

1 Does urbanisation decrease diversity in ground beetle (Carabidae)
2 assemblages?

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22 Running title: Urbanisation and carabid diversity

23

24 **ABSTRACT**

25

26 **Aim** We tested whether urbanisation has similar effects on biodiversity in different
27 locations, comparing the responses of ground beetle (Coleoptera, Carabidae)
28 assemblages to an urbanisation gradient. We also examined if urbanisation had a
29 homogenising effect on ground beetle assemblages.

30 **Locations** Nine forested temperate locations in Europe, Canada and Japan.

31 **Methods** Published results of the Globenet Project were used. At all locations, three
32 stages were identified: a forested (rural) area, a suburban area where the original
33 forest was fragmented and isolated, and remnants of the original forest in urban parks.
34 These habitats formed an urbanisation series. Study arrangements (number and
35 operation of traps) and methods (pitfall trapping) were identical, conforming to the
36 Globenet protocol. Assemblage composition and diversity patterns were evaluated.
37 Diversity relationships were analysed by the Renyi diversity ordering method
38 considering all ground beetles and – separately – the forest specialist species.
39 Taxonomic homogenisation was examined by multivariate methods using assemblage
40 similarities.

41 **Results** Overall biodiversity (compared by species richness and diversity ordering)
42 showed inconsistent trends by either urbanisation intensity or by geographic position.
43 However, when only forest species were compared, diversity was higher in the
44 original rural (forested) areas than in urban forest fragments. Within–country
45 similarities of carabid assemblages were always higher than within–urbanisation stage
46 similarities.

47 **Main conclusions** Urbanisation does not appear to cause a decrease in ground beetle
48 diversity *per se*. Forest species decline as urbanisation intensifies but this trend is

49 masked by an influx of non–forest species. The rural faunas were more similar to the
50 urban ones within the same location than similar urbanisation stages were to each
51 other, indicating that urbanisation did not homogenise the taxonomic composition of
52 ground beetle faunas across the studied locations.

53

54 **KEYWORDS:**

55 Urbanisation, diversity, Globenet Project, scalable diversity comparison,
56 fragmentation, disturbance, biotic homogenisation

57

58 INTRODUCTION

59 Significant parts of biodiversity today are in non-protected environments under
60 varying degree of human manipulation (Tschardt *et al.*, 2005). One of the most
61 intensively modified of human environments is the urbanised area. Urbanised areas
62 are on the increase world-wide. By 2007, the majority of humankind was estimated to
63 live in cities (UNPD, 2005). Urbanisation profoundly modifies the original habitat,
64 with the loss of its plant and animal species (Marzluff *et al.*, 2001) and their place is
65 often taken by non-natives (Blair, 1996; 2004; La Sorte & Boecklen, 2005). The
66 urbanisation process seems to go through similar event sequences in different parts of
67 the world, and species tolerating or thriving under such conditions can be
68 cosmopolitan, leading to increasing biological homogenisation (Lövei, 1997;
69 McKinney & Lockwood, 1999; Rahel, 2002; Olden & Poff, 2003). Urbanisation has
70 different levels, and these differ in the density of humans present, the amount of the
71 original habitat left, and often the intensity and type of management (Blair, 2004;
72 McDonald, 2008).

73 Urban areas, however, are not devoid of plants and animals. Such areas can
74 provide ephemeral or more permanent habitats for species, dispersal corridors, or
75 resting places for migrating organisms (Gaston *et al.*, 2005). Further, biodiversity is
76 linked to important environmental services in urbanised areas, including the removal
77 of dust, mitigation of microclimatic extremes, and modulation of humidity (Bolund &
78 Hunhammar, 1999). A further significant ecological service people derive from urban
79 biodiversity is the psychological benefits resulting from biophilia (Wilson, 1984;
80 Fuller *et al.*, 2007).

81 While urban ecology is quickly developing, we do not yet have a detailed
82 understanding of the effects of urbanisation on biodiversity or its functioning

83 (Vandruuff *et al.*, 1995). Therefore it is important to document biodiversity changes
84 during urbanisation to identify:

- 85 a) what level of biodiversity remains in urbanised areas;
- 86 b) which elements of the original biota remain, and are these specific by bionomics,
87 size, or other features;
- 88 c) if it is possible to increase biodiversity in urbanised areas by management and to
89 what degree;
- 90 d) which ecological services (Daily, 1997) remain, and at what intensity do they
91 function in urbanised areas, how do we ensure their sustained activity, and, if
92 possible, increase them?

93 This is an ambitious agenda, whose logical first step is the documentation of
94 biodiversity in urbanised areas. In this paper, we try to answer some of the above
95 questions, using published data from nine geographical locations of the international
96 Globenet Project (Niemelä *et al.*, 2000).

97 Specifically, we tested the following predictions regarding the possible impact
98 of urbanisation on arthropod diversity (exemplified by ground beetles):

99 (1) Urbanisation, starting from an originally forested habitat, will decrease the
100 diversity of ground beetles (Gray's (1989) "increasing disturbance hypothesis"). This
101 hypothesis predicts an overall decrease of diversity as a result of urbanisation.

102 (2) According to the "habitat specialist hypothesis" of Magura *et al.* (2008c),
103 different elements of an assemblage will react differently, because the specialists are
104 expected to decrease with urbanisation while the generalist species could be favoured.

105 (3) Urbanisation will homogenise the taxonomic composition of ground beetle
106 faunas and create similar assemblages in cities; thus the ground beetle assemblages in
107 urban forest fragments will be more similar to each other than to their rural

108 counterparts, at least within a geographical region. For example, the carabid fauna of
109 urban sites in NW Europe would be more similar to each other than the average
110 similarity of the forest-urban comparisons of the same NW European studies. This
111 “homogenisation hypothesis” has had support (Olden & Rooney, 2006; Olden *et al.*,
112 2006), but has rarely been tested on arthropods (but see Blair, 2001).

113 In the present study, we found qualified support for the habitat specialist
114 hypothesis. However, neither the decreasing diversity nor the homogenisation
115 hypothesis was supported: in general, diversity did not decrease, and local effects
116 seemed to override the impact of urbanisation on ground beetle diversity.

