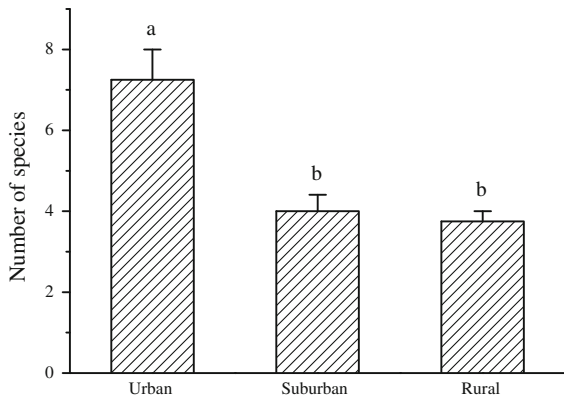
Species	Habitat affinity	Urban	Suburban	Rural
Dysderidae				
<i>Harpactea rubicunda</i> (C. L. Koch, 1838)	Generalist	3	2	0
<i>Harpactea</i> sp.	–	0	1	0
Theridiidae				
<i>Enoplognatha thoracica</i> (Hahn, 1833)	Open-habitat	1	0	0
Linyphiidae				
<i>Ceratinella wideri</i> (Thorell, 1871)	Forest	1	0	0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

247 The ratio of spider species associated with forest  
 248 was significantly higher in the rural area than in the  
 249 suburban and urban ones ( $F = 9.0588$ ; d.f. = 2,9;  
 250  $P = 0.0070$ ; Fig. 2a). An opposite tendency was  
 251 observed for the open-habitat spider species, whose  
 252 ratio decreased along the urban–rural gradient and was  
 253 significantly lower in the rural area compared to the  
 254 urban and suburban ones ( $F = 11.4168$ ; d.f. = 2,9;  
 255  $P = 0.0034$ ; Fig. 2c). There were no statistically

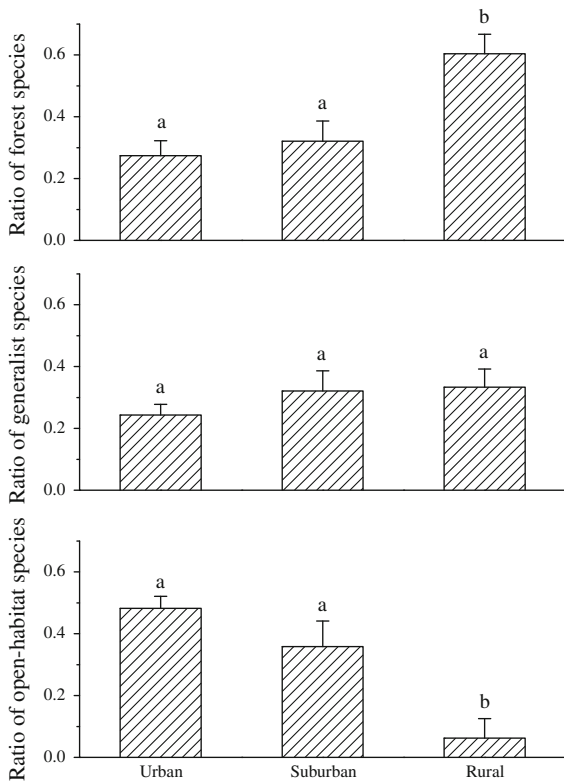
significant differences in the ratio of generalist species  
 among the studied areas ( $F = 0.7975$ ; d.f. = 2,9;  
 $P = 0.4799$ ; Fig. 2b). 256  
 257  
 258

