



RESEARCH
PAPER

Does urbanization decrease diversity in ground beetle (Carabidae) assemblages?

Tibor Magura^{1†}, Gábor L. Lövei^{2*} and Béla Tóthmérész³

¹Hortobágy National Park Directorate, H-4002 Debrecen, PO Box 216, Hungary, ²Department of Integrated Pest Management, Aarhus University, Faculty of Agricultural Sciences, Flakkebjerg Research Centre, DK-4200 Slagelse, Denmark, ³Department of Ecology, University of Debrecen, H-4010 Debrecen, PO Box 71, Hungary

ABSTRACT

Aim We wanted to test whether urbanization has similar effects on biodiversity in different locations, comparing the responses of ground beetle (Coleoptera, Carabidae) assemblages with an urbanization gradient. We also wanted to see if urbanization had a homogenizing effect on ground beetle assemblages.

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

Methods Published results of the Globenet Project were used. At all locations, three stages were identified: (1) a forested (rural) area, (2) a suburban area where the original forest was fragmented and isolated, and (3) remnants of the original forest in urban parks. These habitats formed an urbanization series. Study arrangements (number and operation of traps) and methods (pitfall trapping) were identical, conforming to the Globenet protocol. Assemblage composition and diversity patterns were evaluated. Diversity relationships were analysed by the Rényi diversity ordering method considering all ground beetles and – separately – the forest specialist species. Taxonomic homogenization was examined by multivariate methods using assemblage similarities.

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

Main conclusions Urbanization does not appear to cause a decrease in ground beetle diversity *per se*. Forest species decline as urbanization intensifies but this trend is masked by an influx of non-forest species. The rural faunas were more similar to the urban ones within the same location than similar urbanization stages were to each other, indicating that urbanization did not homogenize the taxonomic composition of ground beetle faunas across the studied locations.

Keywords

Biotic homogenization, disturbance, diversity, fragmentation, Globenet Project, scalable diversity comparison, urbanization.

*Correspondence: Gábor L. Lövei, Department of Integrated Pest Management, Aarhus University, Faculty of Agricultural Sciences, Flakkebjerg Research Centre, 4200 Slagelse, Denmark.

E-mail: gabor.lovei@agrsci.dk

†All three authors contributed equally to this paper.

INTRODUCTION

Significant amounts of biodiversity today are in non-protected environments under varying degrees of human manipulation (Tscharrntke *et al.*, 2005). One of the most intensively modified human environments is urbanized areas. Urbanized areas are on

the increase world-wide. By 2007, the majority of humankind was estimated to live in cities (UNPD, 2005). Urbanization profoundly modifies the original habitat, with the loss of its plant and animal species (Marzluff *et al.*, 2001), their place often being taken by non-natives (Blair, 1996, 2004; La Sorte & Boecklen, 2005). The urbanization process seems to go through a similar

sequence of events in different parts of the world, and species tolerating or thriving under such conditions can be cosmopolitan, leading to increasing biological homogenization (Lövei, 1997; McKinney & Lockwood, 1999; Rahel, 2002; Olden & Poff, 2003). Urbanization occurs at different levels, and these differ in the density of humans present, the amount of the original habitat left, and often the intensity and type of management (Blair, 2004; McDonald, 2008).

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

While urban ecology is quickly developing, we do not yet have a detailed understanding of the effects of urbanization on biodiversity or its functioning (Vandruff *et al.*, 1995). Therefore it is important to document changes in biodiversity during urbanization to identify:

1. What level of biodiversity remains in urbanized areas.
2. Which elements of the original biota remain, and whether these are specific to bionomics, size or other features.
3. If it is possible to increase biodiversity in urbanized areas by management, and to what degree.
4. Which ecological services (Daily, 1997) remain, and at what intensity do they function in urbanized areas; how do we ensure their sustained activity, and, if possible, increase it?

