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Abstract

Effects of urbanization on rove beetles were studied along a rural-suburban-urban forested gradient characterized by increasing human disturbance in and around Debrecen city (Hungary). Three classical and six novel hypotheses regarding the response of species to urbanization were tested. We found that overall species richness increased significantly with decreasing urbanization (i) as it is predicted by the increasing disturbance hypothesis, and contradicting (ii) the intermediate disturbance hypothesis that predicts the highest species richness in the moderately disturbed suburban area. (iii) The number of forest-associated species was significantly lower in the urban area compared to suburban and rural areas, as predicted by the habitat specialist hypothesis. All of the proposed novel hypotheses are about habitat alteration caused by the urbanization were corroborated. The (iv) richness of hygrophilous species was the highest in the rural area (hygrophilous species hypothesis), while (v) the number of thermophilous species was higher in the urban area (thermophilous species hypothesis). The richness of species directly or indirectly feeding on decaying organic materials ((vi) saprophilous, (vii) phytodetriticol, (viii) myrmecophilous, (ix) mycetophilous species hypotheses) was also highest in the rural area compared to the urban one. We stress that overall species richness is not the most appropriate indicator of the impacts of urbanization and accompanying disturbance on these beetles. Instead, habitat affinity and ecological traits of the species give more information about what habitat properties and environmental variables change drastically during urbanization.

Keywords (separated by '-') Diversity - Disturbance - Forest specialist species - GlobeNet - Habitat affinity - Staphilinids

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2 **Rove beetles respond heterogeneously to urbanization**

3 **Tibor Magura · Dávid Nagy · Béla Tóthmérész**

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36

Keywords Diversity · Disturbance · Forest specialist 37
species · GlobeNet · Habitat affinity · Staphilinids 38

Introduction 39

The process of urbanization includes spatial expansion, 40
population growth in urban settlements and the stretch 41
of the urban life's form. Currently, urbanization and its 42
accompanying environmental impacts are a most important 43
challenge for humanity. Urbanization radically alters 44
native environments and forms new, artificial habitats. 45
Nowadays, 3.5 billion people on Earth are living in cities. 46
Globally, urban populations are projected to increase to 6.4 47
billion in 2050 (United Nations 2009). Thus, a better 48
understanding of the relationship between the urbanization 49
and ecosystem functioning is important for developing 50
strategies to mitigate unwanted environmental impacts of 51
urbanization for humans. 52

Urban landscapes typically consist of densely built and 53
highly developed urban core areas surrounded by suburban 54
and rural areas characterized by decreasing intensity of 55
development and increasing naturalness. Rural-urban 56

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57 gradients have this general appearance all over the world,
 58 although the exact type of ecosystems involved differs
 59 (McDonnell et al. 1997; Niemelä 1999; Niemelä et al.
 60 2000). From rural areas to urban centers the number and
 61 the density of human inhabitants increases, along with road
 62 density, area covered by artificially created surfaces, and
 63 air and soil pollution. Nitrogen (N) deposition, heavy metal
 64 content of soil and plants, and decomposition rate are
 65 all higher in urban areas than their rural surroundings
 66 (Carreiro and Tripler 2005; Simon et al. 2011a, b, 2012a, b,
 67 2013a, b). In addition, ecosystem processes, litter decom-
 68 position and soil N dynamics vary significantly along the
 69 urban–rural gradient (McDonnell et al. 1997). As habitat is
 70 lost to urban development, the habitat that supports the
 71 biota becomes increasingly fragmented into more numer-
 72 ous but smaller remnant patches (Collins et al. 2000). In
 73 addition to buildings and sealed surfaces, natural habitat for
 74 native species is also lost to managed areas (residential,
 75 commercial, and other regularly maintained green spaces),
 76 ruderal spaces (empty lots, abandoned farmland, and other
 77 green space that is cleared but not managed) and remnant
 78 patches of native habitats invaded non-native plants
 79 (Deutschewitz et al. 2003). As a consequence of frag-
 80 mentation, connection between the natural habitat patches
 81 is often minimal in the urban areas and this appears to
 82 reduce species richness (number of species). There are,
 83 however, many factors that can affect the rate and consis-
 84 tency of species loss and gain along the gradient, so
 85 empirical studies are crucial in measuring urban impacts
 86 (McKinney 2008).

87 A number of anthropogenic activities, such as urbani-
 88 zation, farming and forestry create modified land types that
 89 exhibit similar patterns throughout the world (Paillet et al.
 90 2009). To assess the general trends of urbanization on
 91 arthropods, there is an urgent need to investigate responses
 92 of a range of taxa along the rural–urban gradient. The
 93 family of rove beetles (*Coleoptera: Staphylinidae*) is one
 94 of the largest families of beetles, with about 32,000 known
 95 species (Newton 1990). Rove beetles are distributed
 96 worldwide and are found in practically all types of ter-
 97 restrial ecosystems. About half of rove beetle species are
 98 found in litter, and they are among the most common and
 99 ecologically important insect components of the soil fauna.
 100 Taxonomy, habitat requirements and ecological traits of
 101 European rove beetle species are reasonably well known
 102 (Boháč 1999). They are fairly easy to collect, and being
 103 mobile and relatively short-lived, they adjust rapidly to
 104 changes in abiotic and biotic environmental variables and
 105 human disturbances. For all of these reasons they have
 106 excellent potential as monitoring group (Boháč 1999;
 107 Klimaszewski and Langor 2009). In spite of this, staphy-
 108 lylinids are used less often than other beetles in indicator
 109 studies.