Spiders and environmental factors 259

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 260  
 261  
 262



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

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

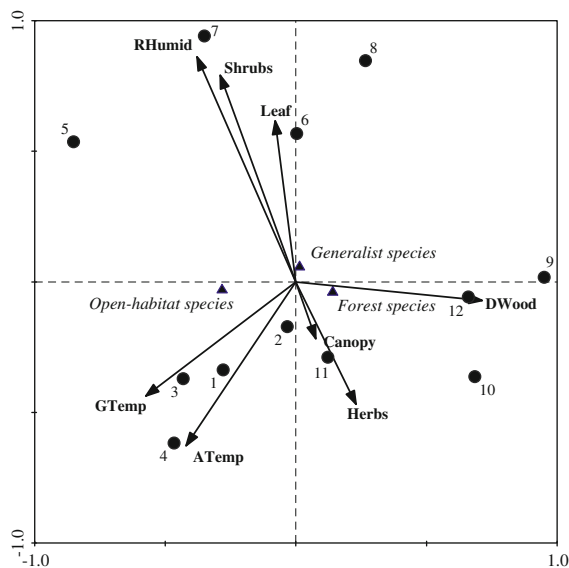
The urban sites were characterized by higher  
 267 ground and air temperature. The suburban sites  
 268 disposed of higher relative humidity and cover of  
 269 leaf litter and shrubs, but of lower cover of herbs and  
 270 canopy. The rural sites had higher amount of  
 271 decaying wood material, herbs and higher canopy  
 272 cover. The triplot graph also showed that the forest  
 273 spiders were characteristic of the rural sites with  
 274 higher amount of decaying woods. Open-habitat  
 275 spiders were associated with the urban sites of higher  
 276 ground and air temperature, whereas the generalist  
 277 spiders seemed to not be influenced by the changes of  
 278 the studied environmental factors, as indicated by  
 279 their position near the origin (Fig. 3). A total of  
 280 92.1% of the species and 99.8% of the species-  
 281 environment variation were accounted for by the four  
 282 axes of the DCCA using all of the studied variables.  
 283

## Discussion

### Disturbance and overall diversity

In their study of ground-dwelling spiders, Alarukka  
 286 et al. (2002) failed to uncover any significant  
 287 differences in overall species richness along an  
 288 urban-rural gradient in Finland. Thus, similarly to  
 289 our results, the increasing disturbance hypothesis was  
 290 not supported. Although, we found significantly  
 291 higher number of species in the urban area.  
 292 A possible reason for the lack of support of the  
 293 increasing disturbance hypothesis may be that the  
 294 gradient is a complex system where many factors  
 295 (temperature, moisture, edaphic conditions, acidity,  
 296 pollution, decomposition) interact (McDonnell et al.  
 297 1997; Niemelä 1999). In the case of urban and  
 298 suburban forests path appear, increasing edges or  
 299 edge-like habitats, which modify species patterns  
 300 (Lövei et al. 2006). A more obvious reason for the  
 301 lack of support for the increasing disturbance hypo-  
 302 thesis is the variability of responses of spider species  
 303 with differing habitat affinities to disturbance. Forest  
 304 species may have narrower tolerance limits and  
 305 consequently suffer, whereas generalist and open-  
 306 habitat species may benefit from the disturbance and  
 307 habitat alteration caused by urbanization. It is likely  
 308 that diversity itself, as measured by overall species  
 309 richness, is not the most appropriate indicator of  
 310 disturbance. Therefore, species with different habitat  
 311





**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

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

314 Several studies examining forest patches with  
315 different level of human disturbance found that  
316 overall diversity (overall species richness or value  
317 of a particular diversity index) did not differ among  
318 these patches, although the composition of spider  
319 assemblages differed considerably among the patches  
320 (Alaruiikka et al. 2002; Hsieh et al. 2003; Chen and  
321 Tso 2004). These findings highlight that species with  
322 different habitat affinity respond differently to the  
323 human-generated disturbance. Our results also  
324 showed that the overall diversity was not the most  
325 appropriate indicator of disturbance. To evaluate the  
326 effect of urbanization on ground-dwelling spiders  
327 based on overall species richness, the conclusion  
328 would be that urbanization has no harmful conse-  
329 quence on the spiders. Moreover, it causes a signif-  
330 icant increase in diversity. However, the increase in  
331 diversity was mostly due to species penetrating from  
332 the neighbouring grassland and arable land matrix  
333 (open-habitat species). Simultaneously, the ratio of

the forest species significantly decreased in the 334  
disturbed urban sites. 335