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

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

1. Urbanization, starting from an originally forested habitat, will decrease the diversity of ground beetles (the 'increasing disturbance hypothesis'; Gray, 1989). This hypothesis predicts an overall decrease in diversity as a result of urbanization.
2. According to the 'habitat specialist hypothesis' of Magura *et al.* (2008c), different elements of an assemblage will react differently, because the specialists are expected to decrease with urbanization while the generalist species could be favoured.
3. Urbanization will homogenize the taxonomic composition of ground beetle faunas and create similar assemblages in cities; thus the ground beetle assemblages in urban forest fragments will be more similar to each other than to their rural counterparts, at least within a geographical region. For example, the carabid fauna of urban sites in north-west Europe would be more similar to each other than the average similarity of the forest-urban comparisons of the same north-west European studies. This 'homogenization hypothesis' has had support

(Olden & Rooney, 2006; Olden *et al.*, 2006) but has rarely been tested on arthropods (but see Blair, 2001).

In the present study, we found qualified support for the habitat specialist hypothesis. However, neither the decreasing diversity nor the homogenization hypothesis were supported: in general diversity did not decrease, and local effects seemed to override the impact of urbanization on ground beetle diversity.

MATERIALS AND METHODS

The Globenet Project

The aim of the Globenet Project is to study the impact of urbanization on biodiversity, specifically using the responses of arthropods (Niemelä *et al.*, 2000). The set-up requires the presence of a common original habitat type (native forest) that has been gradually transformed by urbanization from an expanding city (a rural-urban gradient approach; Pickett *et al.*, 2001). Remnants of the original forested habitat should remain, even if in patches, in all other urbanization stages. In the Globenet Project, three kinds of forested habitats are compared that represent different (increasing) levels of urbanization: forested rural areas, suburban forested areas and remnants of the original forest in urban parks. The two endpoints were unequivocally characterized: forested rural habitats had no built-up area, while urban parks had $\geq 80\%$ of the surroundings (usually within 1 km of the study site) built up. Suburban habitats had a complex of houses, roads and parks/forest patches, and an intermediate level of urbanization in relation to the two local endpoints. There was an unknown degree of variation in the conditions of the suburban habitats (including the size and distribution of the forest patches, their connectedness, the number and width of paths) between locations. Due to this variation, data from suburban habitats were only evaluated along the gradient, and no cross-comparisons between locations were made. Invertebrate biodiversity was sampled by a common methodology (pitfall trapping), using an identical design (see below). Ground beetles (family Carabidae) were selected as the reference group, since they are sufficiently varied both taxonomically and ecologically, taxonomically well known, abundant, easy to collect and also sensitive to disturbance (Lövei & Sunderland, 1996).

Sampling design and the data sets used

The standardized Globenet protocol (Niemelä *et al.*, 2000) requires that within each of the three urbanization stages, four replicate sites be selected. Within each site, 10 pitfall traps were set in a random arrangement. Individual traps were at least 10 m apart, ensuring that the assemblage structure of the catch was not distorted (Niemelä *et al.*, 2000). The pitfall traps consisted of pots, usually with a capacity of 500 ml and a diameter of c. 15 cm. They were sunk into the ground so that their opening was level with the soil surface, were unbaited and contained a killing-preserving liquid (usually a 70% ethylene glycol solution with a drop of detergent to reduce surface tension). Traps were covered to protect the catch from scavengers and to avoid a

by-catch of small mammals and frogs. Traps were checked weekly or fortnightly, when the catch was sieved, transferred to 70% alcohol and transported to the laboratory for further sorting and identification to species level. In most locations studied so far, the trapping period covered the entire growing season (but see Sapia *et al.*, 2006). This set-up resulted in 1320–5280 trap-weeks of sampling effort, and collected 1627–15,643 individuals (Table 1). The varying length of the growing season caused differences in the length of the trapping period, and thus in the trapping effort (Table 1).

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

Evaluation methods

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

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

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

At four values of the scale parameter α , the value of the Rényi diversity index corresponds to other well-known diversity indices (Tóthmérész, 1998; Lövei, 2005): (1) at $\alpha = 0$, the value of the Rényi diversity is the logarithm of the number of species of the community; (2) at $\alpha \rightarrow 1$, the Rényi diversity is identical to the Shannon diversity; (3) at $\alpha = 2$, the value of the Rényi diversity is related to the Simpson diversity; and (4) at $\alpha \rightarrow +\infty$, the value of the Rényi diversity is closely related to the Berger–Parker dominance index (Berger & Parker, 1970).

