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

Tibor Magura$^1$, Gábor L. Lövei$^2$* and Béla Tóthmérész$^3$

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

*Address for correspondence:
Gabor 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
Tel. +45-89993636

$ The three authors contributed equally to this paper

Running title: Urbanisation and carabid diversity
ABSTRACT

Aim We tested whether urbanisation has similar effects on biodiversity in different locations, comparing the responses of ground beetle (Coleoptera, Carabidae) assemblages to an urbanisation gradient. We also examined if urbanisation had a homogenising 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: a forested (rural) area, a suburban area where the original forest was fragmented and isolated, and remnants of the original forest in urban parks. These habitats formed an urbanisation 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 Renyi diversity ordering method considering all ground beetles and – separately – the forest specialist species. Taxonomic homogenisation was examined by multivariate methods using assemblage similarities.

Results Overall biodiversity (compared by species richness and diversity ordering) showed inconsistent trends by either urbanisation 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–urbanisation stage similarities.

Main conclusions Urbanisation does not appear to cause a decrease in ground beetle diversity per se. Forest species decline as urbanisation 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 urbanisation stages were to each other, indicating that urbanisation did not homogenise the taxonomic composition of ground beetle faunas across the studied locations.

KEYWORDS:

Urbanisation, diversity, Globenet Project, scalable diversity comparison, fragmentation, disturbance, biotic homogenisation
INTRODUCTION

Significant parts of biodiversity today are in non-protected environments under varying degree of human manipulation (Tscharntke et al., 2005). One of the most intensively modified of human environments is the urbanised area. Urbanised areas are on the increase world-wide. By 2007, the majority of humankind was estimated to live in cities (UNPD, 2005). Urbanisation profoundly modifies the original habitat, with the loss of its plant and animal species (Marzluff et al., 2001) and their place is often taken by non-natives (Blair, 1996; 2004; La Sorte & Boecklen, 2005). The urbanisation process seems to go through similar event sequences in different parts of the world, and species tolerating or thriving under such conditions can be cosmopolitan, leading to increasing biological homogenisation (Lövei, 1997; McKinney & Lockwood, 1999; Rahel, 2002; Olden & Poff, 2003). Urbanisation has 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 urbanised areas, including the removal of dust, mitigation of microclimatic extremes, and modulation of humidity (Bolund & Hunhammar, 1999). A further significant ecological service people derive from urban biodiversity is the psychological benefits resulting from 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 urbanisation on biodiversity or its functioning.
(Vandruff *et al.*, 1995). Therefore it is important to document biodiversity changes during urbanisation to identify:

a) what level of biodiversity remains in urbanised areas;

b) which elements of the original biota remain, and are these specific by bionomics, size, or other features;

c) if it is possible to increase biodiversity in urbanised areas by management and to what degree;

d) which ecological services (Daily, 1997) remain, and at what intensity do they function in urbanised areas, how do we ensure their sustained activity, and, if possible, increase them?

This is an ambitious agenda, whose logical first step is the documentation of biodiversity in urbanised 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 urbanisation on arthropod diversity (exemplified by ground beetles):

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

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 urbanisation while the generalist species could be favoured.

3. Urbanisation will homogenise 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 NW Europe would be more similar to each other than the average similarity of the forest-urban comparisons of the same NW European studies. This “homogenisation 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 homogenisation hypothesis was supported: in general, diversity did not decrease, and local effects seemed to override the impact of urbanisation on ground beetle diversity.

MATERIAL AND METHODS

The Globenet Project

The Globenet Project aims to study the impact of urbanisation on biodiversity, specifically using responses of arthropods (Niemelä et al., 2000). The setup requires the presence of a common original habitat type (native forest) that has been gradually transformed by urbanisation by 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 urbanisation stages. In the Globenet Project, the three kinds of forested habitats are compared that represent different (increasing) levels of urbanisation: forested rural areas, suburban forested areas, and remnants of the original forest in urban parks. The two endpoints were unequivocally characterised: forested rural habitats had no built-up area, while urban parks had ≥80% of the surroundings (usually within 1 km from the study site) built-up. Suburban habitats had a complex of houses, roads and parks/forest patches, and an intermediate level of urbanisation with 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 later). 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 standardised Globenet protocol (Niemelä *et al.*, 2000) requires that within each of
the three urbanisation stages, four replicate sites be selected. Within each site, 10
pitfall traps were set in a random arrangement. Individual traps were at least 10m
apart, ensuring that the assemblage structure of the catch was not distorted (Niemelä
*et al.*, 2000). The pitfall traps consisted of pots, usually of 500 ml in size and ca. 15
cm in diameter, 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. In most locations studied so far, the trapping period
covered the entire growing season (but see Sapia *et al.*, 2006). This setup resulted in
1,320-5,280 trap-weeks of sampling effort, and collected 1,627-15,643 individuals
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 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 underway (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 urbanisation.

