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Abstract	<p>We studied ground-dwelling spiders along a rural–suburban–urban forest gradient representing increasing human disturbance using pitfall traps. We tested four known and two novel hypotheses: (1) increasing disturbance hypothesis (species richness is decreasing by disturbance); (2) matrix species hypothesis (the richness of open-habitat species is increasing by disturbance); (3) opportunistic species hypothesis (the richness of generalist species is increasing by disturbance); and (4) habitat specialist hypothesis (the number of the forest specialist species is decreasing by disturbance). As a consequence of urbanization, urban forests become drier and more open; thus, according to the new hypotheses, the number of (5) xerophilous species and (6) light-preferring species are increasing in the urban area. Our result did not support the increasing disturbance hypothesis, as the overall species richness increased from the rural sites to the urban ones. As predicted, the number of both the open-habitat and the generalist species increased towards the urban sites. The number of forest specialist species was higher in the suburban area than in the rural and urban area. Both</p>	

xerophilous and light-preferring species were the most numerous in the urban area, supporting the xerophilous species and the light-preferring species hypotheses. Canonical correspondence analysis showed that the forest specialist species associated with the rural sites with higher amounts of decaying woods and more herbs or with the suburban sites with higher cover of leaf litter and higher relative humidity. Two generalist species and one open habitat species were characteristic of urban sites with higher ground surface and air temperature.

Keywords (separated by '-') Globenet - Disturbance - Xerophilous species - Light-preferring species - Environmental factors

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7 **a case study of ground-dwelling spiders along a rural–urban**
8 **gradient in a lowland forest in Hungary**

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33 disturbance hypothesis, as the overall species richness
34 increased from the rural sites to the urban ones. As
35 predicted, the number of both the open-habitat and the
36 generalist species increased towards the urban sites.
37 The number of forest specialist species was higher in the
38 suburban area than in the rural and urban area. Both
39 xerophilous and light-preferring species were the most
40 numerous in the urban area, supporting the xerophilous
41 species and the light-preferring species hypotheses.
42 Canonical correspondence analysis showed that the
43 forest specialist species associated with the rural sites

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or with the suburban sites with higher cover of leaf litter 45
and higher relative humidity. Two generalist species and 46
one open habitat species were characteristic of urban 47
sites with higher ground surface and air temperature. 48

Keywords Globenet · Disturbance · Xerophilous 49
species · Light-preferring species · Environmental 50
factors 51

Introduction 52

The human population is rising exponentially and cur- 53
rently more than 7 billion people live in the world. More 54
than 50 % of humanity lives in and around cities 55
(UNPD 2005). The prediction shows that this propor- 56
tion will be more than 60 % by 2025 (Antrop 2000). 57
Increased human activities affect almost all species live 58
on Earth. These are resulting in a vast amount of bio- 59
diversity loss, modifications, and alteration of natural 60
habitats. The most intensively managed, modified, and 61
fragmented areas by humans are the urbanized habitats 62
primarily in the bigger cities (Gibb and Hochuli 2002; 63
Miyashita et al. 1998; Shochat et al. 2004). Urbanization 64
processes are similar all around the world and these 65
effects are major in the city centers than in the rural 66
parts of cities (Magura et al. 2010a). The urban forests 67
are usually more fragmented, more polluted, warmer, 68
more open, and drier than the natural ones (Marshall 69
and Shortle 2005; Venn et al. 2003). Therefore, the 70
urbanized habitat patches are considerably different 71
from the rural habitats. From the surrounding habitats 72
more non-native and invasive species can penetrate in 73
urban forest fragments (McIntyre 2000; Tóthmérész 74
et al. 2011). Besides, more exotic plant and animal spe- 75
cies may appear in the fragmented urban patches. In 76
contrast, lots of original plant and animal species dis- 77
appear from these habitats or decrease their number 78

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79 (Marzluff et al. 2001). Therefore, the negative environ- 138
80 mental effects should be minimized. 139

81 The aim of an international research framework, 140
82 called Globenet, was to assess and compare the influence 141
83 of urbanization on arthropods biodiversity in different 142
84 countries worldwide (Niemelä et al. 2000). The Globenet 143
85 program regards a rural–suburban–urban forested gra- 144
86 dient, representing different levels of human disturbance 145
87 (Pickett et al. 2001), using a common sampling meth- 146
88 odology (pitfall trap) and some target of ground-dwell- 147
89 ing invertebrates (ground beetles, isopods, and spiders) 148
90 across different parts of the world. Most of the published 149
91 articles within this framework focus on ground beetles 150
92 (Elek and Lövei 2007; Gaublomme et al. 2008; Ishitani 151
93 et al. 2003; Magura et al. 2004, 2008b, c, d, 2010a; 152
94 Niemelä et al. 2002; Sadler et al. 2006; Tóthmérész et al. 153
95 2011), while the study of other arthropod taxa are lim- 154
96 ited (for spiders: Alarukka et al. 2002; Magura et al. 155
97 2008d, 2010b; for isopods: Hornung et al. 2007; Magura 156
98 et al. 2008a, d; Vilisics et al. 2007). To assess whether 157
99 there are general trends of urbanization on arthropods, 158
100 therefore other indicator taxa (like spider; e.g., Horváth 159
101 et al. 2001, 2009; Lawes et al. 2005; Willett 2001) should 160
102 also be investigated along rural–urban gradients. 161