At small values of the scale parameter, the value of the Rényi diversity is influenced by rare species; as the scale parameter increases, the diversity value is increasingly influenced by the common species (see above). Near infinity, only the abundance of the most common species will determine the diversity (Tóthmérész, 1998). This approach gives a diversity profile and

not a single value as ‘the’ diversity of an assemblage, allowing a more synthetic assessment of diversity relations among different assemblages than the often-used single-value diversity indices (Patil & Taillie, 1982; Lövei, 2005).

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

As the diversity of the total assemblage may show idiosyncratic responses to urbanization due to the different species pools and local conditions, the diversity evaluation procedure was repeated using the subassemblages of forest-associated species only. To identify species that can be considered as ‘forest specialists’, relevant ecological information was extracted from the habitat association categorization of European species by Koch (1989), supplemented by relevant bionomics information (Lindroth, 1961–1969, 1985, 1986; Freude *et al.*, 1976; Húrka 1996); where in doubt, we sought confirmation from experts (see the Acknowledgements). The above sources give verbal descriptions of habitat affinity that may vary, but we accepted only unequivocal indications that the species is rarely found outside forest, and at some point in its life history it depends on some particular forest characteristic. Species linked to forest edges, clearings and forest generalists were not included in this category. This way we created a subassemblage of the original catch, containing only individuals belonging to forest specialist species. At all locations, these included only some of the species captured in forested habitats (Table 1).

To test whether urbanization would homogenize ground beetle faunas and create similar assemblages in cities, we analysed the species composition from the rural and urban areas by cluster analysis using the Sørensen index of similarity and the Ward fusion method (Rencher, 2002) as well as by multidimensional scaling ordination. Calculations were made with the `NuCoSA` package (Tóthmérész, 1993b). Further, we compared the average similarity (calculated by the Sørensen index of similarity) between rural and urban areas using the unpaired two-tailed Student’s t -test. We considered $P < 0.05$ as the level of significance in all tests.

RESULTS

Patterns of species richness

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

The faunas were nowhere fully nested – the forest fragments in urban habitats contributed new species to the species pool in all countries, i.e. the total number of species was higher than the

Table 1 Summary characteristics of the ground beetle assemblages along rural–urban urbanization gradients in nine northern temperate locations arranged according to their geographical latitude.

Country and urbanization stage	Number of		Trapping effort (trap-weeks)	Total number of		Activity density (ind./trap-week)	Number of forest		Relative frequency of			
	Traps	Weeks		Individuals	Species		Individuals	Species	Forest individuals	Forest species	Rare species*	Common species†
FINLAND‡	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
DENMARK	120	22	2640	10,319	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
BELGIUM	78	26	2028	12,096	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
ENGLAND	240	22	5280	10,648	36	2.02	10,600	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
HUNGARY	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
ROMANIA	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
BULGARIA	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
CANADA (total)	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	10,559	25	24.0	278	3	0.03	0.12	0.72	0.16
CANADA (natives)	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
JAPAN	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

*Species with relative frequency < 0.01 were categorized as rare.

†Species with relative frequency > 0.05 were categorized as common.

‡Data from: Niemelä *et al.* (2002) (Finland, Bulgaria, Alberta, Canada); Elek & Lövei (2005) (Denmark); Gaublomme *et al.* (2005) (Belgium); Sadler *et al.* (2006) (England); Magura *et al.* (2004) (Hungary); Máthé & Balázs (2006) (Romania); Ishitani *et al.* (2003) (Japan).