**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, $S$ the total number of species and $\alpha$ is the scale parameter ($\alpha \geq 0$, $\alpha \neq 1$).
At four values of the scale parameter $\alpha$, the Rényi diversity index value corresponds to well-known diversity indices (Tóthmérész, 1998; Lövei, 2005): (i) at $\alpha = 0$, the value of the Rényi diversity is the logarithm of the number of species of the community; (ii) at $\alpha \to 1$, the Rényi diversity is identical to the Shannon diversity. (iii) at $\alpha = 2$, the value of the Rényi diversity is related to the Simpson diversity, and (iv) at $\alpha \to +\infty$, 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 Rényi diversity value 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 whose diversity profile 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 urbanisation due to the different species pools and local conditions, the diversity evaluation procedure was repeated using the sub-assemblages of forest-associated species only. To identify species that can be considered "forest specialists", relevant ecological information was extracted from the habitat association categorisation of
European species by Koch (1989), supplemented by relevant bionomics information (Lindroth, 1961-69; 1985; 1986; Freude et al., 1976; Hůrka, 1996); where in doubt, we sought confirmation from experts (see Acknowledgements). The above sources give verbal descriptions of habitat affinity that may vary, but we accepted only unequivocal indication 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 sub-assemblage of the original catch, containing only individuals belonging to forest specialist species. At all locations, these included only a part of the species captured in forested habitats (Table 1).

To test whether urbanisation would homogenise ground beetle faunas and create similar assemblages in cities, we analyzed 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 multi-dimensional scaling ordination. Calculations were made with the NuCoSA package (Tóthméresz, 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 number of species in the forested rural areas (Table 1, Fig. 1). An expected impoverishment of the ground beetle fauna along the urbanisation 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 urbanisation 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 urbanisation in Alberta, Belgium, and Hungary can be unequivocally ordered. However, the hypothesis that forest assemblages are more diverse than the other ones, living in more urbanised 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 forest 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 urbanisation gradient

When we considered only the diversity of the sub – assemblage of forest specialist species, the picture was less complicated (Fig. 3). Carabids in the original forest were the most diverse in Belgium, Finland and Romania, and the urban fragments supported the least diverse sub – assemblage 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: at all nine studies, the forest specialist sub-assemblages 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 urbanisation correlated with pronounced differences in the diversity pattern of the forest specialist species.

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

Three subgroups could be separated by the 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 (Alberta, Japan). In all three subgroups, the rural faunas were more similar to their local urban counterpart than any urbanisation stage to each other within the given region (Fig. 4).

The assemblages showed a similar pattern when a cluster analysis using the 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 urbanisation. In most cases, the similarity between the two urbanisation gradient extremes (forest – urban forest fragment) was higher than between the urbanised 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 *forest* faunas were more similar to each other than the urban ones. This gave further
support to the notion that urbanisation did not homogenise 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 vs. Denmark, for example). We do not
make the claim, either, that these nine locations representatively cover the conditions
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 vs. urban) of the urbanisation series can be well
characterised by the extent of 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 vs. Romania), and
urban parks may have differences in management regimes. In Denmark, plant debris
resulting from gardening operations is not taken away even from the park but returned
to the understory 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
exotic tree species, so the effect of urbanisation on the original native fauna can be
more extreme than these studies have found.

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 cause unexpected trends.

329

**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 one. However, in Bulgaria (Niemelä et al., 2002), and Denmark (Elek & Lövei, 2007), no significant differences exist.

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 disturbance. Forest specialist species may have narrower tolerance limits and consequently suffer, while generalist and matrix species can benefit from the habitat alteration and disturbance caused by urbanisation. 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 on diversity. Therefore, species with different habitat affinity should be analyzed separately to evaluate the effect of urbanisation,
otherwise basic ecological patterns may remain hidden. The biology of organisms cannot be neglected for the understanding of 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 urbanisation 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 to the rural ones. Habitat alteration caused by urbanisation appears to eliminate the combination of factors necessary for forest specialist species (Desender et al., 1999) and contributes to their decline.

Nevertheless, urbanisation is not necessarily detrimental to ground beetle diversity: urbanisation 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.

Homogenisation by urbanisation

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

Assemblages of plants (Kuhn & 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 homogenisation in
different geographical regions. Our results showed that urbanisation seemingly did not
homogenise ground beetle faunas (judged by their taxonomic composition), at least in
the studied cities. This can 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 habitats contain several microhabitats that matrix
species can easily colonise (Magura et al., 2004; Elek & Lövei, 2007). However, it
seems that the success of such colonisation events in cities is unpredictable. Such
unpredictable colonisation success may lead to heterogeneous and different
assemblages in the urban areas, providing a strong local influence and preventing
taxonomic homogenisation 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 urbanisation
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 urbanised 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 setup 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 urbanisation does not cause a decrease in ground
beetle diversity \textit{per se}. Forest species decline as urbanisation 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
urbanised habitats. Further, it seems that ground beetle assemblages living in urban
remnants of an originally forested habitat are not homogenised by urbanisation.