Urbanization is usually considered as a form of environ- 110
 mental disturbance (Rebele 1994). There are several hypoth- 111
 eses to explain the effects of disturbance on biotic 112
 communities. Most of these hypotheses make predictions 113
 about effects on overall species richness. However, species 114
 with different ecological traits respond variously to natural 115
 and anthropogenic disturbances (Lövei et al. 2006; Magura 116
 et al. 2010a). Therefore, it is important to investigate the 117
 groups of species with different ecological traits separately. 118
 The aim of the present study was to investigate the effects of 119
 urbanization on rove beetles, a beetle taxon that has not yet 120
 been studied in the frame of the international Globenet project. 121
 In particular, we tested three classical and six novel hypoth- 122
 eses regarding the response of species to urbanization: (i) The 123
 increasing disturbance hypothesis claims that species richness 124
 monotonously decreases with the increasing levels of distur- 125
 bance (Gray 1989). (ii) The intermediate disturbance 126
 hypothesis predicts that species richness is the highest in the 127
 moderately disturbed suburban area (Connell 1978). (iii) The 128
 habitat specialist hypothesis predicts that the species richness 129
 of forest-associated species decreases with the increasing 130
 disturbance (Magura et al. 2004). Our novel hypotheses are 131
 related to the habitat alteration caused by the urbanization. 132
 Urbanization radically alters the original habitat, the urban 133
 forest patches become more open, drier and warmer compared 134
 to the suburban and rural ones. Therefore, (iv) the richness of 135
 hygrophilous species should be the highest in the rural area 136
 (hygrophilous species hypothesis), while (v) the richness of 137
 thermophilous species should be the highest in the urban area 138
 (thermophilous species hypothesis). In the urban area and 139
 somewhat in the suburban area decaying organic material are 140
 usually removed during the management of forest patches. 141
 Therefore, (vi) the richness of saprophilous species (saprophil- 142
 ous species hypothesis), and (vii) the richness of species 143
 living in decaying plant debris (phytodetriticol species 144
 hypothesis) should be the highest in the less modified rural 145
 area. As ants and fungi prefer habitats with dense dead and 146
 decaying organic material, therefore (viii) the richness of 147
 myrmecophilous species (myrmecophilous species hypothe- 148
 sis), and (ix) the richness of species preferring the fungi 149
 (mycetophilous species hypothesis) also should be the highest 150
 in the rural area. 151

152 Methods

153 Study area

The study area was in and around Debrecen city (47°32'N; 154
 21°38'E), the second largest city of Hungary (208,000 inhab- 155
 itants in 2011), located in the eastern plains area near the 156
 country's eastern border (Magura et al. 2004). Three forested 157
 areas, representing rural, suburban and urban habitats, were 158

159 selected along an rural–urban gradient running from the adja- 208
 160 cent Nagyerdő Forest Reserve into the city. These areas had 209
 161 formerly (a few hundred years ago) been part of a continuous 210
 162 aged (older than 100 years) native *Convallario-Quercetum* 211
 163 forest association. All sampled areas were larger than 6 ha 212
 164 (urban: 6–10 ha, suburban: 6–8 ha, rural: 6–12 ha). Intensity of 213
 165 urbanization was characterized by the ratio of the anthropo- 214
 166 genically modified areas (buildings, roads and asphalt covered 215
 167 paths) to natural habitats, as calculated in a GIS (ArcGIS) based 216
 168 on an aerial photograph made in 2009. In the rural area none of 217
 169 the land was covered by built-up surfaces. In contrast, on 218
 170 average 30 % of the suburban area was modified, and >60 % of 219
 171 the surface area in the urban area was built up. In addition, the 220
 172 intensity of the habitat maintenance operations also differed 221
 173 among the three categories of land. In the rural area there were 222
 174 only occasional low-intensity forestry management operations. 223
 175 In habitat management of suburban forest, however, fallen trees 224
 176 and branches were removed, although understory vegetation 225
 177 was largely undisturbed. The urban forest patches were largely 226
 178 park-like; fallen trees and branches were regularly removed, the 227
 179 shrub layer was thinned and highly disturbed, and grass 228
 180 between urban forest patches was frequently mowed and 229
 181 removed. The distance between the sampling areas (rural, 230
 182 suburban and urban) was 1–3 km. 231