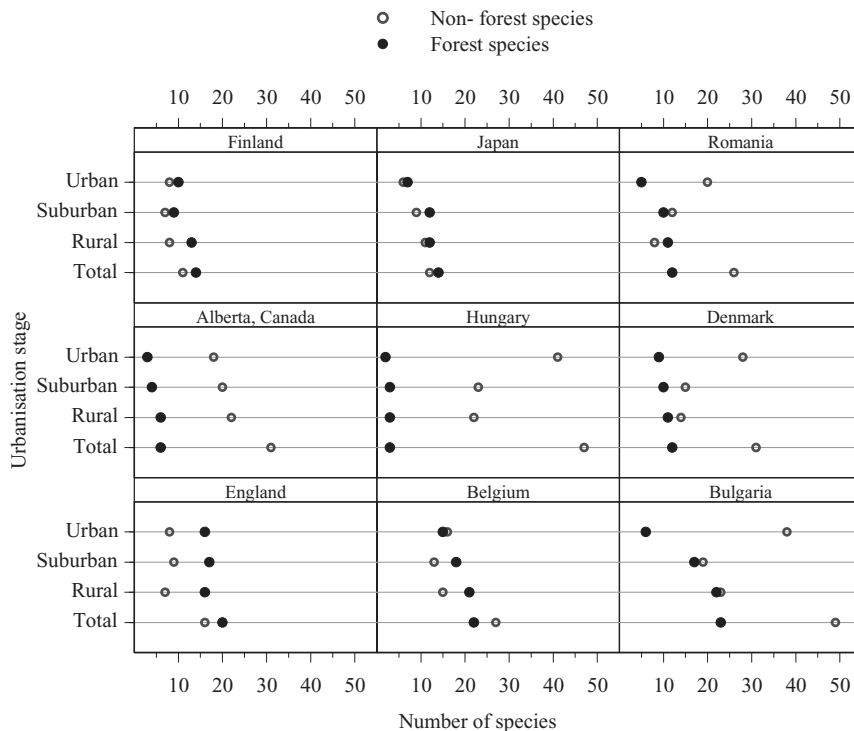


Figure 1 Patterns in the species richness (total number of species collected) of forest-associated and non-forest ground beetle species in three stages of forested habitats along an urbanization gradient in nine northern temperate locations. The panel sequence of the individual dot plots starts with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

number of species in the forested rural areas (Table 1, Fig. 1). An expected impoverishment of the ground beetle fauna along the urbanization gradient, as predicted by the increasing disturbance hypothesis, was only found in Alberta (when considering only the native species) and Japan.

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

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

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

Patterns in diversity of the carabid assemblages

Considering all species, only the carabid assemblages living in habitats differing in urbanization in Alberta, Belgium and Hungary can be unequivocally ordered. However, the hypothesis that the original forest assemblages are more diverse than the other ones living in more urbanized habitats held only in Belgium and Alberta (Fig. 2). In Alberta, the diversity ordering gave the same results with and without the invasive species

(results not shown). In Belgium, the urban carabid assemblage was more diverse than the suburban one (Fig. 2).

A 'softer' formulation of the hypothesis, that carabid assemblages are unequivocally less diverse in urban forest fragments than in the original forest habitats, found support for Belgium, Alberta and Japan only. There was, however, some qualified support for this latter hypothesis from Finland, where only the initial section of the Rényi diversity profile of the urban assemblage ran above the rural curve (Fig. 2). In other locations there was no support for even this 'softer' hypothesis. Forest fragments in urban habitats did not harbour less diverse faunas than the corresponding rural areas (Fig. 2).

Diversity relationships of forest specialist carabids along the urbanization gradient

When we considered only the diversity of the subassemblage of forest specialist species the picture was less complicated (Fig. 3). Carabids in the original forest were the most diverse in Belgium, Finland, Bulgaria and Romania, and the urban fragments supported the least diverse subassemblage in all locations except Bulgaria and Belgium (Fig. 3). In spite of the different patterns, there was a robust relationship in the diversity of the forest specialist species: in all nine locations studied the forest specialist subassemblages were more diverse over the entire range of the scale parameter in the rural area than in the urban one (Fig. 3). This indicates that urbanization correlated with pronounced differences in the diversity pattern of the forest specialist species.