\textbf{ACKNOWLEDGEMENTS}

We thank L. Penev and M. Koivula for information on the habitat affinity of some
species, the anonymous reviewers and the handling editor for their constructive
comments on earlier versions, the former Danish Institute of Agricultural Sciences
(now Aarhus University, Faculty of Agricultural Sciences), the Domus Hungarica
Foundation, Budapest, Hungary (GLL), the Hungarian Scientific Research Fund
(OTKA research grant no. F61651, to TM) and the Bolyai Research Fellowship of the
Hungarian Academy of Sciences (TM) for supporting this research. This is publication no. 8 in the Danglobe Project.
REFERENCES


FIGURE LEGENDS

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 is gradually increasing downwards.

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; overseas locations are at the two last positions. Dotted line denotes rural habitats, broken line: suburban habitats, continuous line: urban habitats.

Figure 3 The Rényi diversity profiles of the forest specialist sub-assemblage 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; overseas locations are at the two last positions. Dotted line denotes rural habitats, broken line: suburban habitats, continuous line: urban habitats.

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 Ward fusion method.
Figure 5 Multi-dimensional 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, those in circles denote urban habitats.
BIOSKETCH

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.

Gábor 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 characterisation, scalable proximity measures and the multivariate analysis of communities.
Table 1. Summary characteristics of the ground beetle assemblages along rural-urban urbanisation gradients in nine northern temperate locations.

Locations are arranged according to their geographical latitude.

