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Review

Carabid beetle assemblages along urban to rural gradients: A review

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ABSTRACT

Urbanisation causes similar landscape patterns across the world; cities are characterised by a densely populated and highly disturbed urban core, a less disturbed suburban zone and a least disturbed rural surroundings. In 1998, we set up a project to investigate the effects of this urbanisation gradient on the responses of carabid beetles (Carabidae, Coleoptera) in different cities across the globe. To date, eight cities have participated in this project and the findings can be summarised as follows. In general, carabid abundance and species richness increased from the city centres to the rural surroundings. Forest specialist species tended to be more common in suburban and rural zones, while open-habitat species predominate in the urban core. The highly disturbed urban environments were also generally characterised by a few dominant species and species capable of flight, while suburban and rural areas were characterised by larger-sized species and species incapable of flight. Deviations from these general patters do occur, notably the occurrence and high abundance of introduced carabid species in urban Edmonton, Canada. The challenge now is to infer process from these patterns. In particular, community and species specific responses need to be related to characteristics of the urbanised landscape, i.e. the urban–rural gradient needs to be operationalised in terms of specific disturbance features. Furthermore, the results should now be communicated to decision-makers so that they can be considered in planning.

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1. Introduction

In a rapidly urbanising world, knowledge of ecosystem responses to urbanisation is needed to ensure that cities are planned for the well-being of residents and nature (McDonnell and Pickett, 1990; Niemelä, 1999). The effects of urbanisation on biotic communities can be illuminated through studies across urban–rural gradients (Blair, 1996; McDonnell et al., 1997; Niemelä, 1999, 2000; Niemelä et al., 2000, 2002). Such gradients, from densely built city cores to increasingly rural surroundings occur all over the world, and they provide a useful framework for comparative work on a global scale, as they reflect, in general, similar anthropogenic patterns and processes (Niemelä, 2000).

To assess the responses of species and communities to a change in urban landscapes we developed the GLOBENET programme that uses a common field methodology (pitfall trapping) to sample the same taxonomic group (carabid beetles) in visually similar land-mosaics (urban–suburban–rural), in different parts of the world (Niemelä et al., 2000). The goal is to provide a framework for ecolo-

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Table 1
Summary statistics (mean ± SE) of the number of carabid individuals, species and rarefied species richness across urban–suburban–rural gradients of the cities investigated.

	Urban	Suburban	Rural
Number of individuals			
Brussels (Bel)	2993 (±360)	**4746** (±827)	4035 (±1107)
Sofia (Bul)	425 (±109)	737 (±507)	**781** (±155)
Edmonton (Can)	302 (±74.1)	**361** (±118)	245 (±43.5)
Edmonton (Can⁺)	**2640** (±738)	919 (±296)	327 (±73.3)
Birmingham (Eng)	934 (±211)	**1033** (±196)	695 (±115)
Helsinki 1998 (Fin)	83.3 (±20.5)	176 (±37.0)	**292** (±118)
Helsinki 2000 (Fin)	134 (±34.7)	226 (±10.5)	**331** (±163)
Debrechen (Hun)	236 (±38.3)	257 (±68.0)	**495** (±192)
Hiroshima (Jap)	71.8 (±3.07)	115 (±10.2)	**221** (±10.0)
Number of species			
Brussels (Bel)	23.7 (±2.19)	35.3 (±5.15)	**55.0** (±4.71)
Sofia (Bul)	**23.8** (±2.56)	20.3 (±4.10)	22.0 (±3.89)
Edmonton (Can)	12.3 (±0.48)	14.3 (±0.48)	**19.3** (±1.70)
Edmonton (Can⁺)	15.5 (±0.50)	16.5 (±1.04)	**20.3** (±1.70)
Birmingham (Eng)	11.0 (±2.12)	13.3 (±2.39)	**13.5** (±1.44)
Helsinki 1998 (Fin)	9.50 (±1.04)	9.25 (±1.03)	**11.0** (±1.15)
Helsinki 2000 (Fin)	9.75 (±1.49)	**12.0** (±2.27)	11.0 (±0.71)
Debrechen (Hun)	**30.8** (±1.60)	22.0 (±1.15)	22.3 (±1.65)
Hiroshima (Jap)	9.25 (±0.48)	14.0 (±1.47)	**15.8** (±1.11)
Rarefied species richness			
Brussels (Bel) (*N* = 1350)	18.1 (±1.92)	30.9 (±3.46)	**46.5** (±3.33)
Sofia (Bul) (*N* = 180)	**19.0** (±1.90)	16.2 (±1.18)	15.9 (±3.27)
Edmonton (Can) (*N* = 130)	10.5 (±0.82)	12.2 (±0.91)	**16.1** (±1.61)
Edmonton (Can⁺) (*N* = 140)	7.94 (±0.52)	11.7 (±0.52)	**16.0** (±1.37)
Birmingham (Eng) (*N* = 380)	8.96 (±2.09)	10.3 (±1.72)	**11.6** (±0.94)
Helsinki 1998 (Fin) (*N* = 40)	**7.54** (±0.82)	6.60 (±0.30)	7.23 (±0.51)
Helsinki 2000 (Fin) (*N* = 60)	7.65 (±0.66)	8.22 (±1.46)	**8.43** (±0.62)
Debrechen (Hun) (*N* = 140)	**25.9** (±0.59)	19.0 (±0.47)	14.5 (±0.23)
Hiroshima (Jap) (*N* = 60)	8.82 (±0.51)	**11.3** (±1.22)	10.3 (±0.51)