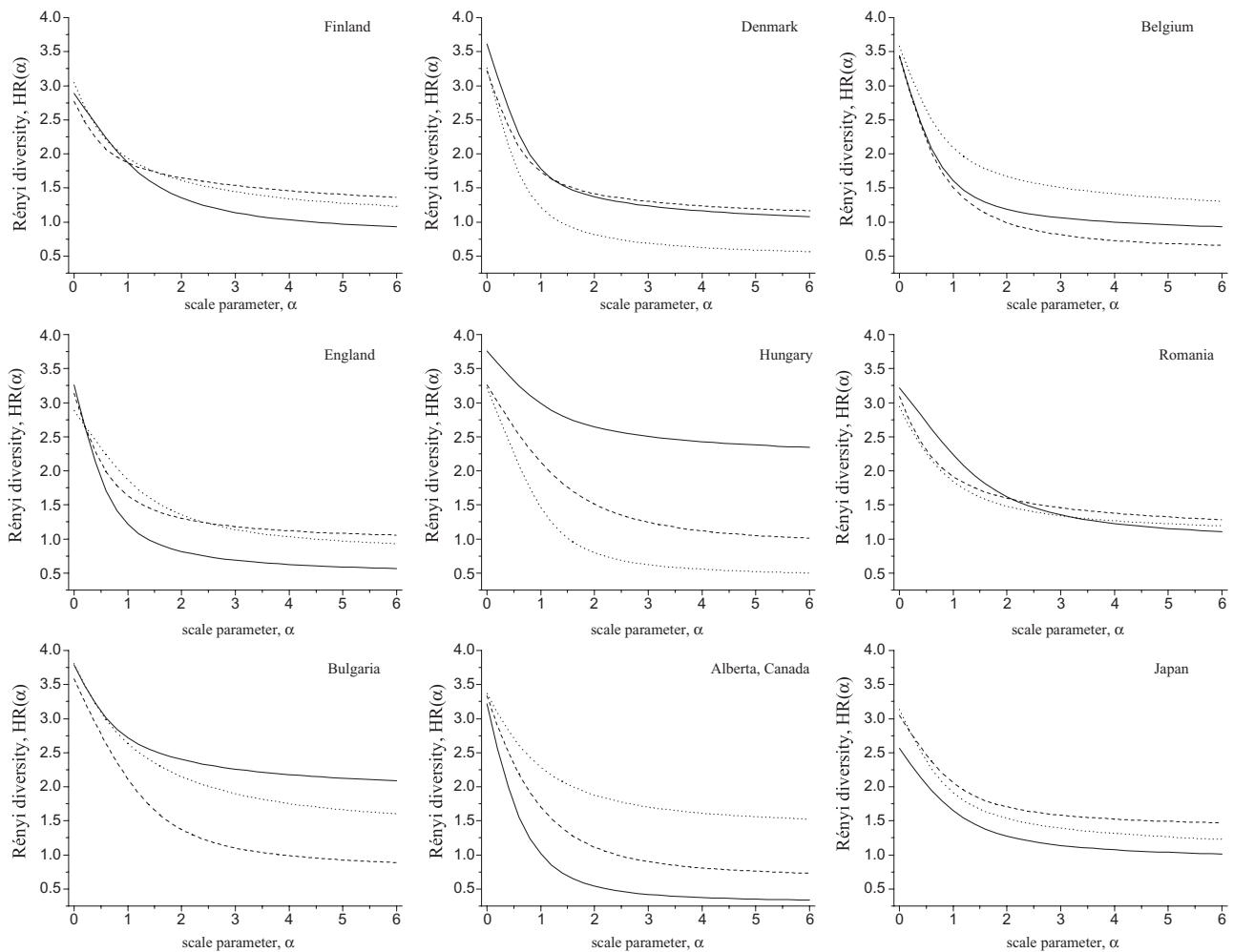


Figure 2 The Rényi diversity profiles of the ground beetle assemblages in forested habitats in rural, suburban and urban areas in nine northern temperate locations. Panels are arranged by geographical latitude (northernmost on top) for the European locations; the other locations are in the two last positions. The dotted line denotes rural habitats, the broken line suburban habitats and the continuous line urban habitats.