183 Sampling design 232

184 Two sites, at least 100 m apart, were selected within each 233
 185 of the three sampling areas. Rove beetles were collected 234
 186 using ten unbaited pitfall traps placed randomly at least 235
 187 10 m apart from each other at each site. This resulted in a 236
 188 total of 60, 10 traps in two replicated forest stand at each 237
 189 stage of the gradient. All traps were at least 50 m from the 238
 190 nearest forest edge, in order to avoid edge effects (Molnár 239
 191 et al. 2001). Pitfall traps were plastic cups (diameter 240
 192 65 mm) containing about 100 ml of 4 % formaldehyde as a 241
 193 killing-preserving solution. Traps were covered by a square 242
 194 (20 × 20 cm) of fiberboard minimize accumulation of litter 243
 195 and rain. Rove beetles species were collected fortnightly 244
 196 from the end of April to the end of October 2009. 245

197 Data analyses 246

198 Catches were pooled for the year for analysis. We used nested 247
 199 (sites within sampling areas) GLMs to test differences in the 248
 200 overall rove beetle species richness and the species richness of 249
 201 the rove beetles with different ecological traits among the 250
 202 three areas and among the 6 sites. The response variable 251
 203 (species richness) was a Poisson distribution (with log link 252
 204 function), assuming that the mean and variance of the data 253
 205 were equal. However, because the variance is expected to be 254
 206 larger than the mean overdispersion was also incorporated into 255
 207 the model using quasi-Poisson distribution (Zuur et al. 2009). 256

When the overall GLMs revealed a significant difference 208
 between the means, an LSD test was performed for multiple 209
 comparisons among means. Ecological traits of rove beetles 210
 (forest, hygrophilous, thermophilous, saprophilous, phytodet- 211
 ritorial, mycetophilous, and myrmecophilous species) were 212
 obtained from the literature (Irmler and Gürlich 2007; Koch 213
 1989; Stan 2008; Table 1). Composition of rove beetle 214
 assemblages along the gradient was compared at trap level 215
 using nonmetric multidimensional scaling based on presence- 216
 absence data using the Rogers-Tanimoto index of similarity 217
 (Legendre and Legendre 1998). 218

219 Results 220

Altogether 3105 individuals belonging to 84 species were 220
 trapped during the study (Table 1). This included 1,229 221
 from 60 species in the rural area, 1,204 individuals of 50 222
 species in suburban forest and 672 individuals of 49 spe- 223
 cies in urban sites. The most numerous species was 224
Omalium caesum; 761 individuals were trapped comprising 225
 24.5 % of the total catch and it was the most abundant 226
 species in all three sampling areas (Table 1). 227

The overall species number decreased significantly from 228
 the rural sites to the urban ones ($\chi^2 = 75.7$; $df = 2, 3$; 229
 $p < 0.0001$, Fig. 1a). Number of forest-associated species 230
 was significantly lower in the urban than in either the 231
 suburban or rural areas ($\chi^2 = 37.0$; $df = 2, 3$; $p < 0.0001$, 232
 Fig. 1b). Number of species that appear to respond to 233
 environmental conditions based on their lifestyle or habitat 234
 use varied significantly along the gradient. For example, 235
 number of hygrophilous species decreased significantly 236
 from the rural area towards the urban forest ($\chi^2 = 60.0$; 237
 $df = 2, 3$; $p < 0.0001$, Fig. 2a), while number of ther- 238
 mophilous species was significantly higher in the urban 239
 area compared to the suburban and rural forests ($\chi^2 = 7.7$; 240
 $df = 2, 3$; $p = 0.0214$, Fig. 2b). Number of species relat- 241
 ing directly or indirectly to decaying organic materials also 242
 changed significantly along the gradient. Numbers of 243
 saprophilous, phytodetriticol species and myrmecophilous 244
 species were significantly highest in the rural area ($\chi^2 =$ 245
 16.47 ; $df = 2, 3$; $p = 0.0003$; $\chi^2 = 45.81$; $df = 2, 3$; $p <$ 246
 0.0001 ; $\chi^2 = 39.31$; $df = 2, 3$; $p < 0.0001$, respectively; 247
 Fig. 3a-c). The number of mycetophilous species did not 248
 differ between rural and suburban areas but was signifi- 249
 cantly higher than in the urban forest ($\chi^2 = 19.4$; 250
 $df = 2, 3$; $p < 0.0001$, Fig. 3d). 251

The rove beetle assemblages of the rural, suburban and 252
 urban areas were clearly separated from each other by the 253
 ordination (Fig. 4). Assemblages from rural forests were 254
 separated from those of suburban and urban habitats along 255
 the first axis. Clearly, composition of the rove beetle 256

Table 1 Habitat affinity, ecological traits and the trapped number of individuals of the rove beetle species along the urbanization gradient