103 Species with different ecological demands respond 162
104 variously to the natural and anthropogenic disturbances 163
105 (Langor and Spence 2006; Lövei et al. 2006; Magura 164
106 et al. 2010a). Therefore, it is important to investigate the 165
107 groups of species with different ecological demands 166
108 separately. These studies can provide help for experts 167
109 before planning different managements. We selected 168
110 spiders (Araneae) for this study because they are fairly 169
111 easy to collect and preserve, diverse and abundant, 170
112 taxonomically and ecologically well known, include 171
113 sensitive specialist and less sensitive generalist species. 172
114 Moreover, spiders can be found nearly everywhere, and 173
115 being mobile and relatively short-lived; they may adjust 174
116 rapidly to changes in abiotic and biotic environmental 175
117 variables and human disturbances (Foelix 2011; Wise 176
118 1993). 177

119 There are several hypotheses to explain the effects of 178
120 human disturbances on biotas (Niemelä et al. 2000; 179
121 Rebele 1994). We tested four classical and two novel 180
122 hypotheses regarding the response of species to urbani- 181
123 zation. (1) The *increasing disturbance hypothesis* claims 182
124 that species richness monotonously decreases with the 183
125 increasing levels of disturbance (Gray 1989). Species 184
126 with different ecological demands show specific reactions 185
127 to disturbance. (2) The *matrix species hypothesis* sug- 186
128 gests that the matrix (open habitat) species penetrating 187
129 from the surrounding open habitat; therefore, the 188
130 dominance of these species increase from the rural sites 189
131 to the urban ones (Tóthmérész et al. 2011). (3) Oppor- 190
132 tunistic species are able to benefit from the high level of 191
133 disturbance, and their dominance should be the highest 192
134 in the heavily disturbed urban sites (*opportunistic species* 193
135 *hypothesis*) (Gray 1989). (4) The *habitat specialist* 194
136 *hypothesis* predicts that the abundance and species 195
137 richness of forest specialist species decreases with the 196

138 increasing disturbance from the rural area to the urban 139
140 one (Magura et al. 2004). 141

142 In the habitat choice of spiders, the light and 143
144 humidity conditions of the environment play vital role. 145
146 Buchar and Ruzicka (2002) pointed out that the light 147
148 and humidity demands of a species may differ. For 149
150 example, a light-preferring species may also be humid- 151
152 ity-preferring; therefore, we also tested two novel 153
154 hypotheses: (5) urbanization decreases the humidity of 155
156 forest; thus, the abundance of xerophilous species 157
158 should increase from the rural habitat to the urban one 159
160 (*xerophilous species hypothesis*). (6) As a result of 161
162 urbanization, the urban forest become more open and 163
164 lighter; therefore the diversity of light-preferring species 165
166 increase along the gradient from the rural area towards 167
168 the urban one (*light-preferring species hypothesis*). We 169
170 also tested the effects of urbanization on the occurrence 171
172 of the most frequent spider species along a rural– 173
174 suburban–urban gradient. The abundance of the most 175
176 frequent spider species, which the number of individuals 177
178 made up at least 5 % of the total catch, was also studied 179
180 along the rural–urban gradient. We also investigated the 181
182 relationships between the abundance of the most fre- 183
184 quent spider species and several environmental variables 185
186 along the gradient. 187

163 Methods 164

165 Study area 166

167 The study areas were along a rural–urban gradient in 168
169 and around Debrecen city (eastern Hungary, 47°32'N; 169
170 21°38'E), the second largest city of Hungary near the 170
171 eastern border of Hungary (Magura et al. 2004). We 171
172 selected three sampling areas (rural, suburban, and 172
173 urban forests) along an urbanization gradient in the city 173
174 and in the adjacent forest (Nagyerdő Forest Reserve). 174
175 All selected areas were in a once-continuous old (older 175
176 than 100 years) native *Convallario-Quercetum* forest 176
177 association. All sampling areas were larger than 6 ha. 177
178 We characterized the level of urbanization by the ratio 178
179 of the built-up area (buildings, roads, and asphalt-cov- 179
180 ered paths) to the natural habitats measured by the 180
181 ArcGIS program (ESRI Software 2004) using an aerial 181
182 photograph. In the rural area, the built-up area was 0 % 182
183 (there were no buildings). Therefore, the forest was 183
184 continuous. In the suburban area, about 30 % of the 184
185 surface was built-up or tiled; while in the urban area the 185
186 built-up area exceeded 60 % (this area was very built-up 186
187 and drastically different from the original forest habitat). 187
188 The distance between the forested areas (rural, subur- 188
189 ban, and urban) was 1–3 km. Further disturbance types 189
190 were the presence of people and the intensity of forestry/ 190
191 habitat maintenance operations among the areas. In the 191
192 rural forest area, there were occasional low-intensity 192
193 forestry management operations. Only a small portion 193
194 of the paths was asphalt-covered. In the suburban sites, 194

192 while the understory was not thinned, the fallen trees
193 and branches were also regularly removed. In this area,
194 most paths were not asphalt-covered. In the urban for-
195 ested area the fallen trees and branches were frequently
196 removed, besides in this area there were several asphalt-
197 covered paths, increasing the isolation between the for-
198 ested patches and the shrub layer was strongly thinned,
199 resulting in a park character. Grass between the urban
200 patches was frequently mown, and the mowed grass was
201 removed.