Similarity within the gradient versus within regions

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

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

Further, the urban faunas were not significantly more similar to each other than the rural faunas, either among the north-western European (Student's $t = 0.309$, d.f. = 10, $P = 0.764$) or among the south-eastern European locations (Student's $t = 2.762$, d.f. = 4, $P = 0.051$). In the latter case, the near-significant result emerged because the rural *forest* faunas were more similar to each other than the urban ones. This gave further support to the notion that urbanization did not homogenize the taxonomic composition of ground beetle assemblages.

DISCUSSION

Limitations of the dataset

Due to logistical constraints, there was only one study region per country, and the countries vary enormously in size (Canada versus Denmark, for example). We do not make the claim, either, that these nine locations representatively cover the con-

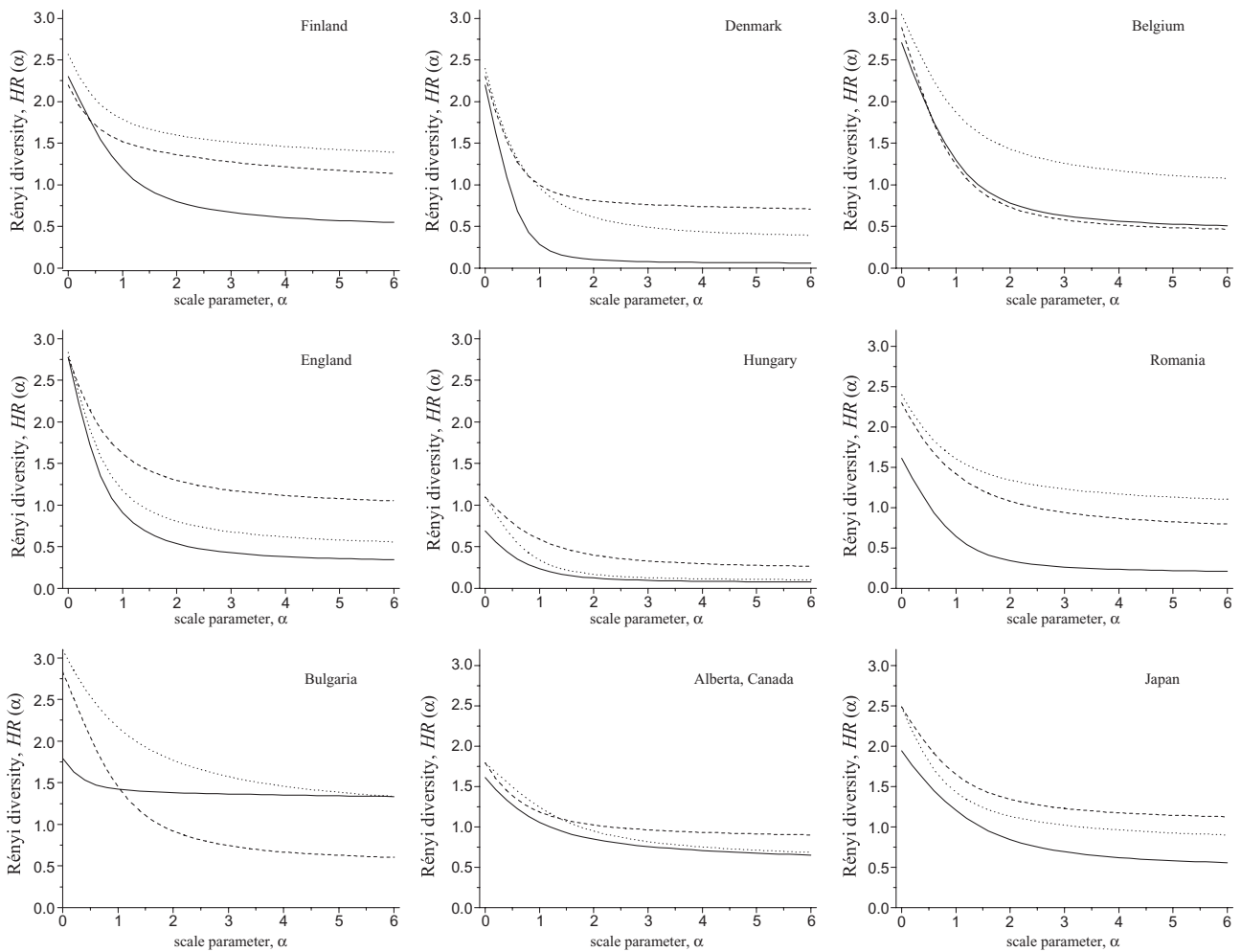


Figure 3 The Rényi diversity profiles of the forest specialist subassemblage of ground beetles in forested habitats in rural, suburban and urban areas in nine northern temperate locations. Panels are arranged by geographical latitude (northernmost on top) for the European locations; the other locations are in the two last positions. The dotted line denotes rural habitats, the broken line suburban habitats and the continuous line urban habitats.