117

118 **MATERIAL AND METHODS**

119 **The Globenet Project**

120 The Globenet Project aims to study the impact of urbanisation on biodiversity,
121 specifically using responses of arthropods (Niemelä *et al.*, 2000). The setup requires
122 the presence of a common original habitat type (native forest) that has been gradually
123 transformed by urbanisation by an expanding city (a rural-urban gradient approach,
124 Pickett *et al.*, 2001). Remnants of the original forested habitat should remain, even if
125 in patches, in all other urbanisation stages. In the Globenet Project, the three kinds of
126 forested habitats are compared that represent different (increasing) levels of
127 urbanisation: forested rural areas, suburban forested areas, and remnants of the
128 original forest in urban parks. The two endpoints were unequivocally characterised:
129 forested rural habitats had no built-up area, while urban parks had $\geq 80\%$ of the
130 surroundings (usually within 1 km from the study site) built-up. Suburban habitats
131 had a complex of houses, roads and parks/forest patches, and an intermediate level of
132 urbanisation with relation to the two local endpoints. There was an unknown degree

133 of variation in the conditions of the suburban habitats (including the size and
134 distribution of the forest patches, their connectedness, the number and width of paths)
135 between locations. Due to this variation, data from suburban habitats were only
136 evaluated along the gradient, and no cross-comparisons between locations were made.
137 Invertebrate biodiversity was sampled by a common methodology (pitfall trapping),
138 using an identical design (see later). Ground beetles (family Carabidae) were selected
139 as the reference group, since they are sufficiently varied both taxonomically and
140 ecologically, taxonomically well known, abundant, easy to collect, and also sensitive
141 to disturbance (Lövei & Sunderland, 1996).

142

143 **Sampling design and the data sets used**

144 The standardised Globenet protocol (Niemelä *et al.*, 2000) requires that within each of
145 the three urbanisation stages, four replicate sites be selected. Within each site, 10
146 pitfall traps were set in a random arrangement. Individual traps were at least 10m
147 apart, ensuring that the assemblage structure of the catch was not distorted (Niemelä
148 *et al.*, 2000). The pitfall traps consisted of pots, usually of 500 ml in size and ca. 15
149 cm in diameter, sunk into the ground so that their opening was level with the soil
150 surface, were unbaited, and contained a killing-preserving liquid (usually a 70%
151 ethylene glycol solution with a drop of detergent to reduce surface tension). Traps
152 were covered to protect the catch from scavengers and to avoid a by-catch of small
153 mammals and frogs. Traps were checked weekly or fortnightly, when the catch was
154 sieved, transferred to 70% alcohol and transported to the laboratory for further sorting
155 and identification to species. In most locations studied so far, the trapping period
156 covered the entire growing season (but see Sapia *et al.*, 2006). This setup resulted in
157 1,320-5,280 trap-weeks of sampling effort, and collected 1,627-15,643 individuals

158 (Table 1). The varying length of the growing season caused differences in the length
159 of the trapping period, and thus in the trapping effort (Table 1).

160 Currently, results from nine locations are available (in chronological order):
161 Bulgaria, Canada and Finland (Alaruikka *et al.*, 2002; Niemelä *et al.*, 2002; Venn *et*
162 *al.*, 2003), Japan (Ishitani *et al.*, 2003), Hungary (Magura *et al.*, 2004; 2005; 2008b),
163 Denmark (Elek & Lövei, 2005; 2007), Belgium (Gaublomme *et al.*, 2005), Romania
164 (Máthé & Balázs, 2006) and England (Sadler *et al.*, 2006). Even though all these
165 studies come from different countries, they are best considered emerging from nine
166 different geographical locations in the northern temperate region. For simplicity,
167 however, we refer to them hereafter by country. In the case of Alberta, Canada, a
168 recent invasion of a few European species grossly distorted the assemblage structures.
169 This invasion started from urban areas, and is still underway (Niemelä & Spence,
170 1991). We present summary data with and without the inclusion of invaders (Table 1),
171 but we removed the invaders from other comparisons that evaluate the reaction of
172 forest ground beetle assemblages to urbanisation.

173

174 **Evaluation methods**

175 The diversity of the carabid assemblages was evaluated by a scalable diversity
176 comparison using the Rényi diversity function (Southwood & Henderson, 2000),
177 calculated by the DivOrd program package (Tóthmérész, 1993a). The Rényi diversity,
178 $HR(\alpha)$ is defined as:

$$179 \quad HR(\alpha) = \frac{1}{1-\alpha} \left(\log \sum_{i=1}^S p_i^\alpha \right),$$

180 where p_i is the relative frequency of the i -th species, S the total number of species and
181 α is the scale parameter ($\alpha \geq 0$, $\alpha \neq 1$).

182 At four values of the scale parameter α , the Rényi diversity index value
183 corresponds to well-known diversity indices (Tóthmérész, 1998; Lővei, 2005): (i) at α
184 = 0, the value of the Rényi diversity is the logarithm of the number of species of the
185 community; (ii) at $\alpha \rightarrow 1$, the Rényi diversity is identical to the Shannon diversity.
186 (iii) at $\alpha = 2$, the value of the Rényi diversity is related to the Simpson diversity, and
187 (iv) at $\alpha \rightarrow +\infty$, the value of the Rényi diversity is closely related to the Berger-Parker
188 dominance index (Berger & Parker 1970).

189 At small values of the scale parameter, the Rényi diversity value is influenced
190 by rare species; as the scale parameter increases, the diversity value is increasingly
191 influenced by the common species (see above). Near infinity, only the abundance of
192 the most common species will determine the diversity (Tóthmérész, 1998). This
193 approach gives a diversity profile and not a single value as “the” diversity of an
194 assemblage, allowing a more synthetic assessment of diversity relations among
195 different assemblages than the often-used single-value diversity indices (Patil &
196 Taillie, 1982; Lővei, 2005).

197 If two diversity profiles do not intersect each other, the assemblage whose
198 diversity profile runs above the other one is unequivocally more diverse. If the
199 profiles cross, the assemblages cannot be unequivocally ordered, as one assemblage is
200 more diverse for the rare species, while another is more diverse for the frequent
201 species. This situation may reflect important ecological processes (Tóthmérész, 1998).