202 Sampling design

203 We selected two sites per urbanization stage, at least
204 100 m apart, within each sampling area (rural, subur-
205 ban, and urban). We collected spiders using pitfall traps
206 from three sampling areas of two sites. We placed ten
207 traps randomly at least 10 m apart from each other at
208 each site. The result was a total of 60 traps scattered
209 along the rural–urban gradient (3 areas \times 2 sites \times 10
210 traps). In order to avoid edge effects, each pitfall trap
211 was at least 50 m from the nearest forest edge (Horváth
212 et al. 2002). The pitfall traps were unbaited, and made of
213 plastic cups (65 mm in diameter) filled with approxi-
214 mately 100 ml of 4 % formaldehyde as a killing-pre-
215 serving liquid. We covered the traps with fiberboard to
216 protect them from litter and rain. We collected spider
217 species fortnightly from the end of April to the end of
218 October 2009. For the statistical analyses, we pooled
219 pitfall samples for the whole year.

220 Data analyses

221 We grouped the ecological demands (forest, generalist,
222 and open-habitat species, as well as xerophilous and
223 light-preferring species) of the collected species from the
224 literature (Alaruikka et al. 2002; Buchar and Ruzicka
225 2002; Electronic Supplementary Material (ESM)
226 Table 1).

227 GLMs based on Poisson distribution were used to
228 test differences in the overall spider species richness and
229 the species richness of the spiders with different ecolog-
230 ical demands among the three sampling areas (rural,
231 suburban, urban), among the six sites. We used data

from the individual traps. Sites were nested within the 232
sampling areas; therefore, we used nested design. The 233
response variable (species richness or abundance) was 234
defined as following a Poisson distribution (with log link 235
function). The Poisson distribution assumes that the 236
mean and variance are equal. Real data do not follow 237
this, and the variance is often much larger than the mean 238
(O'Hara and Kotze 2010). This biological reality (over- 239
dispersion) was also incorporated into the model using 240
the Pearson Chi-square (quasi-Poisson distribution). 241
That is, GLMs based on quasi-Poisson distribution were 242
used. For multiple comparisons among means, a Tukey 243
test was performed, when GLM showed a significant 244
difference between the means (StatSoft Inc. 2010). 245

246 We measured eight environmental variables that were
247 assumed to affect the distribution of spiders (Oxbrough
248 et al. 2005; Pearce et al. 2004). We measured ground
249 temperature at 2 cm depth, air temperature, and relative
250 humidity on the soil surface at each trap monthly on the
251 morning of a typical sunny day. The statistical analyses
252 were based on the averages of the monthly measures. We
253 also estimated the percentage cover of leaf litter,
254 decaying wood material, herbs, shrubs, and canopy
255 cover around each trap within a 2×2 m quadrat
256 (Table 1).

257 We examined the relationships between the environ-
258 mental measurements and the abundance of the most
259 frequent species using the detrended canonical corre-
260 spondence analysis by second-order polynomials
261 (DCCA) calculated by the CANOCO package (ter
262 Braak and Šmilauer 2002). Biplot scaling in the ordi-
263 nation was symmetric (focusing on both the inter-species
264 and inter-samples distances). We analyzed the most
265 frequent five species because the abundance of the other
266 species was low.

267 Results

268 During the study, we trapped altogether 4,959 individ-
269 uals belonging to 69 species (Table 1 in ESM). In the
270 rural area, we collected 1,521 individuals belonging to 40
271 species, 46 species and 1,636 individuals in the suburban
272 area, and in the urban area 1,802 individuals repre-
273 senting 46 species. The dominant species was *Pardosa*
274 *alacris*, which made up 32 % of the total catch. This

Table 1 Average values (\pm SE) of the environmental variables in three study areas

Environmental variables	Rural	Suburban	Urban
Ground temperature (°C)	21.1 \pm 0.266	22.1 \pm 0.109	25.9 \pm 0.361
Air temperature (°C)	27.3 \pm 0.257	27.3 \pm 0.075	31.4 \pm 0.206
Relative humidity (%)	59.6 \pm 0.682	77.4 \pm 0.625	60.1 \pm 0.743
Cover of leaf litter (%)	21.1 \pm 3.480	69.9 \pm 2.045	11.8 \pm 2.756
Cover of decaying wood material (%)	10.4 \pm 2.110	4.4 \pm 0.765	4.1 \pm 0.688
Cover of herbs (%)	70.8 \pm 3.282	20.5 \pm 2.693	48.4 \pm 7.251
Cover of shrubs (%)	12.3 \pm 3.541	55.4 \pm 4.165	28.7 \pm 5.508
Canopy cover (%)	56.7 \pm 2.741	55.0 \pm 3.639	42.3 \pm 3.920