<table>
<thead>
<tr>
<th>Country and urbanization stage</th>
<th>Number of Traps</th>
<th>Trapping effort, trap-wk</th>
<th>Total number of Individuals</th>
<th>Activity density, ind./trap-wk</th>
<th>Number of forest individuals</th>
<th>Relative frequency of forest species</th>
<th>Relative frequency of rare species*</th>
<th>Relative frequency of common species**</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finland***</td>
<td>120 22</td>
<td>2640</td>
<td>2203</td>
<td>25</td>
<td>0.83</td>
<td>1520</td>
<td>14</td>
<td>0.69</td>
</tr>
<tr>
<td>Rural</td>
<td>40</td>
<td>880</td>
<td>1167</td>
<td>21</td>
<td>1.33</td>
<td>695</td>
<td>13</td>
<td>0.60</td>
</tr>
<tr>
<td>Suburban</td>
<td>40</td>
<td>880</td>
<td>703</td>
<td>16</td>
<td>0.80</td>
<td>583</td>
<td>9</td>
<td>0.83</td>
</tr>
<tr>
<td>Urban</td>
<td>40</td>
<td>880</td>
<td>333</td>
<td>18</td>
<td>0.38</td>
<td>242</td>
<td>10</td>
<td>0.73</td>
</tr>
<tr>
<td>Denmark</td>
<td>120 22</td>
<td>2640</td>
<td>10319</td>
<td>43</td>
<td>3.91</td>
<td>5320</td>
<td>12</td>
<td>0.52</td>
</tr>
<tr>
<td>Rural</td>
<td>40</td>
<td>880</td>
<td>4255</td>
<td>25</td>
<td>4.84</td>
<td>3151</td>
<td>11</td>
<td>0.74</td>
</tr>
<tr>
<td>Suburban</td>
<td>40</td>
<td>880</td>
<td>1670</td>
<td>25</td>
<td>1.90</td>
<td>1142</td>
<td>10</td>
<td>0.69</td>
</tr>
<tr>
<td>Urban</td>
<td>40</td>
<td>880</td>
<td>4394</td>
<td>37</td>
<td>4.99</td>
<td>1027</td>
<td>9</td>
<td>0.23</td>
</tr>
<tr>
<td>Belgium</td>
<td>78 26</td>
<td>2028</td>
<td>12096</td>
<td>49</td>
<td>5.96</td>
<td>9490</td>
<td>22</td>
<td>0.78</td>
</tr>
<tr>
<td>Rural</td>
<td>26</td>
<td>676</td>
<td>4047</td>
<td>36</td>
<td>5.99</td>
<td>3332</td>
<td>21</td>
<td>0.82</td>
</tr>
<tr>
<td>Suburban</td>
<td>26</td>
<td>676</td>
<td>3547</td>
<td>31</td>
<td>5.25</td>
<td>3026</td>
<td>18</td>
<td>0.85</td>
</tr>
<tr>
<td>Urban</td>
<td>26</td>
<td>676</td>
<td>4502</td>
<td>31</td>
<td>6.66</td>
<td>3132</td>
<td>15</td>
<td>0.70</td>
</tr>
<tr>
<td>England</td>
<td>240 22</td>
<td>5280</td>
<td>10648</td>
<td>36</td>
<td>2.02</td>
<td>10600</td>
<td>20</td>
<td>1.00</td>
</tr>
<tr>
<td>Rural</td>
<td>80</td>
<td>1760</td>
<td>2781</td>
<td>23</td>
<td>1.58</td>
<td>2772</td>
<td>16</td>
<td>0.99</td>
</tr>
<tr>
<td>Suburban</td>
<td>80</td>
<td>1760</td>
<td>4130</td>
<td>26</td>
<td>2.35</td>
<td>4106</td>
<td>17</td>
<td>0.99</td>
</tr>
<tr>
<td>Urban</td>
<td>80</td>
<td>1760</td>
<td>3737</td>
<td>24</td>
<td>2.12</td>
<td>3722</td>
<td>16</td>
<td>0.99</td>
</tr>
<tr>
<td>Hungary</td>
<td>120 34</td>
<td>4080</td>
<td>2140</td>
<td>50</td>
<td>0.52</td>
<td>1177</td>
<td>3</td>
<td>0.55</td>
</tr>
<tr>
<td>Rural</td>
<td>40</td>
<td>1360</td>
<td>1206</td>
<td>25</td>
<td>0.89</td>
<td>867</td>
<td>3</td>
<td>0.72</td>
</tr>
<tr>
<td>Region</td>
<td>Suburban</td>
<td>Urban</td>
<td>Romania</td>
<td>Rural</td>
<td>Suburban</td>
<td>Urban</td>
<td>Bulgaria</td>
<td>Rural</td>
</tr>
<tr>
<td>----------------------</td>
<td>----------</td>
<td>-------</td>
<td>---------</td>
<td>-------</td>
<td>----------</td>
<td>-------</td>
<td>----------</td>
<td>-------</td>
</tr>
<tr>
<td></td>
<td>40</td>
<td>40</td>
<td>120</td>
<td>40</td>
<td>40</td>
<td>40</td>
<td>132</td>
<td>24</td>
</tr>
<tr>
<td></td>
<td>1360</td>
<td>1360</td>
<td>2640</td>
<td>880</td>
<td>880</td>
<td>880</td>
<td>3168</td>
<td>1056</td>
</tr>
<tr>
<td></td>
<td>457</td>
<td>477</td>
<td>3651</td>
<td>999</td>
<td>300</td>
<td>1700</td>
<td>7035</td>
<td>3125</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>19</td>
<td>38</td>
<td>22</td>
<td>25</td>
<td>44</td>
<td>72</td>
<td>45</td>
</tr>
<tr>
<td></td>
<td>0.34</td>
<td>0.35</td>
<td>1.38</td>
<td>2.67</td>
<td>0.34</td>
<td>1.61</td>
<td>2.22</td>
<td>2.96</td>
</tr>
<tr>
<td></td>
<td>246</td>
<td>929</td>
<td>2624</td>
<td>1553</td>
<td>142</td>
<td>905</td>
<td>5147</td>
<td>2502</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>11</td>
<td>12</td>
<td>10</td>
<td>5</td>
<td>6</td>
<td>23</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>0.54</td>
<td>0.66</td>
<td>0.72</td>
<td>0.66</td>
<td>0.47</td>
<td>0.79</td>
<td>0.73</td>
<td>0.80</td>
</tr>
<tr>
<td></td>
<td>0.12</td>
<td>0.45</td>
<td>0.47</td>
<td>0.45</td>
<td>0.2</td>
<td>0.47</td>
<td>0.64</td>
<td>0.49</td>
</tr>
<tr>
<td></td>
<td>0.54</td>
<td>0.55</td>
<td>0.19</td>
<td>0.55</td>
<td>0.2</td>
<td>0.57</td>
<td>0.57</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>0.19</td>
<td>0.47</td>
<td>0.21</td>
<td>0.47</td>
<td>0.4</td>
<td>0.57</td>
<td>0.57</td>
<td>0.57</td>
</tr>
<tr>
<td></td>
<td>0.21</td>
<td>0.21</td>
<td>0.16</td>
<td>0.21</td>
<td>0.21</td>
<td>0.21</td>
<td>0.21</td>
<td>0.21</td>
</tr>
</tbody>
</table>
Species with <0.01 relative frequency were categorised as rare; **Species with >0.05 relative frequency were categorised as common. ***Data from:

Niemela 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).
Fig. 4.
Fig 5.