202 As the diversity of the total assemblage may show idiosyncratic responses to
203 urbanisation due to the different species pools and local conditions, the diversity
204 evaluation procedure was repeated using the sub-assemblages of forest-associated
205 species only. To identify species that can be considered "forest specialists", relevant
206 ecological information was extracted from the habitat association categorisation of

207 European species by Koch (1989), supplemented by relevant bionomics information
208 (Lindroth, 1961-69; 1985; 1986; Freude *et al.*, 1976; Húrka, 1996); where in doubt,
209 we sought confirmation from experts (see Acknowledgements). The above sources
210 give verbal descriptions of habitat affinity that may vary, but we accepted only
211 unequivocal indication that the species is rarely found outside forest, and at some
212 point in its life history, it depends on some particular forest characteristic. Species
213 linked to forest edges, clearings, and forest generalists were not included in this
214 category. This way we created a sub-assemblage of the original catch, containing only
215 individuals belonging to forest specialist species. At all locations, these included only
216 a part of the species captured in forested habitats (Table 1).

217 To test whether urbanisation would homogenise ground beetle faunas and
218 create similar assemblages in cities, we analyzed the species composition from the
219 rural and urban areas by cluster analysis using the Sørensen index of similarity and
220 the Ward fusion method (Rencher, 2002) as well as by multi-dimensional scaling
221 ordination. Calculations were made with the NuCoSA package (Tóthmérész, 1993b).
222 Further, we compared the average similarity (calculated by the Sørensen index of
223 similarity) between rural and urban areas using the unpaired two-tailed Student's *t*-
224 test. We considered $p < 0.05$ as the level of significance in all tests.

225

226 **RESULTS**

227 **Patterns of species richness**

228 Overall, the nine studies had a total trapping effort of 26,436 trap-weeks, and
229 collected 65,262 individuals belonging to 213 species (Table 1). The number of
230 individuals ranged from 1627 (the Japanese study) to 15,543 (Alberta, Canada) and
231 the number of species captured at individual locations varied from 25 (Finland) to 72
232 (Bulgaria).

233 The faunas were nowhere fully nested – the forest fragments in urban habitats
234 contributed new species to the species pool in all countries, i.e., the total number of
235 species was higher than the number of species in the forested rural areas (Table 1, Fig.
236 1). An expected impoverishment of the ground beetle fauna along the urbanisation
237 gradient, as predicted by the increasing disturbance hypothesis, was only found in
238 Alberta (when considering only the native species) and Japan.

239 The forest species group showed a near – complete nestedness: there were no
240 or few forest specialist species in the other urbanisation stages that were not present in
241 the rural area. The number of such individuals, if any, was minimal (0 – 21
242 individuals).

243 Non-forest species were lowest in number in Finland, and highest in Hungary.
244 In the three most species – rich locations (Denmark, Bulgaria, Hungary), plus in
245 Romania, these species mostly occurred in the forest fragments in urban parks (Fig.
246 1).

247 In Alberta, total carabid activity density was hugely inflated by a few non –
248 native species that dominated the urban, and – to a lesser degree – suburban habitats
249 (Table 1). Their impact on the original forest habitat was small. Only two of the four
250 invader species were captured in the forest, and only in small numbers (Table 1).

251

252 **Patterns in diversity of the carabid assemblages**

253 Considering all species, only the carabid assemblages living in habitats differing in

254 urbanisation in Alberta, Belgium, and Hungary can be unequivocally ordered.

255 However, the hypothesis that forest assemblages are more diverse than the other ones,

256 living in more urbanised habitats held only in Belgium and Alberta (Fig. 2). In

257 Alberta, the diversity ordering gave the same results with and without the invasive

258 species (results not shown). In Belgium, the urban carabid assemblage was more

259 diverse than the suburban one (Fig. 2).

260 A "softer" formulation of the hypothesis, that carabid assemblages are

261 unequivocally less diverse in urban forest fragments than in the original forest

262 habitats, found support for Belgium, Alberta and Japan only. There was, however,

263 some qualified support for this latter hypothesis from Finland, where only the initial

264 section of the Rényi diversity profile of the urban assemblage ran above the forest

265 curve (Fig 2). In other locations, there was no support for even this "softer"

266 hypothesis. Forest fragments in urban habitats did not harbour less diverse faunas than

267 the corresponding rural areas (Fig. 2).

268

269 **Diversity relationships of forest specialist carabids along the urbanisation**

270 **gradient**

271 When we considered only the diversity of the sub – assemblage of forest specialist

272 species, the picture was less complicated (Fig. 3). Carabids in the original forest were

273 the most diverse in Belgium, Finland and Romania, and the urban fragments

274 supported the least diverse sub – assemblage in all locations except Bulgaria and

275 Belgium (Fig. 3). In spite of the different patterns, there was a robust relationship in

276 the diversity of the forest specialist species: at all nine studies, the forest specialist
277 sub-assemblages were more diverse over the entire range of the scale parameter in the
278 rural area than in the urban one (Fig. 3). This indicates that urbanisation correlated
279 with pronounced differences in the diversity pattern of the forest specialist species.

280

281 **Similarity within the gradient vs. within regions**

282 Three subgroups could be separated by the cluster analysis using the Sørensen index
283 of similarity (Fig. 4): north – western Europe (Belgium, Denmark, England, Finland),
284 south-eastern Europe (Bulgaria, Hungary, Romania) and the two locations outside
285 Europe (Alberta, Japan). In all three subgroups, the rural faunas were more similar to
286 their local urban counterpart than any urbanisation stage to each other within the
287 given region (Fig. 4).

288 The assemblages showed a similar pattern when a cluster analysis using the
289 Bray-Curtis similarity (results not shown) or an ordination was performed (Fig. 5). In
290 the latter, the western European locations could be grouped together, but even within
291 this group, urban assemblages were not made similar to each other by urbanisation. In
292 most cases, the similarity between the two urbanisation gradient extremes (forest –
293 urban forest fragment) was higher than between the urbanised habitats at different
294 geographical locations.

295 Further, the urban faunas were not significantly more similar to each other
296 than the rural faunas either among the north-western European (Student's $t= 0.309$,
297 d.f.= 10, $p=0.764$) or among the south-eastern European locations (Student's $t= 2.762$,
298 d.f.= 4, $p=0.051$). In the latter case, the near – significant result emerged because the
299 *forest* faunas were more similar to each other than the urban ones. This gave further

300 support to the notion that urbanisation did not homogenise the taxonomic composition
301 of ground beetle assemblages.