275 species was the most numerous in the suburban and
 276 urban habitats, while in the rural habitat *Diplostyla*
 277 *concolor* was the most numerous (here *Pardosa alacris*
 278 was the second numerous species). In all habitats,
 279 *Ozyptila praticola* and *Trochosa terricola* were also
 280 numerous. In the rural forest, *Liocranoeca striata* was
 281 numerous. In the suburban area, *Diplostyla concolor* and
 282 *Cozyptila blackwalli*; and in the urban habitat, *Trachy-*
 283 *zelotes pedestris*, *Liocranoeca striata* and *Cozyptila*
 284 *blackwalli* were also numerous (Table 1 in ESM).
 285 Regarding the ecological demands of the spider species,
 286 there were 3,141 individuals of 29 forest species, whereas
 287 1,467 individuals belonged to 29 generalist species, 340
 288 individuals represented ten open-habitat species, 1,689
 289 individuals belonged to six xerophilous species, 330
 290 individuals represented ten light-preferring species, and
 291 11 individuals of one species, which could be determined
 292 only at genus level (Table 1 in ESM).

293 The total species number increased significantly from
 294 the rural sites to the urban ones ($\chi^2 = 32.0581$; $df =$
 295 $2,3$; $p < 0.001$, Fig. 1a). There was a similar tendency
 296 in the case of open-habitat and generalist spiders, whose
 297 species number were significantly lower in the rural and
 298 suburban habitats than in the urban sites (species
 299 number of open-habitat species: $\chi^2 = 19.0246$; $df =$
 300 $2,3$; $p < 0.001$, Fig. 1b; species number of generalist
 301 species: $\chi^2 = 65.7374$; $df = 2,3$; $p < 0.001$, Fig. 1c).

302 The species number of forest specialist spider was sig-
 303 nificantly higher in the suburban area than in the rural
 304 and urban ones ($\chi^2 = 26.0006$; $df = 2,3$; $p < 0.001$,
 305 Fig. 1d). The number of xerophilous species was sig-
 306 nificantly higher in the urban sites than in the rural and
 307 suburban ones ($\chi^2 = 43.0912$; $df = 2,3$; $p < 0.001$,
 308 Fig. 2a). The species number of light-preferring spider
 309 species was significantly higher in the urban area than in
 310 the rural area ($\chi^2 = 13.5226$; $df = 2,3$; $p < 0.001$,
 311 Fig. 2b).

312 Two of the five most abundant species were forest
 313 specialist species (*D. concolor*, *P. alacris*), two were
 314 generalist species (*O. praticola*, *T. terricola*) and one was
 315 open-habitat species (*T. pedestris*). One of the two forest
 316 specialist species (*D. concolor*) was more abundant in the
 317 rural areas than in the suburban and urban ones
 318 ($\chi^2 = 300.3505$; $df = 2,3$; $p < 0.001$, Fig. 3a). The
 319 other forest species (*P. alacris*) was most numerous in
 320 the suburban sites ($\chi^2 = 28.6329$; $df = 2,3$; $p < 0.001$,
 321 Fig. 3b). The generalist species showed significant vari-
 322 ation along the urbanization gradient. *O. praticola* was
 323 more abundant in the urban area, compared to the rural
 324 and suburban sites ($\chi^2 = 45.9617$; $df = 2,3$; $p < 0.001$,
 325 Fig. 3c), while the number of individuals of *T. terricola*
 326 increased continuously from the rural area to the urban
 327 sites ($\chi^2 = 82.3959$; $df = 2,3$; $p < 0.001$, Fig. 3d). The
 328 open-habitat species (*T. pedestris*) was more numerous