ditions from Canada to Japan. The published studies covered only a single year (except Magura *et al.*, 2008b) and assume that the trends found in the year of study were typical. The two end-points (rural versus urban) of the urbanization series can be well characterized by the extent of the built-up area (and these arguably correlate with increasing levels of disturbance; Gray, 1989). However, cities in the different locations have different energy use per inhabitant and the resulting pollution loads, for example, are probably different (consider the situation in Japan versus Romania); and urban parks may have differences in management regimes. In Denmark, plant debris resulting from gardening operations is not taken away from the park but is returned to the understorey of the forest patches (Elek & Lövei, 2005). In Hungary, leaf litter, and trimmed branches are removed from the urban habitats (Magura *et al.*, 2004). The forest fragments in parks included in this study were all fragments of an original, continuous forest cover. Many urban parks are newly planted, and contain numerous

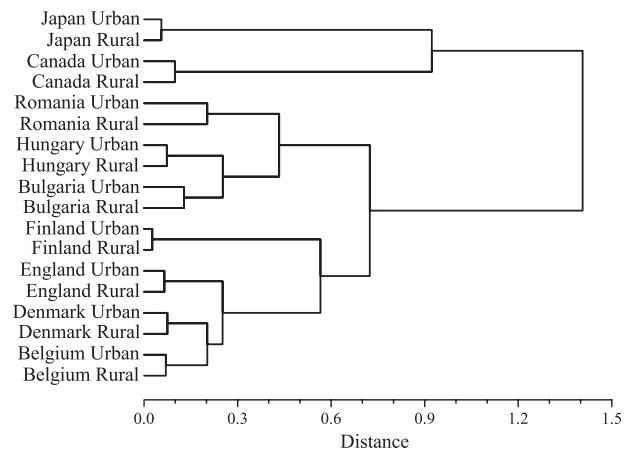


Figure 4 Cluster analysis of the species compositions of the rural and urban carabid assemblages in the nine studied northern temperate locations using the Sørensen index of similarity and the Ward fusion method.

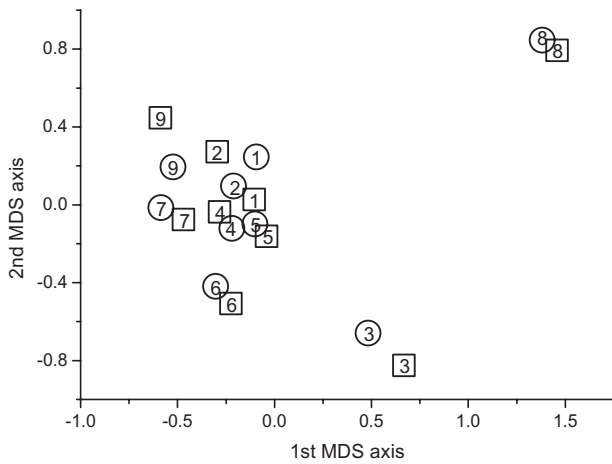


Figure 5 Multidimensional scaling (MDS) ordination of the species compositions of urban and rural carabid assemblages in the nine studied northern temperate locations based on the Sørensen index of similarity (stress = 8.480763). The numbers indicate countries: 1, Belgium; 2, Bulgaria; 3, Canada; 4,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

exotic tree species, so the effect of urbanization on the original native fauna can be more extreme than that found by these studies.