Species	Habitat affinity and ecological traits	Rural	Suburban	Urban
<i>Abemus chloropterus</i>	For, Hyg	62	115	28
<i>Aleochara erythroptera</i>	Hyg, Myc, Phy	6	1	0
<i>Anotylus rugosus</i>	Hyg, Myc, Phy, Sap	5	1	1
<i>Anthobium atrocephalum</i>	Phy	14	16	11
<i>Astenus immaculatus</i>	Hyg, Phy	1	0	3
<i>Atheta gagatina</i>	Myc, Phy	1	1	9
<i>Atheta sodalis</i>	For, Myc, Phy	0	4	1
<i>Atheta triangulum</i>	Myc, Phy, Sap	4	2	4
<i>Bolitochara bella</i>	Myc	1	0	0
<i>Byraxis curtisii orientalis</i>	Phy	1	2	0
<i>Dropephylla ioptera</i>	For, Hyg, Myc,	0	1	0
<i>Drusilla canaliculata</i>	Phy	1	0	0
<i>Enalodroma hepatica</i>	For	1	0	1
<i>Gabrius osseticus</i>	Hyg, Phy	89	11	5
<i>Geostiba circellaris</i>	Hyg, Myc	3	2	3
<i>Gyrophypnus angustatus</i>	Hyg, Phy	24	58	81
<i>Habrocerus capillaricornis</i>	Myc, Phy	2	3	1
<i>Heterothops dissimilis</i>	Phy	7	1	2
<i>Ilyobates bennetti</i>	Hyg, Phy	13	15	0
<i>Ilyobates nigricollis</i>	For, Hyg, Phy	0	4	1
<i>Lathrobium brunnipes</i>	Hyg, Phy	4	0	0
<i>Lathrobium geminum</i>	Hyg, Phy	14	0	1
<i>Liogluta granigera</i>	Myc, Phy	4	0	0
<i>Liogluta longiuscula</i>	Hyg, Myc, Phy	90	49	20
<i>Mocyta fungi</i>	Hyg, Myc, Phy	6	1	0
<i>Mocyta orbata</i>	Hyg, Myc, Phy	3	1	0
<i>Mycetoporus eppelsheimianus</i>	For, Myc	1	0	2
<i>Mycetoporus erichsonianus</i>	Myc	0	1	0
<i>Mycetoporus forticornis</i>	For, Hyg	0	1	0
<i>Mycetoporus lepidus</i>	Phy	0	4	0
<i>Mycetota laticollis</i>	Phy	0	0	1
<i>Ocalea badia</i>	Hyg, Phy	2	0	0
<i>Ocypus brunnipes</i>	For, Hyg, Myc, Phy	0	2	6
<i>Ocypus mus</i>	For, Myc	7	40	0
<i>Ocypus nitens</i>	For, Hyg	21	43	1
<i>Oligota pusillima</i>	Myc, Phy	0	1	0
<i>Omalium caesum</i>	Hyg, Myc, Phy	257	277	227
<i>Omalium rivulare</i>	Hyg, Myc, Phy, Sap	142	156	90
<i>Ontholestes haroldi</i>	Phy	73	231	50
<i>Othius punctulatus</i>	For, Phy	16	4	0
<i>Oxypoda abdominalis</i>	Myc, Phy	2	8	0
<i>Oxypoda acuminata</i>	Hyg, Myc, Phy	87	13	22
<i>Oxypoda longipes</i>	Phy	0	1	0
<i>Oxypoda opaca</i>	Myc, Phy	5	0	0
<i>Oxypoda vittata</i>	Myr	30	5	1
<i>Paederus balcanicus</i>	Hyg	0	0	1
<i>Pella laticollis</i>	Myr	10	0	0
<i>Pella lugens</i>	Myr	39	4	1

Table 1 continued

Species	Habitat affinity and ecological traits	Rural	Suburban	Urban
<i>Pella ruficollis</i>	For, Myr	7	0	0
<i>Philonthus carbonarius</i>	Phy	1	0	0
<i>Philonthus intermedius</i>	Phy, Sap	1	0	0
<i>Philonthus laminatus</i>	Myc, Phy, Sap	4	0	0
<i>Philonthus succicola</i>	Myc, Phy	1	0	0
<i>Philonthus tenuicornis</i>	Myc, Phy	0	1	0
<i>Phyllodrepa floralis</i>	Phy	1	0	0
<i>Platydracus fulvipes</i>	For, Hyg	5	14	4
<i>Platystethus cornutus</i>	Hyg	0	1	0
<i>Pselaphus heisei</i>	Phy	0	1	0
<i>Quedius curtippennis</i>	Hyg, Phy	18	4	1
<i>Quedius fuliginosus</i>	Hyg, Phy	2	0	1
<i>Quedius limbatus</i>	For, Hyg, Myc	2	5	0
<i>Quedius longicornis</i>	Hyg	0	0	2
<i>Quedius molochinus</i>	Hyg, Phy	3	0	0
<i>Quedius ochripennis</i>	Phy	0	0	1
<i>Quedius scintillans</i>	Phy	0	1	2
<i>Rugilus rufipes</i>	Hyg, Phy	26	78	24
<i>Sepedophilus marshami</i>	Myc, Phy	2	2	4
<i>Sepedophilus obtusus</i>	Phy, The	0	1	2
<i>Staphylinus erythropterus</i>	For, Hyg	9	0	1
<i>Stenus humilis</i>	Hyg, Phy	2	0	9
<i>Stenus ludyi</i>	For, Hyg, Phy	3	0	2
<i>Stenus ochropus</i>	Hyg, The	0	0	1
<i>Sunius fallax</i>	Phy	0	0	4
<i>Tachinus rufipes</i>	Myc, Sap	10	0	0
<i>Tachyporus formosus</i>	For, Hyg	3	0	0
<i>Tachyporus hypnorum</i>	Hyg, Myc, Phy	0	2	1
<i>Tachyporus nitidulus</i>	Myc, Phy	0	1	0
<i>Tasgius melanarius</i>	Phy	21	5	2
<i>Tasgius morsitans</i>	Phy, The	5	6	16
<i>Tasgius winkleri</i>	Phy	0	0	2
<i>Xantholinus dvoraki</i>	Phy	0	0	1
<i>Xantholinus linearis</i>	Phy	1	0	2
<i>Xantholinus tricolor</i>	For, Phy	53	3	15
<i>Zyras haworthi</i>	Myr, The	1	0	1