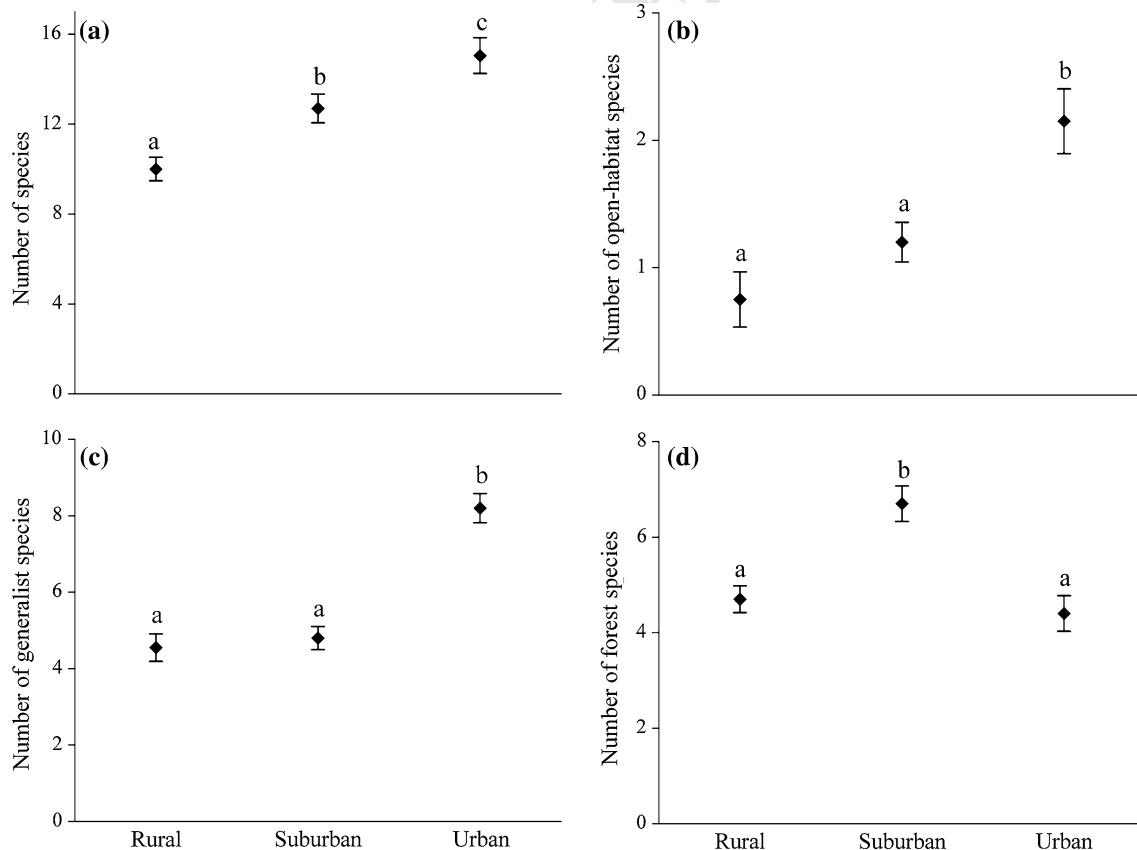


Fig. 1 Average values of overall species (a), open-habitat species (b), generalist species (c), and forest spider species richness (d) (\pm SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by Tukey test ($p < 0.05$)

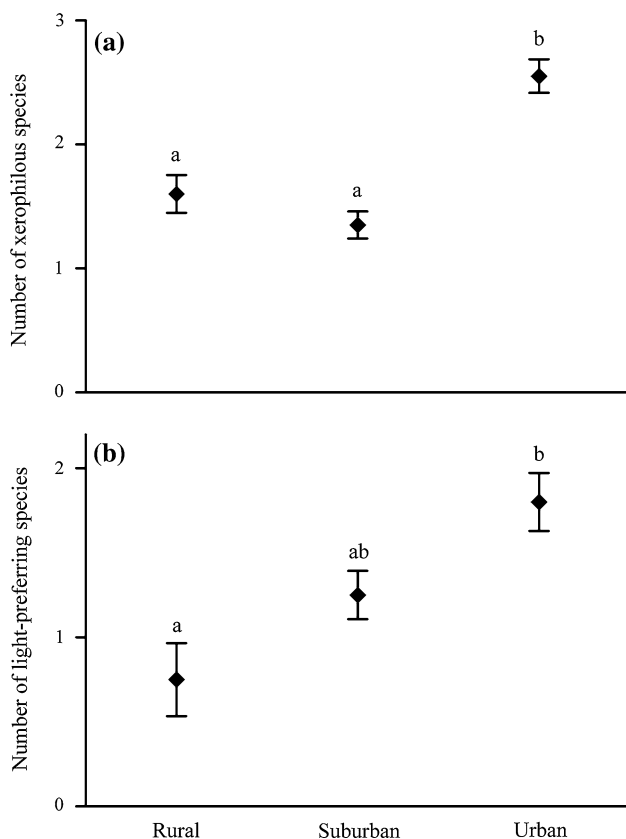


Fig. 2 Average values of xerophilous species (a) and light-preferring species richness (b) (\pm SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by Tukey test ($p < 0.05$)

329 in the urban sites than in the suburban and rural sites
 330 ($\chi^2 = 47.4325$; $df = 2,3$; $p < 0.001$, Fig. 3e).

331 The DCCA triplot showed that there was a clear
 332 separation among the traps along the rural–urban gra-
 333 dient based on the number of individuals of the five most
 334 frequent species. The rural traps differed from the sub-
 335 urban and urban traps, which were more similar to each
 336 other. The rural traps are located on the right part,
 337 whereas the suburban and urban traps on the left part of
 338 the ordination scatter-plot. The suburban and urban
 339 traps separated along the second axis of the ordination
 340 scatter-plot (Fig. 4). Furthermore, the rural sites char-
 341 acterized by higher amounts of decaying wood material
 342 and higher cover of herbs. The suburban sites disposed
 343 of higher relative humidity and cover of leaf litter and
 344 shrubs. The urban sites had higher ground and air
 345 temperature and lower canopy cover. The triplot graph
 346 also demonstrated that *D. concolor* was associated with
 347 the rural sites of higher amounts of decaying wood and
 348 more herbs. *P. alacris* favored the moderate disturbed
 349 suburban sites with higher cover of leaf litter and higher
 350 relative humidity. Three species (*O. praticola*, *T. terri-*
 351 *cola*, and *T. pedestris*) were characteristic to urban sites
 352 with higher ground, air temperature, and lower canopy
 353 cover.