Disturbance and the ratio of species penetrating 336  
from the matrix 337

Considering the habitat affinity of spiders, we have 338  
shown that the open-habitat spiders occurred most 339  
frequently in the urban sites. These open-habitat 340  
spiders were not characteristic of forests, because 341  
they can survive and reproduce in the surrounding 342  
matrix (grasslands and arable lands, Buchar and 343  
Ruzicka 2002). Alaruiikka et al. (2002) did not find 344  
any significant difference in the richness of species 345  
with different habitat affinity along the urbanization 346  
gradient in Finland. This could be either because we 347  
used species ratios while Alaruiikka et al. (2002) used 348  
absolute species numbers. Another possible reason is 349  
that in Hungary the open habitat matrix, a source of 350  
open habitat immigrant is more extensible than in 351  
Finland. 352

Urbanization causes several forms of disturbance 353  
which all contribute to the alteration of indigenous 354  
habitats (Gilbert 1989; Niemelä 1999). In the present 355  
study, this habitat alteration was the most pronounced 356  
in the urban sites, where the forest patches were 357  
significantly fragmented by asphalt-covered paths, 358  
and the habitat structure was heavily modified by 359  
removal of dead wood and thinning of the shrub 360  
layer. All these modifications also caused significant 361  
changes in environmental conditions. Alteration of 362  
habitat structure with accompanying changes in 363  
environmental conditions may alter spider commu- 364  
nity structure (Shochat et al. 2004; Schowalter and 365  
Zhang 2005). For example, in their studies of 366  
community structure of forest spiders, Pajunen et al. 367  
(1995) and Pearce et al. (2004) studying community 368  
structure of spiders in forests, showed that the 369  
abundance and species richness of large, hunting- 370  
spider species (Gnaphosidae, Lycosidae) increased by 371  
disturbance. Jocqué and Alderweireldt (2005) showed 372  
that the abundance of Lycosidae is higher in open 373  
habitats with low vegetation, than in dense forests. 374  
However, our results contradicted these findings, as 375  
the ratio of lycosid specimens did not differ signif- 376  
icantly among sites, moreover the ratio of this species 377  
in the assemblage increased significantly from 378  
the urban area toward the rural one. Ratios of both 379  
the Gnaphosidae specimens and species in the 380

381 assemblage were significantly higher at the urban  
 382 sites, probably due to the high numbers of *Trachy-*  
 383 *zelotes pedestris* (C. L. Koch, 1837, Table 1).  
 384 Disturbed forest patches could be invaded by gener-  
 385 alist species and by species from the surrounding  
 386 matrix (Buddle et al. 2000; Gurdebeke et al. 2003).  
 387 The matrix surrounded the studied forest patches  
 388 were grasslands and arable lands. The open-habitat  
 389 species can be regarded as a species characteristic of  
 390 the matrix habitats. The disturbed, thinned urban park  
 391 with increased ground and air temperature contained  
 392 several favorable microhabitats for open-habitat  
 393 species.

#### 394 Disturbance and the ratio of forest species

395 Several studies emphasized that alteration of habitat  
 396 structure alters spider community structure (Hurd and  
 397 Fagan 1992; Schowalter et al. 2003; Shochat et al.  
 398 2004; Schowalter and Zhang 2005). Forest species  
 399 are associated with rural sites and their abundance  
 400 increased with the increasing of the amount of  
 401 decaying wood. Oxbrough et al. (2005) similarly  
 402 showed that forest spider species were positively  
 403 correlated with twig materials; perhaps these spiders  
 404 prey on invertebrates in and on decaying wood.  
 405 Urbanization causes an extensive alteration of habitat  
 406 structure (e.g. by strong thinning and removing  
 407 decaying wood material, creating asphalt-covered  
 408 paths). These alterations generally cause unfavorable  
 409 changes in the microclimatic abiotic and biotic  
 410 conditions of the area. All these changes affected  
 411 directly the forest species. Lawes et al. (2005), in  
 412 studying forests that spanned a gradient from rela-  
 413 tively undisturbed to highly disturbed forest patches,  
 414 also showed that the abundance of a spider species  
 415 characteristic to the undisturbed forests decreased  
 416 with increasing disturbance. Langelotto and Denno  
 417 (2004) argued that habitat simplification affects  
 418 spiders' ability to capture prey eliminating enough  
 419 refuge from intraguild predation, and providing no  
 420 alternative resources (e.g. alternative prey). All these  
 421 may contribute to the decreased ratio of forest spiders  
 422 at the disturbed urban sites. Habitat alteration caused  
 423 by urbanization also has indirect effects on forest  
 424 spiders. Creating sealed paths fragments the habitat  
 425 into even smaller patches. The division of the original  
 426 forested area into small, isolated patches causes also a  
 427 loss of forest species through a reduction in the