302

303 **DISCUSSION**

304 **Limitations of the dataset**

305 Due to logistical constraints, there was only one study region per country, and the
306 countries vary enormously in size (Canada vs. Denmark, for example). We do not
307 make the claim, either, that these nine locations representatively cover the conditions
308 from Canada to Japan. The published studies covered only a single year (except
309 Magura *et al.*, 2008b) and assume that the trends found in the year of study were
310 typical. The two end-points (rural vs. urban) of the urbanisation series can be well
311 characterised by the extent of built – up area (and these arguably correlate with
312 increasing levels of disturbance; Gray, 1989). However, cities in the different
313 locations have different energy use per inhabitant and the resulting pollution loads, for
314 example, are probably different (consider the situation in Japan vs. Romania), and
315 urban parks may have differences in management regimes. In Denmark, plant debris
316 resulting from gardening operations is not taken away even from the park but returned
317 to the understory of the forest patches (Elek & Lövei, 2005). In Hungary, leaf litter,
318 and trimmed branches are removed from the urban habitats (Magura *et al.*, 2004). The
319 forest fragments in parks included in this study were all fragments of an original,
320 continuous forest cover. Many urban parks are newly planted, and contain numerous
321 exotic tree species, so the effect of urbanisation on the original native fauna can be
322 more extreme than these studies have found.

323 The pattern of species richness of forest-associated species rests on the
324 important assumption that the species will have the same habitat affinity over their

325 whole distribution area. This is often assumed, but there are counterexamples (e.g.
326 Tyler, 2008). Differences in behaviour and/or habitat affinity by the same species in
327 different parts of its distribution range could cause unexpected trends.

328

329 **Diversity pattern along the gradients**

330 Inconsistent trends in ground beetle diversity were found in previously published
331 studies of the rural – suburban – urban gradient. For example, in Belgium
332 (Gaublomme *et al.*, 2005), the number of species decreases significantly from the
333 rural area towards the urban one. However, in Bulgaria (Niemelä *et al.*, 2002), and
334 Denmark (Elek & Lövei, 2007), no significant differences exist.

335 Such conflicting results reappeared in our evaluation of species richness
336 (measured as the average number of species/trap) trends. One possible reason for
337 these different responses may be that the gradient from rural to urban is a complex
338 system where many factors interact: temperature, moisture, edaphic conditions,
339 acidity, pollution, and decomposition (McDonnell *et al.*, 1997; Niemelä, 1999). These
340 factors are likely to be different in the different countries, which could lead to
341 variation in the responses of invertebrates along the rural – urban gradients (Ishitani *et*
342 *al.*, 2003). An additional reason for the inconsistent results could be the diverse
343 responses of ground beetles to disturbance. Forest specialist species may have
344 narrower tolerance limits and consequently suffer, while generalist and matrix species
345 can benefit from the habitat alteration and disturbance caused by urbanisation. For
346 that reason, it is likely that diversity itself, measured either by the mean number of
347 species/trap, species richness or diversity ordering, is not the most appropriate
348 indicator of the impact of disturbance on diversity. Therefore, species with different
349 habitat affinity should be analyzed separately to evaluate the effect of urbanisation,

350 otherwise basic ecological patterns may remain hidden. The biology of organisms
351 cannot be neglected for the understanding of their ecological responses (Lövei &
352 Magura, 2006).

353 The habitat specialist hypothesis suggested that “species richness of forest
354 specialists should decrease from the rural areas to the urban ones” (Magura *et al.*,
355 2004). This hypothesis is related to the “increasing disturbance hypothesis” (Gray,
356 1989) that has received some support in earlier evaluations of the impact of
357 urbanisation on ground beetles, spiders and woodlice (Vilisics *et al.*, 2007, Magura *et*
358 *al.*, 2008a).

359 The habitat specialist hypothesis was supported in this study as well: we found
360 a pronounced impoverishment of forest specialist species in urban habitat (forest)
361 fragments compared to the rural ones. Habitat alteration caused by urbanisation
362 appears to eliminate the combination of factors necessary for forest specialist species
363 (Desender *et al.*, 1999) and contributes to their decline.

364 Nevertheless, urbanisation is not necessarily detrimental to ground beetle
365 diversity: urbanisation provides habitat for species that are not present in the original
366 forest. These species can be non-native, invasive species (as in Alberta), but native
367 non-forest species can also appear in urban habitats. Urban habitats could contribute
368 to the survival of a species if its original habitats are under severe pressure, such as
369 grasslands in Hungary.

370

371 **Homogenisation by urbanisation**

372 Urbanisation is regarded as one of the most homogenising of human activities and in
373 turn, a major negative consequence of urbanisation. As cities expand across the globe,
374 the same species adapted to modified urban habitats may become increasingly

375 widespread and locally abundant (McKinney, 2006, La Sorte & McKinney, 2007).
376 The appearance of these urban – adaptable (synanthropic) species and the consequent
377 loss of native species may cause an increasing similarity between different urban
378 regions, leading to biological homogenisation.

379 Assemblages of plants (Kuhn & Klotz, 2006; Schwartz *et al.*, 2006), fishes,
380 amphibians, reptiles (Olden *et al.*, 2006), birds (Clergeau *et al.*, 2006; Soh *et al.*,
381 2006) and mammals (Olden *et al.*, 2006) suffer such biological homogenisation in
382 different geographical regions. Our results showed that urbanisation seemingly did not
383 homogenise ground beetle faunas (judged by their taxonomic composition), at least in
384 the studied cities. This can indicate the influence of matrix species that can have a
385 large effect on species richness patterns in habitat fragments (Lövei *et al.*, 2006). The
386 altered forest fragments in urban habitats contain several microhabitats that matrix
387 species can easily colonise (Magura *et al.*, 2004; Elek & Lövei, 2007). However, it
388 seems that the success of such colonisation events in cities is unpredictable. Such
389 unpredictable colonisation success may lead to heterogeneous and different
390 assemblages in the urban areas, providing a strong local influence and preventing
391 taxonomic homogenisation and the development of similar, urban-specific ground
392 beetle faunas. However, these conclusions rest on findings at only nine (although
393 widely dispersed) locations, and their generality should be tested at more locations.

394

395 **Final comments and conclusion**

396 Finally, we would like to modify the traditional Globenet view of the urbanisation
397 gradient. Several published papers (e.g. Niemelä *et al.*, 2000; Ishitani *et al.*, 2003)
398 present the experimental setup as an “urban – rural” gradient. In our view, this is
399 slightly misleading. The question is not how much can biodiversity be enriched by

400 moving from an urban forest patch to a little – disturbed continuous forest. The
401 question is precisely the opposite: how much of the biodiversity present in rural
402 habitats can remain under urbanised conditions? Unfortunately, lax word usage in
403 some publications disguises the important distinction that the object of study is not the
404 biodiversity of ground beetles in urban parks, but their diversity in remnants of the
405 original, forested habitat in urban settings. This setup itself indicates that the basis for
406 comparison should be the original biodiversity in the forested habitat. Consequently,
407 the appropriate view is “from the forest”, and comparisons should be made in relation
408 to the biodiversity existing there. Therefore, in this paper we consciously used the
409 term "rural – urban gradient" and hope others will follow suit.