Discussion

355 Our results showed that there were significant effects of
 356 urbanization on ground-dwelling spider assemblages, as
 357 the intensity of disturbance increase from the rural sites
 358 to the urban ones. Besides the four classical hypotheses,
 359 we also studied two novel hypotheses. We pointed out
 360 that the overall species richness increased from the rural
 361 area to the urban one; therefore, this result did not
 362 support the increasing disturbance hypothesis. Richness
 363 of the open-habitat and the generalist species were the
 364 highest in the urban sites, supporting the matrix and
 365 opportunistic species hypotheses. Species richness of the
 366 forest specialist spiders was the highest in the suburban
 367 sampling sites, contradicting the habitat specialist
 368 hypothesis. Our results verified the two new hypotheses,
 369 because the species richness of both the xerophilous and
 370 light-preferring species were the most numerous in the
 371 urban area. Analyzing the abundance of the most fre-
 372 quent spider species supported the matrix species, the
 373 opportunistic species and the habitat specialist hypoth-
 374 esis, too. As the frequent open-habitat and generalist
 375 species were significantly more numerous in the urban
 376 area, while the most abundant forest specialist spider
 377 species were significantly more abundant in the less
 378 disturbed areas (in the rural or in the suburban area).

379 Alaruikka et al. (2002) studied ground-dwelling spi-
 380 ders along a rural–urban forest gradient in Finland, but
 381 they did not find any significant differences in overall
 382 species richness, while Magura et al. (2010b) showed
 383 that the total number of spider species was significantly
 384 higher in the urban area than in the suburban and rural
 385 area in Hungary. Our results, and those of Alaruikka
 386 et al. (2002) and Magura et al. (2010b), showed that the
 387 increasing disturbance hypothesis was not supported;
 388 moreover, we found that the overall species richness
 389 increased significantly from the rural sites to the urban
 390 ones. A possible explanation for the lack of support of
 391 the increasing disturbance hypothesis may be that
 392 because of urbanization the habitat patches are enor-
 393 mously diverse in the urban area. Patches with more
 394 open canopy layer, moderately closed patches, and fully
 395 closed forest patches appear simultaneously in the urban
 396 area. Less and moderately closed patches may be more
 397 suitable for the open-habitat and generalist species. They
 398 can easily colonize these patches, increasing the diversity
 399 in the urban area. Furthermore, in the urban forest
 400 patches, edge-like habitats may appear, which modify
 401 significantly species patterns (Lövei et al. 2006). Several
 402 studies that investigated spiders in forests with different
 403 levels of disturbance found that overall species richness
 404 did not differ significantly among the studied sites, but
 405 the species composition changed along the gradient
 406 (Chen and Tso 2004; Hsieh et al. 2003; Ulrich et al.
 407 2010). The studies of other taxa (for ground beetles:
 408 Magura et al. 2004; for isopods: Hornung et al. 2007) in
 409 Debrecen showed differences from our investigation.
 410 Hornung et al. (2007) did not find significant differences