428 habitat area, an increase in remnant isolation and a  
 429 decrease in habitat connectivity (Didham et al. 1996).  
 430 Miyashita et al. (1998), studying continuous forest  
 431 and fragmented forest patches, also showed that  
 432 smaller fragments had fewer species and lower  
 433 density of individuals. Forest patches divided by  
 434 asphalt-covered paths are isolated from each other, as  
 435 ground-dwelling spiders only rarely cross them  
 436 (Mader et al. 1990). The population size of forest  
 437 spider species in isolated patches could decrease  
 438 because the patches are too small to maintain viable  
 439 populations and there is too little dispersal between  
 440 the patches. Small populations of forest spiders in  
 441 isolated patches are at greater risk of local extinction  
 442 and genetic isolation. Gurdebeke et al. (2000), in  
 443 studying a forest-specific spider species (*Coelotes*  
 444 *terrestris* (Wider, 1834)) in forest patches with  
 445 different degrees of isolation and size, showed that  
 446 there was a very high degree of genetic isolation  
 447 between the spider populations inhabiting the  
 448 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.

**Acknowledgments** We are grateful to Csaba Szinetár for his  
 help during the taxonomic identification of the spiders and for  
 the advice in determining the habitat affinity of the spider  
 species. We are also thankful for Tivadar Molnár and Zoltán  
 Elek for their help during the field work. TM was supported by  
 the Hungarian Scientific Research Fund (OTKA grant no.  
 F61651). TM and RH were supported by the János Bolyai  
 Research Scholarship of the Hungarian Academy of Sciences.

#### References

- Alarukka 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) Kommentierte 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