410 In conclusion, our evaluation of the diversity trends in the nine northern
411 temperate locations revealed that urbanisation does not cause a decrease in ground
412 beetle diversity *per se*. Forest species decline as urbanisation intensifies but this trend
413 is masked by an influx of non-forest species. Results from Canada indicate that such
414 species can be invaders, and can profoundly modify the assemblage structure in
415 urbanised habitats. Further, it seems that ground beetle assemblages living in urban
416 remnants of an originally forested habitat are not homogenised by urbanisation.

417

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595

596 **FIGURE LEGENDS**

597 **Figure 1** Patterns in the species richness (total number of species collected) of forest-
598 associated and non-forest ground beetle species in three stages of forested habitats
599 along an urbanization gradient in nine northern temperate locations. The panel
600 sequence of the individual dot plots starts with the location with the lowest median at
601 the top, and is gradually increasing downwards.

602

603 **Figure 2** The Rényi diversity profiles of the ground beetle assemblages in forested
604 habitats in rural, suburban and urban areas in nine northern temperate locations.
605 Panels are arranged by geographical latitude (northernmost on top) for the European
606 locations; overseas locations are at the two last positions. Dotted line denotes rural
607 habitats, broken line: suburban habitats, continuous line: urban habitats.

608

609 **Figure 3** The Rényi diversity profiles of the forest specialist sub-assemblage of
610 ground beetles in forested habitats in rural, suburban and urban areas in nine northern
611 temperate locations. Panels are arranged by geographical latitude (northernmost on
612 top) for the European locations; overseas locations are at the two last positions.
613 Dotted line denotes rural habitats, broken line: suburban habitats, continuous line:
614 urban habitats.

615

616 **Figure 4** Cluster analysis of the species compositions of the rural and urban carabid
617 assemblages in the nine studied northern temperate locations using the Sørensen index
618 of similarity and Ward fusion method.

619

620

621 **Figure 5** Multi-dimensional scaling (MDS) ordination of the species compositions of
622 urban and rural carabid assemblages in the nine studied northern temperate locations
623 based on the Sørensen index of similarity (stress = 8.480763). The numbers indicate
624 countries: 1: Belgium 2: Bulgaria 3: Canada 4: Denmark 5: England 6: Finland 7:
625 Hungary 8: Japan 9: Romania. Numbers in squares indicate rural habitats, those in
626 circles denote urban habitats.
627

628 **BIOSKETCH**

629

630 Tibor Magura is field biologist at the Hortobágy National Park Directorate, and leader
631 of the Carabidology Research Group at the University of Debrecen. His main research
632 interests include the distribution, biogeography and ecology of ground beetles.

633

634 Gabor L. Lövei is Senior Scientist at the Department of Integrated Pest Management,
635 Aarhus University, where he leads research on agricultural biodiversity, biosafety of
636 transgenic organisms, biological control, and invasion biology.

637

638 Béla Tóthmérész is professor of ecology at the Ecological Institute, University of
639 Debrecen. His research interests include the theory of diversity, with special emphasis
640 on scale-dependent characterisation, scalable proximity measures and the multivariate
641 analysis of communities.

642

643 **Table 1.** Summary characteristics of the ground beetle assemblages along rural-urban urbanisation gradients in nine northern temperate locations.

644 Locations are arranged according to their geographical latitude.

Country and urbanization stage	Number of		Trapping effort, trap*wk	Total number of		Activity density, ind./trap*wk	Number of forest		Relative frequency of			
	Traps	Weeks		Individuals	Species		individuals	species	forest individuals	forest species	rare species*	common species**
<i>Finland***</i>	120	22	2640	2203	25	0.83	1520	14	0.69			
Rural	40		880	1167	21	1.33	695	13	0.60	0.62	0.57	0.24
Suburban	40		880	703	16	0.80	583	9	0.83	0.56	0.56	0.31
Urban	40		880	333	18	0.38	242	10	0.73	0.56	0.44	0.22
<i>Denmark</i>	120	22	2640	10319	43	3.91	5320	12	0.52			
Rural	40		880	4255	25	4.84	3151	11	0.74	0.44	0.64	0.16
Suburban	40		880	1670	25	1.90	1142	10	0.69	0.4	0.72	0.2
Urban	40		880	4394	37	4.99	1027	9	0.23	0.24	0.84	0.11
<i>Belgium</i>	78	26	2028	12096	49	5.96	9490	22	0.78			
Rural	26		676	4047	36	5.99	3332	21	0.82	0.58	0.72	0.11
Suburban	26		676	3547	31	5.25	3026	18	0.85	0.58	0.77	0.13
Urban	26		676	4502	31	6.66	3132	15	0.70	0.48	0.74	0.1
<i>England</i>	240	22	5280	10648	36	2.02	10600	20	1.00			
Rural	80		1760	2781	23	1.58	2772	16	0.99	0.7	0.65	0.17
Suburban	80		1760	4130	26	2.35	4106	17	0.99	0.65	0.81	0.12
Urban	80		1760	3737	24	2.12	3722	16	0.99	0.67	0.83	0.12
<i>Hungary</i>	120	34	4080	2140	50	0.52	1177	3	0.55			
Rural	40		1360	1206	25	0.89	867	3	0.72	0.12	0.6	0.08