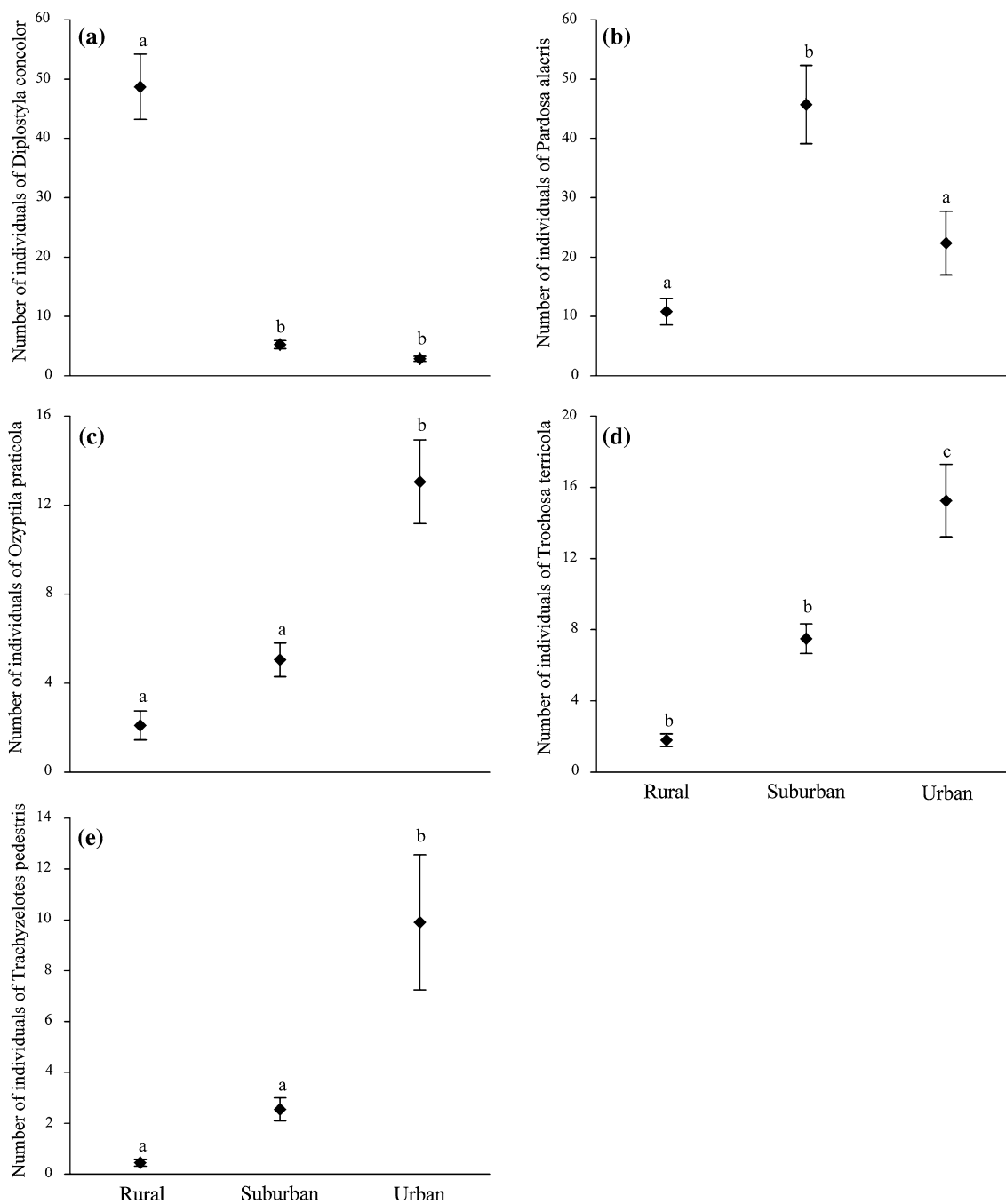


Fig. 3 Average number of individuals of *Diplostyla concolor* (forest species) (a), *Pardosa alacris* (forest species) (b), *Ozyptila praticola* (generalist species) (c), *Trochosa terricola* (generalist species) (d) and *Trachyzelotes pedestris* (open-habitat species) (e) (\pm SE)

along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by Tukey test ($p < 0.05$)

411 in overall isopod species richness along the disturbance
 412 gradient, while Magura et al. (2004) pointed out that the
 413 number of carabid beetle species was significantly higher
 414 in the rural and urban area than in the suburban one.
 415 These results reveal that the different groups of arthro-
 416 pods may respond differently to the urbanization at the
 417 same area.

418 Our results supported the matrix species hypothesis,
 419 as the species richness of the open-habitat species was

420 higher in the urban sampling sites than in the suburban
 421 and urban ones. The urban park differed significantly
 422 from the suburban and rural forested sites, because these
 423 fragments are the most open and the warmest. From the
 424 surrounding matrix, several open-habitat species can
 425 penetrate. The heavily disturbed urban forest patches
 426 have higher air and ground surface temperature; there-
 427 fore, in these sites there are favorable microhabitats
 428 where open-habitat species can survive. Matveinen and

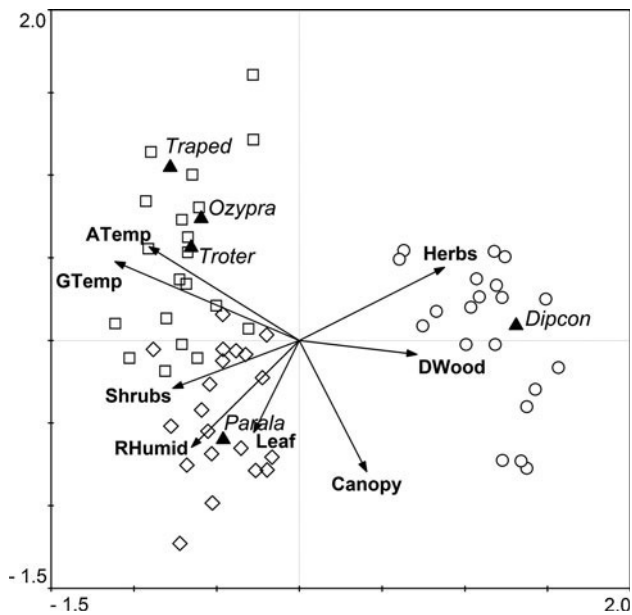


Fig. 4 DCCA for the five frequent spider species where the number of individuals made up at least 5 % of the total catch. Empty symbols represent the pitfall traps (squares urban traps, rhombuses suburban traps, circles rural traps). The arrows denote the increase of the value of the eight environmental variables (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, Canopy cover of canopy layer). Filled triangles and the six-letter abbreviations indicate the species (e.g., Dipcon, *Diplostyla concolor*)

429 Koivula (2008) showed that the most drastic logging
430 methods (clear-cutting and retention felling) increased
431 the abundance of open-habitat spider species in a
432 Finnish boreal forest, as these forest patches became
433 more open. The results of Magura et al. (2008b) were
434 very similar to our results, because the species number of
435 open-habitat carabid beetle was the highest in the urban
436 park in Debrecen.