For forest species, Hyg hygrophilous species, The thermophilous species, Sap saprophilous species, Phy phytodetriticol species, Myc mycetophilous species, Myr myrmecophilous species

257 assemblages of suburban and urban areas was more similar
258 to each other than to the assemblages of the rural area.

259 **Discussion**

260 Overall species richness

261 Our findings did not support the intermediate disturbance
262 hypothesis, as the overall species richness of the rove
263 beetles was not highest in the moderately disturbed sub-
264 urban area. The Romanian research examining ground

beetles (Tóthmérés et al. 2011) were the only ones of the 265
published Globenet studies that supported the intermediate 266
disturbance hypothesis. The other studies, similarly to our 267
results, disprove this hypothesis (for ground beetles: 268
Alaruikka et al. 2002; Niemelä et al. 2002; Magura et al. 269
2004, 2005; Gaublomme et al. 2008; for isopods: Magura 270
et al. 2008a; for spiders: Alaruikka et al. 2002; Magura 271
et al. 2010a). Thus, most of the published results con- 272
tradicted the prediction of the intermediate disturbance 273
hypothesis. Obvious reasons for the failure of the inter- 274
mediate disturbance hypothesis may be due to the rather 275
problematic quantification of the type, frequency and size 276

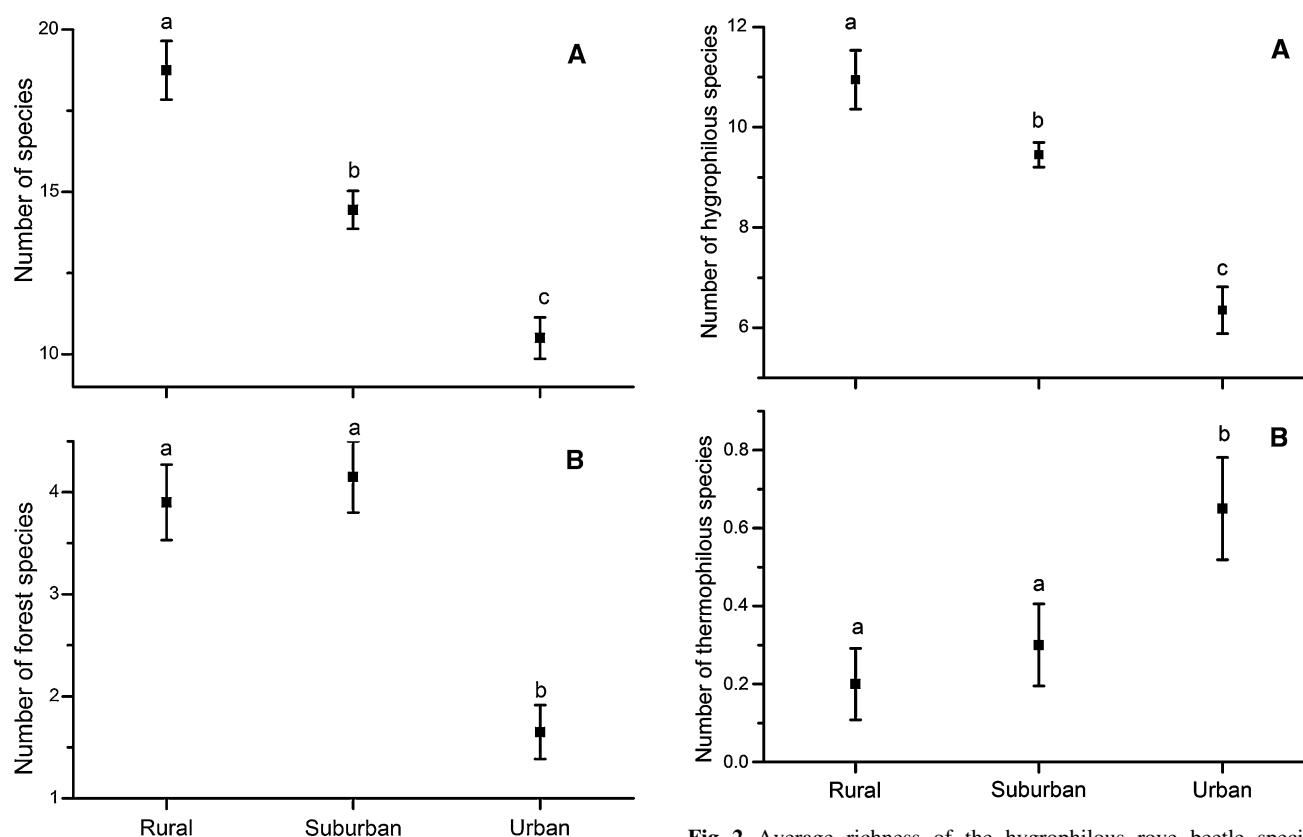


Fig. 1 Average richness of the overall rove beetle species (a) and the forest-associated rove beetle species (b) (\pm SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by LSD test ($p < 0.05$)

Fig. 2 Average richness of the hygrophilous rove beetle species (a) and the thermophilous rove beetle species (b) (\pm SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by LSD test ($p < 0.05$)

277 of the disturbance events along the rural-suburban-urban
278 gradients. Therefore, it is hard to arrange precisely the
279 study areas along a disturbance continuum.

280 The richness of rove beetles increased significantly with
281 decreasing urbanization. This is similar to results with
282 ground beetles for which similar patterns have been reported
283 from Belgium, Canada, Finland, Japan and the United
284 Kingdom (Niemelä et al. 2002; Gaublomme et al. 2008).
285 However, this pattern has not been consistently found. In
286 studies of isopods (Hornung et al. 2007) and ground-dwell-
287 ing spiders from Hungary (Magura et al. 2010a; Horváth