Suburban	40		1360	457	26	0.34	246	3	0.54	0.12	0.54	0.19
Urban	40		1360	477	43	0.35	64	2	0.13	0.05	0.53	0.21
<i>Romania</i>	120	22	2640	3651	38	1.38	2624	12	0.72			
Rural	40		880	999	19	1.14	929	11	0.93	0.58	0.47	0.21
Suburban	40		880	2352	22	2.67	1553	10	0.66	0.45	0.55	0.18
Urban	40		880	300	25	0.34	142	5	0.47	0.2	0.4	0.16
<i>Bulgaria</i>	132	24	3168	7035	72	2.22	5147	23	0.73			
Rural	24		1056	3125	45	2.96	2502	22	0.80	0.49	0.64	0.13
Suburban	24		1056	2210	36	2.09	1740	17	0.79	0.47	0.58	0.11
Urban	24		1056	1700	44	1.61	905	6	0.53	0.14	0.68	0.14
<i>Alberta, Canada, total</i>	120	11	1320	15543	41	11.78	877	6	0.24			
Rural	40		440	1308	29	2.97	218	6	0.17	0.21	0.62	0.21
Suburban	40		440	3676	28	8.35	381	4	0.10	0.14	0.64	0.18
Urban	40		440	10559	25	24.0	278	3	0.03	0.12	0.72	0.16
<i>Alberta, Canada, native spp. only</i>	120	11	1320	3628	37	2.75	877	6	0.24			
Rural	40		440	980	28	2.23	218	6	0.22	0.21	0.5	0.25
Suburban	40		440	1442	24	3.28	381	4	0.26	0.17	0.58	0.25
Urban	40		440	1206	21	2.74	278	3	0.23	0.14	0.57	0.24
<i>Japan</i>	120	22	2640	1627	26	0.62	1146	14	0.70			
Rural	40		880	882	23	1.00	670	12	0.76	0.52	0.57	0.17
Suburban	40		880	458	21	0.52	339	12	0.74	0.57	0.57	0.24
Urban	40		880	287	13	0.33	137	7	0.48	0.54	0.31	0.23

645 *Species with <0.01 relative frequency were categorised as rare; **Species with >0.05 relative frequency were categorised as common. ***Data from:
646 Niemela *et al.*, 2002 (Finland, Bulgaria, Alberta, Canada); Elek & Lövei, 2005 (Denmark); Gaublomme *et al.*, 2005 (Belgium); Sadler *et al.*, 2006
647 (England); Magura *et al.*, 2004 (Hungary); Máthé & Balázs, 2006 (Romania); Ishitani *et al.* 2003 (Japan).
648