437 In accordance with the opportunistic species hypothe-
438 sis, the species richness of the generalist species were the
439 highest in the urban sites compared to the suburban and
440 rural ones. Generalist species are able to benefit from the
441 high level of disturbance, and they easily colonize the
442 habitat patches modified by urbanization. The Finnish
443 (Alaruikka et al. 2002) and earlier Hungarian results
444 (Magura et al. 2010b) did not support this prediction,
445 because there was no significant difference in the number
446 of generalist species along the urbanization gradient. The
447 tendency was similar in case of carabid beetles in Deb-
448 recen, as there were no significant differences in the
449 number of generalist species among the differently distur-
450 bled sites (Magura et al. 2008b).

451 In our study, the number of forest specialist spider
452 species was the highest in the suburban habitat, con-
453 tradicting the habitat specialist hypothesis. These spiders
454 prefer the shadier and more humid sites. In the last
455 several years, the rural sites became drier and more

open, therefore the cover of shrubs and the relative 456
humidity was the highest in the suburban area. Thus, it 457
is not surprising that the species richness of the forest 458
spiders was statistically higher in these sites. In the 459
present situation, the extent of the disturbance in the 460
rural and the suburban area may be not so significantly 461
different. Therefore the spatial distribution and the 462
richness of the forest specialist spiders were rather 463
influenced by the environmental conditions (shadier and 464
moister conditions) than by the level of the disturbance. 465

466 The xerophilous species hypothesis predicts that the
467 dominance of xerophilous species would increase from
468 the rural area to the urban one. Our investigation sup-
469 ported this prediction because the number of xerophi-
470 lous species was higher in the urban sites than in the
471 suburban and rural sites. The urban forest fragments
472 were more open than the suburban and rural fragments,
473 therefore the ground surface and air temperature were
474 the highest in the city center. Due to this process, the
475 dominance of the xerophilous species was the highest in
476 the urban habitat type. Hoffmann and Andersen (2003)
477 pointed out that the hot climate specialist ant species
478 preferred the open habitats, as the temperature is higher
479 in these sites. Menke et al. (2011) assessed that the native
480 ant species that prefer the warmer and drier sites oc-
481 curred in a higher number in the open habitats.

482 Our result corroborated the light-preferring species
483 hypothesis, as the species richness of light-preferring
484 species increased from the rural sites to the urban ones.
485 The species richness was the highest in the urban park.
486 The forest fragments of the urban area were more open;
487 this resulted in a higher light value than in the suburban
488 and urban forests. In the urban forest patches with
489 lighter conditions, light-preferring species found their
490 favorable microhabitats and they can also colonize here.
491 Lütolf et al. (2009), studying butterflies, also showed
492 that dry grassland butterfly species favored the forest
493 patches with more open canopy, and their abundance
494 decreased as the canopy closure increased.

495 Our results showed that urbanization affected the
496 distribution of all frequent species. DCCA pointed out
497 that the rural sites differed from the suburban and urban
498 sites, while the suburban and urban sites were quite
499 similar to each other. Each of the frequent forest
500 specialist species (*D. concolor* and *P. alacris*) responded
501 significantly to urbanization. *D. concolor* occurred in
502 lower number in the urban and suburban sites than
503 in the rural sites, while *P. alacris* was the most frequent
504 in the suburban area. *D. concolor* occurred in high
505 number only in the rural sites with higher amounts of
506 decaying woods and more herbs. *P. alacris* prefers the
507 relatively dry and shady sites with high amount of leaf
508 litter (Vlček 1995). The suburban habitat was the
509 shadiest and it had the thickest leaf litter among the
510 studied sites. The number of individuals of the two
511 generalist species (*O. praticola* and *T. terricola*) (Buchar
512 and Ruzicka 2002) increased continuously from the
513 rural areas to the urban ones. The number of individuals
514 of *T. pedestris*, which is a typical open-habitat species 514

515 (Buchar and Ruzicka 2002) increased from the rural
516 sites to the urban ones, too. It seems that these species
517 prefer the more open and drier sites with higher air and
518 ground surface temperature; therefore, they occurred in
519 the highest number in the urban habitat type.

520 Our result showed that the overall species richness is
521 not suitable indicator of human disturbance along the
522 urbanization gradient. To investigate the urbanization
523 processes based on overall diversity, the consequence
524 would be that the urbanization is useful for the spider
525 assemblages, as the species richness increased continu-
526 ously from the rural sampling sites to the urban ones.
527 The reason for this is that the number of the less
528 disturbance-sensitive open-habitat and generalist species
529 increased towards the urban habitat because these
530 spiders could penetrate from the matrix habitats. The
531 number of xerophilous and light-preferring species also
532 increased from the rural sites to the urban sites, as the
533 urban forest patches are more open than the suburban
534 and rural ones. The forest specialist spider species
535 occurred in higher number only in the less disturbed
536 contiguous rural and/or suburban forest patches. The
537 population size of these species decreased towards
538 the more isolated urban patches because these patches
539 are too small for the spiders to be able to settle down
540 permanently. Thus, these species can survive and repro-
541 duce with major chance in the natural forest patches.

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