The pattern of species richness of forest-associated species rests on the important assumption that the species will have the same habitat affinity over their whole distribution area. This is often assumed, but there are counterexamples (e.g. Tyler, 2008). Differences in behaviour and/or habitat affinity by the same species in different parts of its distribution range could give rise to unexpected trends.

Diversity pattern along the gradients

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

Such conflicting results reappeared in our evaluation of species richness (measured as the average number of species/trap) trends. One possible reason for these different responses may be that the gradient from rural to urban is a complex system where many factors interact: temperature, moisture, edaphic conditions, acidity, pollution and decomposition (McDonnell *et al.*, 1997; Niemelä, 1999). These factors are likely to be different in the different countries, which could lead to variation in the responses of invertebrates along the rural–urban gradients (Ishitani *et al.*, 2003). An additional reason for the inconsistent results could be the diverse responses of ground beetles to dis-

turbance. Forest specialist species may have narrower tolerance limits and would consequently suffer, while generalist and matrix species can benefit from the habitat alteration and disturbance caused by urbanization. For that reason it is likely that diversity itself, measured either by the mean number of species/trap, species richness or diversity ordering, is not the most appropriate indicator of the impact of disturbance. Therefore, species with different habitat affinity should be analysed separately to evaluate the effect of urbanization, otherwise basic ecological patterns may remain hidden. The biology of organisms cannot be neglected in trying to understand their ecological responses (Lövei & Magura, 2006).

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

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

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

Homogenization by urbanization

Urbanization is regarded as one of the most homogenizing of human activities and, in turn, homogenization is a major negative consequence of urbanization. As cities expand across the globe, the same species adapted to modified urban habitats may become increasingly widespread and locally abundant (McKinney, 2006; La Sorte *et al.*, 2007). The appearance of these urban-adaptable (synanthropic) species and the consequent loss of native species may cause an increasing similarity between different urban regions, leading to biological homogenization.

Assemblages of plants (Kühn & Klotz, 2006; Schwartz *et al.*, 2006), fishes, amphibians, reptiles (Olden *et al.*, 2006), birds (Clergeau *et al.*, 2006; Soh *et al.*, 2006) and mammals (Olden *et al.*, 2006) suffer such biological homogenization in different geographical regions. Our results showed that urbanization seemingly did not homogenize ground beetle faunas (judging by their taxonomic composition), at least in the studied cities. This might indicate the influence of matrix species that can have a large effect on species richness patterns in habitat fragments (Lövei *et al.*, 2006). The altered forest fragments in urban habi-

tats contain several microhabitats that matrix species can easily colonize (Magura *et al.*, 2004; Elek & Lövei, 2007). However, it seems that the success of such colonization events in cities is unpredictable. Such unpredictable colonization success may lead to heterogeneous and different assemblages in urban areas, providing a strong local influence, preventing taxonomic homogenization and the development of similar urban-specific ground beetle faunas. However, these conclusions rest on findings at only nine (although widely dispersed) locations, and their generality should be tested at more locations.

Final comments and conclusion

Finally, we would like to modify the traditional Globenet view of the urbanization gradient. Several published papers (e.g. Niemelä *et al.*, 2000; Ishitani *et al.*, 2003) present the experimental setup as an 'urban – rural' gradient. In our view, this is slightly misleading. The question is not how much can biodiversity be enriched by moving from an urban forest patch to a little-disturbed continuous forest. The question is precisely the opposite: how much of the biodiversity present in rural habitats can remain under urbanized conditions? Unfortunately, lax word usage in some publications disguises the important distinction that the object of study is not the biodiversity of ground beetles in urban parks, but their diversity in remnants of the original, forested habitat in urban settings. This set-up itself indicates that the basis for comparison should be the original biodiversity in the forested habitat. Consequently, the appropriate view is 'from the forest', and comparisons should be made in relation to the biodiversity existing there. Therefore, in this paper we consciously used the term 'rural–urban gradient' and hope others will follow suit.

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

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BIOSKETCHES

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

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

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

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