288 et al. 2012), and ground-beetles from Bulgaria and Denmark
289 (Niemelä et al. 2002; Elek and Lövei 2007) there was no
290 decreasing relationship between urbanization and species
291 diversity. Urbanization generates several forms of distur-
292 bance, including loss, alteration, fragmentation and isolation
293 of the original habitats, changes in temperature, moisture,
294 edaphic conditions and air pollution (Niemelä 1999).
295 Moreover, more frequent disturbance seems to homogenize
296 urban forests patches, perhaps eliminating microhabitats
297 favored by some species. Disturbances in urban and subur-
298 ban areas are continuous, directed and long lasting, leading
299 to decreased diversity (Niemelä et al. 2002).

Clearly, results from studies of overall species richness 300
along the rural-urban gradient are inconsistent. For that 301
reason it is likely that overall species richness itself is not 302
easily interpreted as an indicator of the impacts of urban- 303
ization and accompanying disturbance. Some groups of 304
species may decline with habitat loss (e.g., habitat spe- 305
cialists), while other species may increase in number 306
(e.g., opportunistic species) because of the disturbance and 307
habitat alteration caused by urbanization. Thus, impacts on 308
species with different habitat affinity should be analyzed 309
separately to better interpret the effects of urbanization. 310

Species richness of forest-associated rove beetles 311

The number of forest associated rove beetle species was 312
significantly lower in the heavily disturbed urban area 313
compared to moderately and minimally disturbed suburban 314
and rural area. In Hungary the abundance of forest spe- 315
cialist terrestrial isopod species also decreased significantly 316
from the rural area toward urban habitats (Magura et al. 317
2008a). No significant difference in the number of forest 318
specialist spider species was reported across a rural-urban 319
gradient in Finland, while in Hungary the number of forest 320
specialist spiders was significantly highest in the rural area 321

Fig. 3 Average richness of the saprophilous rove beetle species (a), the phytodetriticol rove beetle species (b), the myrmecophilous rove beetle species (c), and the mycetophilous rove beetle species (d) (\pm SE) along the studied urbanization gradient for the pitfall traps. Different letters indicate significant differences by LSD test ($p < 0.05$)