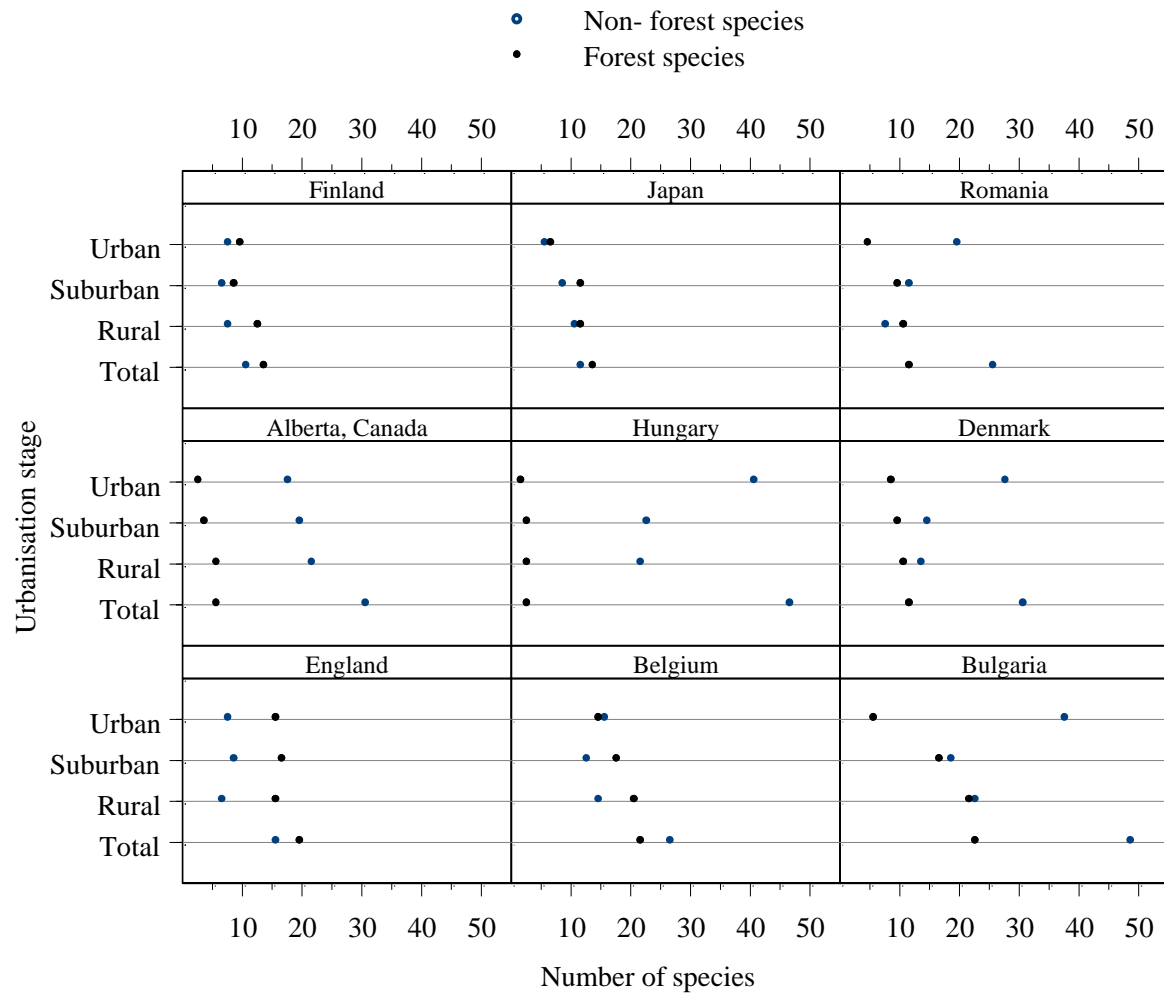


Fig 1

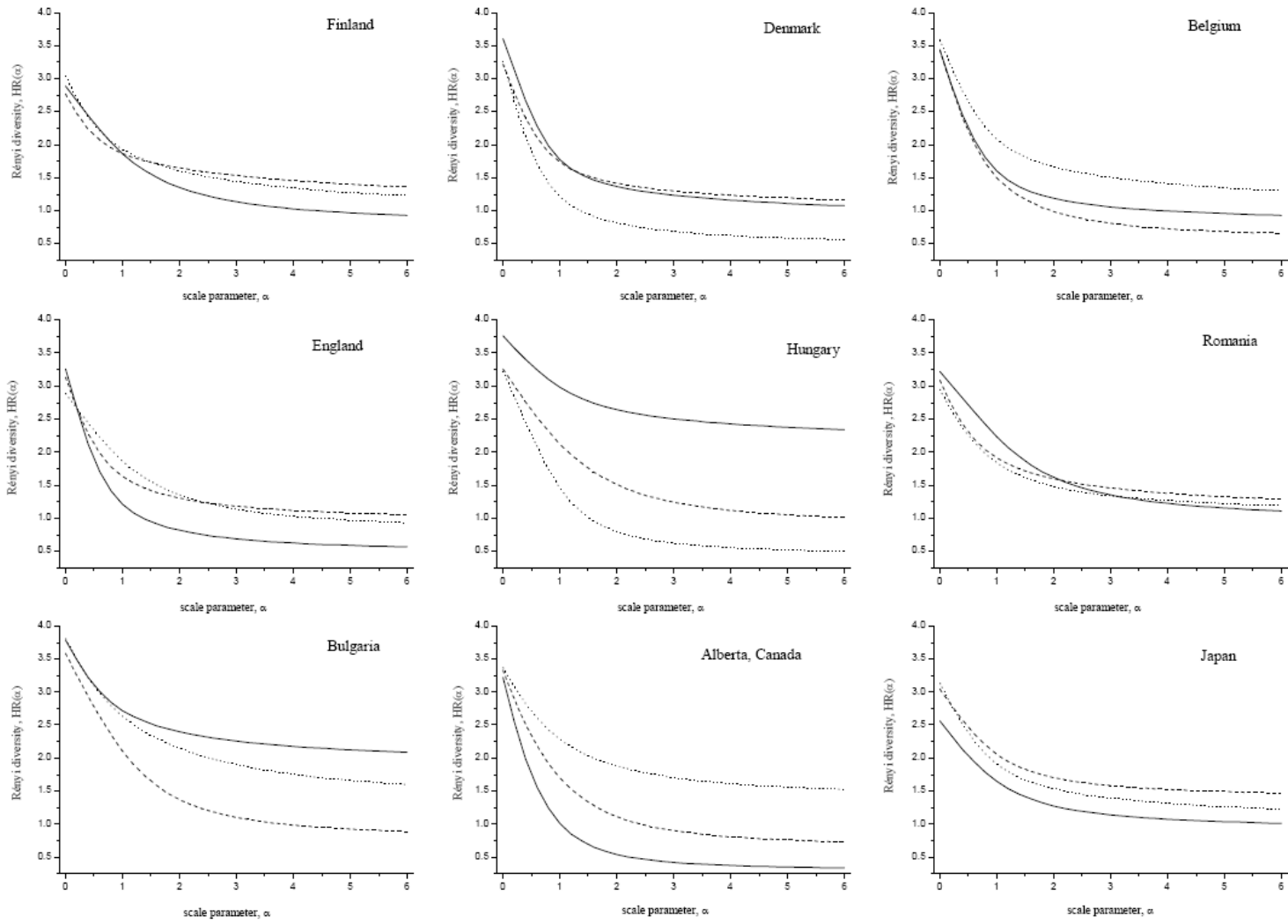
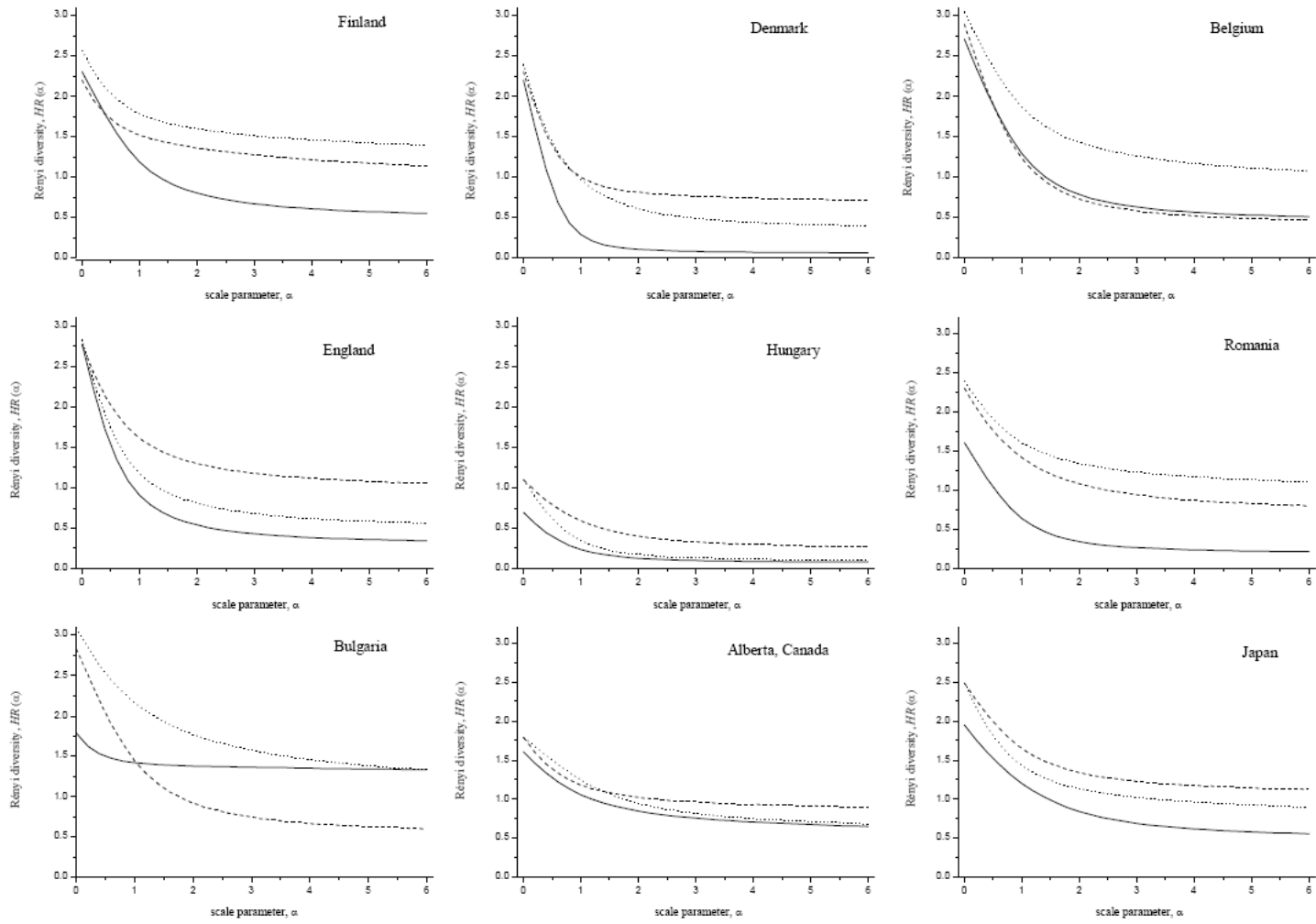
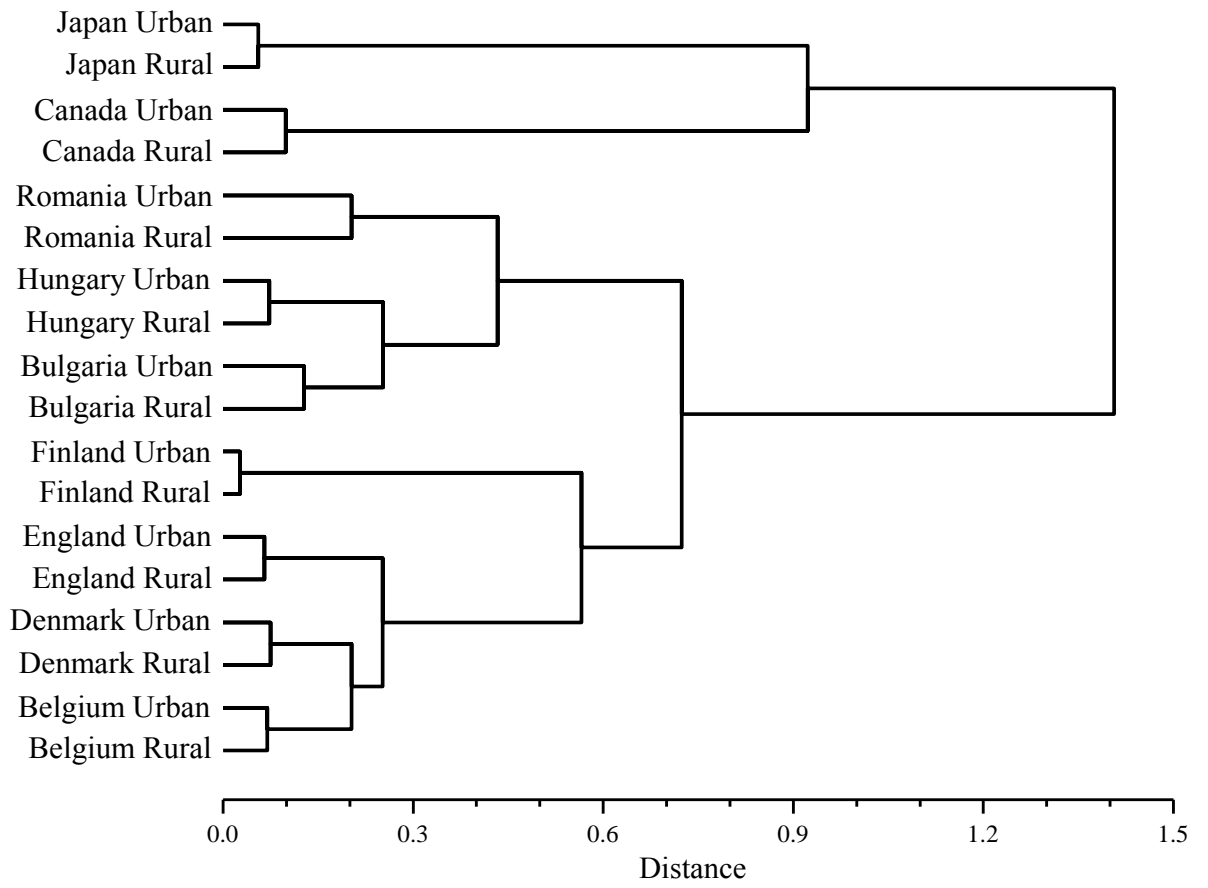