- 476 Buddle CM, Spence JR, Langor DW (2000) Succession of  
477 boreal forest spider assemblages following wildfire and  
478 harvesting. *Ecography* 23:424–436
- 479 Chen KC, Tso IM (2004) Spider diversity on Orchid Island,  
480 Taiwan: A comparison between habitats receiving dif-  
481 ferent degrees of human disturbance. *Zool Stud* 43:598–  
482 611
- 483 Desender K, Small E, Gaublonne E, Verdyck P (2005) Rural-  
484 urban gradients and the population genetic structure of  
485 woodland ground beetles. *Conserv Genet* 6:51–62
- 486 Didham RK, Ghazoul J, Stork NE, Davis AJ (1996) Insects in  
487 fragmented forests: a functional approach. *Trends Ecol*  
488 *Evol* 11:255–260
- 489 Elek Z, Lövei GL (2007) Patterns in ground beetle (Coleoptera:  
490 Carabidae) assemblages along an urbanisation gradient in  
491 Denmark. *Acta Oecol* 32:104–111
- 492 Fernandez-Juricic E (2004) Spatial and temporal analysis of  
493 the distribution of forest specialists in an urban-frag-  
494 mented landscape (Madrid, Spain)—implications for local  
495 and regional bird conservation. *Landsc Urban Plan* 69:17–  
496 32
- 497 Gibb H, Hochuli DF (2002) Habitat fragmentation in an urban  
498 environment: large and small fragments support different  
499 arthropod assemblages. *Biol Conserv* 106:91–100
- 500 Gibbs JP, Stanton EJ (2001) Habitat fragmentation and  
501 arthropod community change: carrion beetles, phoretic  
502 mites, and flies. *Ecol Appl* 11:79–85
- 503 Gilbert OL (1989) The ecology of urban habitats. Chapman  
504 and Hall, London
- 505 Godefroid S, Koedam N (2003) Distribution pattern of the flora  
506 in a peri-urban forest: an effect of the city-forest ecotone.  
507 *Landsc Urban Plan* 65:169–185
- 508 Gray JS (1989) Effects of environmental stress on species rich  
509 assemblages. *Biol J Linn Soc* 37:19–32
- 510 Gurdebeke S, Neiryck B, Maelfait JP (2000) Population  
511 genetic effects of forest fragmentation in Flanders  
512 (Belgium) on *Coelotes terrestris* (Wider) (Araneae: Age-  
513 lenidae) as revealed by allozymes and RAPD. *Ekol-Bra-  
514 tisl* 19:87–96
- 515 Gurdebeke S, De Bakker D, Vanlanduyt N, Maelfait JP (2003)  
516 Plans for a large regional forest in eastern Flanders  
517 (Belgium): assessment of spider diversity and community  
518 structure in the current forest remnants. *Biodivers Conserv*  
519 12:1883–1900
- 520 Honnay O, Piessens K, Van Landuyt W, Hermy M, Gulinck H  
521 (2003) Satellite based land use and landscape complexity  
522 indices as predictors for regional plant species diversity.  
523 *Landsc Urban Plan* 63:241–250
- 524 Hornung E, Tóthmérész B, Magura T, Vilisics F (2005)  
525 Changes of isopod assemblages along an urban-suburban-  
526 rural gradient in Hungary. *Eur J Soil Biol* 43:158–165
- 527 Horváth R, Magura T, Cs Szinetár (2001) Effects of immission  
528 load on spiders living on black pine. *Biodivers Conserv*  
529 10:1531–1542
- 530 Horváth R, Magura T, Péter G, Tóthmérész B (2002) Edge  
531 effect on weevils and spiders. *Web Ecol* 3:43–47
- 532 Hsieh YL, Lin YS, Tso IM (2003) Ground spider diversity in  
533 the Kenting uplifted coral reef forest, Taiwan: a compar-  
534 ison between habitats receiving various disturbances.  
535 *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 afro-  
montane forest condition in South Africa. *Biotropica*  
37:109–118
- Lövei GL, Magura T, Tóthmérész B, Kódöböcz 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 gra-  
dient. *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) assem-  
blages? *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 biodiver-  
sity: 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

- 596 gradients: an international comparison. *Landscape Ecol* 17:387–401 620
- 597 621
- 598 Oxbrough AG, Gittings T, O'Halloran J, Giller PS, Smith GF 622
- 599 (2005) Structural indicators of spider communities across 623
- 600 the forest plantation cycle. *Forest Ecol Manag* 212:171– 624
- 601 183 625
- 602 Pajunen T, Haila Y, Halme E, Niemelä J, Punttila P (1995) 626
- 603 Ground-dwelling spiders (Arachnida, Araneae) in frag- 627
- 604 mented old forests and surrounding managed forests in 628
- 605 southern Finland. *Ecography* 18:62–72 629
- 606 Pearce JL, Venier LA, Eccles G, Pedlar J, McKenney D (2004) 630
- 607 Influence of habitat and microhabitat on epigeal spider 631
- 608 (Araneae) assemblages in four stand types. *Biodivers* 632
- 609 *Conserv* 13:1305–1334 633
- 610 Rebele F (1994) Urban ecology and special features of urban 634
- 611 ecosystems. *Global Ecol Biogeogr Lett* 4:173–187 635
- 612 Sadler JP, Small EC, Fiszpan H, Telfer MG, Niemelä J (2006) 636
- 613 Investigating environmental variation and landscape 637
- 614 characteristics of an urban-rural gradient using woodland 638
- 615 carabid assemblages. *J Biogeogr* 33:1126–1138 639
- 616 Schowalter TD, Zhang YL (2005) Canopy arthropod assem- 640
- 617 blages in four overstorey and three understorey plant species 641
- 618 in a mixed-conifer old-growth forest in California. *For Sci* 642
- 619 242
- Schowalter TD, Zhang YL, Rykken JJ (2003) Litter inverte-  
brate 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
- Vilicis 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

UNCORRECTED