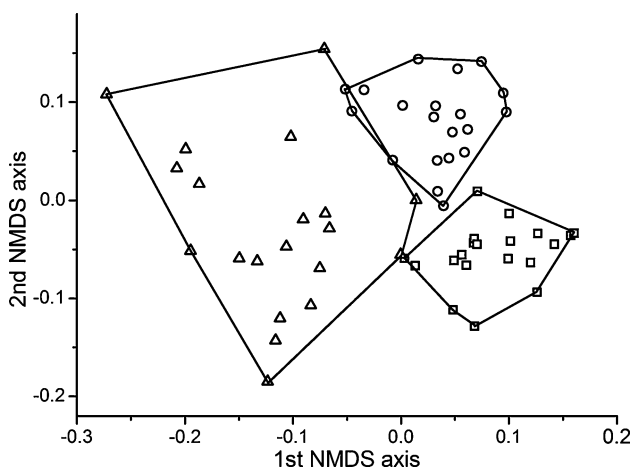
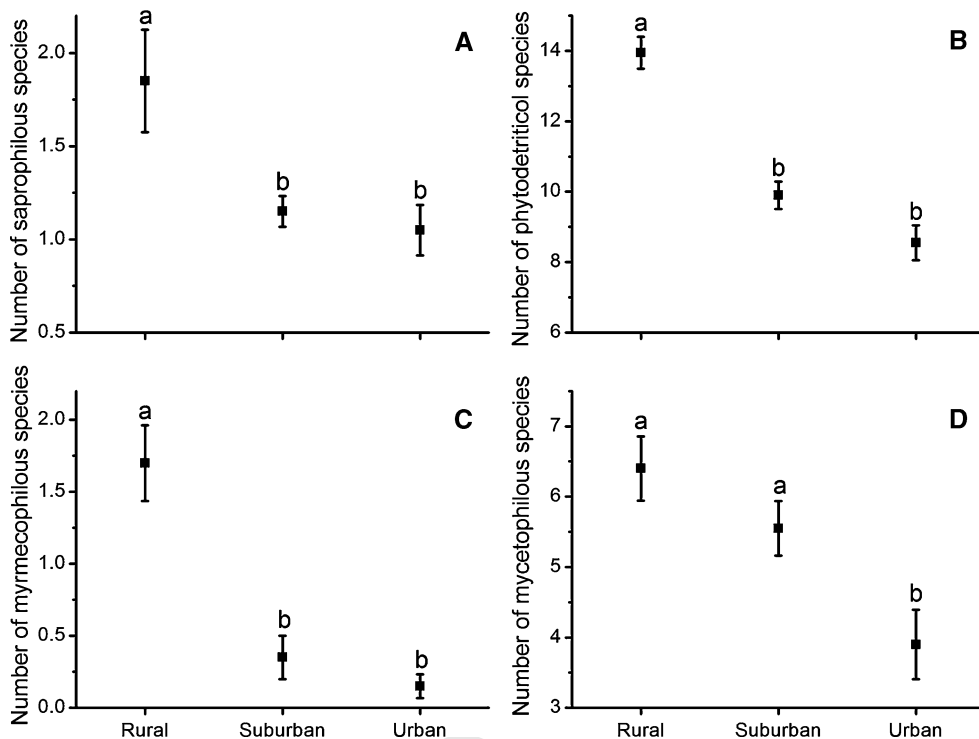


Fig. 4 Ordination (nonmetric multidimensional scaling using the Rogers-Tanimoto index of similarity) of the rove beetle assemblages along the studied rural–urban gradient (unfilled triangles: rural traps, unfilled circles: suburban traps, and unfilled squares: urban traps)

(Magura et al. 2010a). In general it appears that habitat modification associated with urbanization exerts a strong effect upon forest specialist species even in residual forest patches (Niemelä and Kotze 2009; Magura et al. 2010b). Forest specialist species require a particular kind of environmental heterogeneity associated with provision of favorable microclimate, dead and decaying trees, and significant cover of leaf litter, shrubs and herbs, as in an undisturbed forest habitat (Desender et al. 1999). Urbanization appears to eliminate favorable microsities for forest specialist species and thus contributes to the decline of

specialist species' richness in the assemblage. Others have demonstrated that rove beetles are especially sensitive to modification of forested habitat (Boháč 1999; Pohl et al. 2007, 2008; Klimaszewski and Langor 2009), and the proportion of forest specialist staphylinid species decreased, as in the present study, with increasing urbanization in Berlin (Deichsel 2006).

Richness of species indicating habitat alteration

Urbanization drastically modifies the original habitats (McKinney 2008), and in our study the nature of some of these changes was underscored by responses of sensitive species. For example, number of hygrophilous species was highest in the rural area, while the number of thermophilous species was highest in the urban area. The number of the species associated with decaying organic materials (saprophilous species, phytodetriticol species, myrmecophilous species and mycetophilous species) was also highest in the rural area and reached its lowest value in urban habitats. It seems that the fauna responded to increasing dryness and a general reduction in forest floor organic matter on the urban end of the gradient.

The urban forest studied here is considerably fragmented by paved footpaths, increasing edge habitat within the forest patches. This fragmentation together with cutting of the shrub layer, allows sunlight to penetrate more deeply, making urban forest patches drier and warmer (McDonnell et al. 1997). These features of urban patches support survival and/or immigration of open-habitat species that do best under

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361 lighter, warmer and drier conditions. Similar findings have
362 been published for terrestrial isopods (Magura et al. 2008a),
363 ants (Vepsäläinen et al. 2008), ground dwelling spiders
364 (Magura et al. 2010a), ground beetles (Magura et al. 2004,
365 2008b; Tóthmérész et al. 2011), and weevils (Germann et al.
366 2008), suggesting that this situation applies quite generally to
367 invertebrates in urban forest patches.