Fig 2

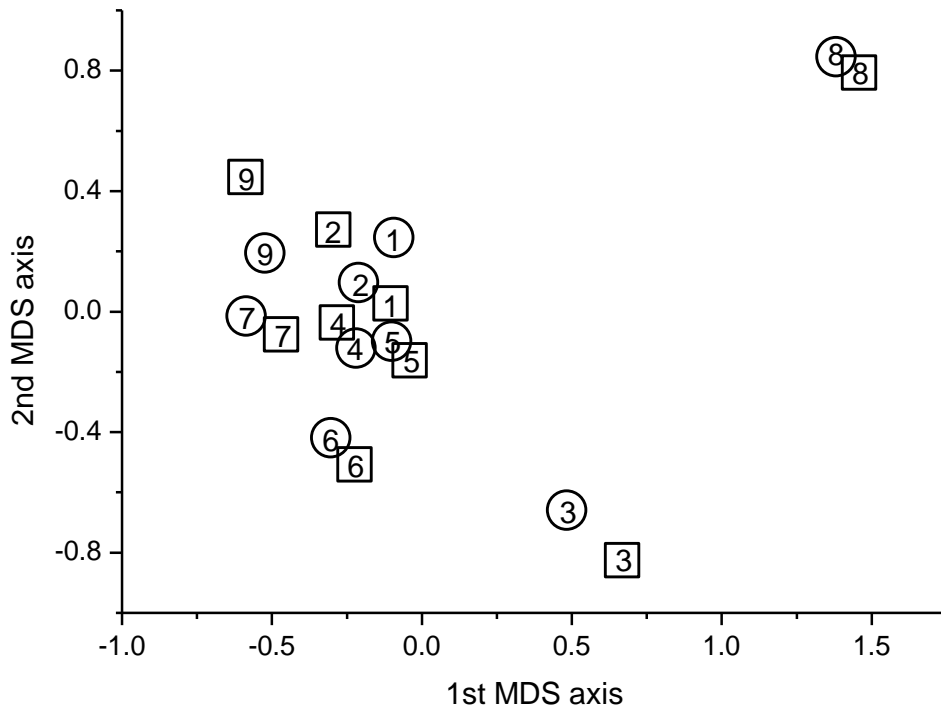




653

654 Fig. 4.

655



657
658
659 Fig 5.