368 In both urban and suburban areas dead and decaying
369 organic materials are commonly removed from forest pat-
370 ches as part of the management regime. Intensity of this
371 sort of habitat management will be generally highest in
372 urban areas, and in our study, it certainly decreased through
373 suburban to rural areas. Decaying wood material provides
374 favorable microclimate, shelter against predators, and sites
375 suitable for feeding, aestivation, hibernation, overwinter-
376 ing, egg and larval development and thus, the number of
377 the saprophilous rove beetle species decreased along the
378 rural–urban gradient. Similarly to our finding, Vepsäläinen
379 et al. (2008) reported that in urban environments ant spe-
380 cies dependent on dead wood were very rare. Similar trend
381 was reported for spiders as forest species requiring pres-
382 ence of dead and decaying wood materials were more
383 species rich in the rural sites characterized by higher
384 amounts of decaying woods (Magura et al. 2010a).

385 Intensity of urbanization is a function of disturbance and
386 the structural simplification of remaining habitat by man-
387 agement practices that remove not only the dead woody
388 and herbaceous material, but the living trees, shrubs and
389 herbs. These practices decrease the habitat quality of
390 remaining habitats (McKinney 2008). In the present study,
391 reductions in coarse woody material and litter doubtlessly
392 were associated with decreasing of the richness of species
393 using decaying plant debris as habitat (phytodetriticol
394 species). Reductions in plant debris are also harmful for
395 rove beetle larvae. As they are soil bound and less mobile
396 than adults (Bohác 1999), disturbance of the litter and soil
397 are important in determining their survival and thus adult
398 population size. Together with similar findings for terres-
399 trial isopods and millipedes (Riedel et al. 2009) and ants
400 (Savitha et al. 2008) our results suggest that dense decaying
401 plant debris and litter promote the establishment and
402 maintenance of species rich assemblages.

403 Myrmecophilous staphylinids are specialized predators
404 that eat ants or saprophages living on waste in or near ant
405 nests (Bohác 1999). Lessard and Buddle (2005) and Ve-
406 psäläinen et al. (2008) reported decreased ant species
407 richness in urban areas relative to surrounding rural areas,
408 and that the decline varied directly with the degree of the
409 urbanization. Vepsäläinen et al. (2008) also reported that
410 ant species dependent on dead wood were rare or absent in
411 urban areas that they studied. Therefore, significant
412 impoverishment of the myrmecophilous rove beetle species
413 in the urban forest patches was expected. The occurrence of

414 aggressive, dominant and competitively dominant non-
415 native species in urban areas could negatively affect not
416 only the other ant species, but also the other ground-
417 dwelling arthropods (Lessard and Buddle 2005).

418 Mycetophilous rove beetles live in or near fungi (Bohác
419 1999). Fungi are sensitive to environmental changes,
420 specialized in substrate requirements, and depend on
421 decomposing organic plant material as their living sub-
422 strate (Rayner and Boddy 1988). Thus, urbanization is
423 associated with decreases in abundance and species rich-
424 ness in urban areas (McDonnell et al. 1997). In conse-
425 quence of the impoverishment of fungi at the urban forest
426 patches, our hypothesis assumed significant decrease of the
427 mycetophilous rove beetle species along the rural–urban
428 gradient. Earlier results also showed that urbanization
429 negatively affected both the fungivorous microinvertebrates
430 (nematods, microarthropods) and the fungi. Moreover, the
431 larvae of the rove beetles are more sensitive to air pollution
432 (Bohác 1999), so damage of the larvae could negatively
433 affect the abundance and species richness of imagoes.

434 Conclusions

435 Our results show that urbanization had a strong effect on rove
436 beetles, with their overall species richness decreasing sig-
437 nificantly with urbanization. Thus, this group, although not
438 frequently used as such, are reliable indicators of urbaniza-
439 tion. Species composition of rove beetle assemblages chan-
440 ged remarkably along the studied rural-suburban-urban
441 gradient, something that likely reflects disproportionate
442 effects on species associated with organic matter and the
443 degree of openness in forest habitats. We conclude that
444 overall species richness is not a sufficient indicator of
445 urbanization and its accompanying disturbance because it
446 does not include an understanding of these disproportionate
447 effects. Therefore, species with different habitat affinity
448 should be analyzed separately to evaluate the real effects of
449 urbanization. In this way we showed, that in accordance with
450 the habitat specialist hypothesis, the number of forest-asso-
451 ciated rove beetle species was significantly lower in the
452 heavily disturbed and altered urban area compared to the
453 suburban and rural area. Beside the habitat affinity of the
454 species, the ecological traits of the species are also important.
455 Namely, species with different ecological traits may also
456 response variously to the urbanization and the accompanying
457 processes. Thus, ecological traits of the species should be
458 considered to detect accurately those environmental vari-
459 ables that changed drastically during the urbanization.

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