Can = carabid beetles collected from Edmonton with the four exotic species excluded. Can⁺ = the four exotic species included. Most studies consisted of four urban, four suburban and four rural sites. The Brussels study consisted of three urban sites (urbanisation = 74.99–90.32%), six suburban sites (urbanisation = 35.03–59.31%) and four rural (13.45–25.80%) sites (see Gaublomme et al., 2008). The Sofia study consisted of four urban, three suburban and four rural sites. Mean differences were not tested here (see original publications for statistical results), but highest values were indicated in bold face. Abundance and species richness values are not standardised in any way as the total number of trapping days and trap losses were not reported in most of the GLOBENET publications, yet values and trends are consistent with those presented in the individual publications. Rarefied species richness values are standardised to the site with the lowest number of individuals collected from that city.

gists to identify general patterns in the responses of communities to urbanisation across the world, and to distinguish these from more locally occurring phenomena. Furthermore, the compiled knowledge could foster collaboration among researchers and managers in finding ways to mitigate the adverse ecological effects of urbanisation. It is important to note that in the GLOBENET programme we do not compare cities *per se*, but patterns along urbanisation gradients between cities. Thus far, GLOBENET studies have only been conducted in forested habitats, primarily in the boreal and temperate zones.

Specific hypotheses can be derived from the gradient approach and can subsequently be tested in different cities. Here we examine whether predictions on how the community responds to stressors (Gray, 1989) hold for carabid beetles in urban environments, i.e. (a) diversity should increase from a low in urban areas to a high in rural areas, (b) opportunistic species (i.e. habitat generalists) should gain dominance in urban areas, and (c) mean body size of the dominating species should increase from more disturbed to less disturbed habitat (Blake et al., 1994, 1996), here from urban to rural areas.

GLOBENET studies have been performed in forested habitats, which are usually small and fragmented in urban areas. Therefore, – and based on earlier studies – we assume that forest-associated species will be less common in urban areas than in suburban or rural areas where there are more forested habitats. Open-habitat species are expected to be more common even in urban forests, which are characteristically smaller with more edge habitat, and more open than are rural forests. Furthermore, it is expected that species with good dispersal abilities are better in colonising patchy and small habitat fragments in urban areas, while species with poorer dispersal abilities would mainly be able to persist in suburban and especially in rural areas where green areas are more continuous and larger in size.

Ground beetles (Coleoptera, Carabidae) were selected for these studies as they are sufficiently varied taxonomically and ecologically, abundant, and are sensitive to human-caused disturbances to be a reliable monitoring group (Lövei and Sunderland, 1996), and have been widely studied in relation to land use throughout the world (e.g. Rainio and Niemelä, 2003).

In this paper we summarise the results of studies in different parts of the world (spanning eight cities in the boreal and temperate zones) that have used the GLOBENET protocol since its launch in 1998. We are particularly interested in identifying general, recurring patterns and distinguishing them from local, unique ones. Most of the papers examined or tested patterns in relation to the hypotheses presented above, and we summarise the results in the context of these hypotheses. We also discuss improvements to the protocol, in particular on how to quantify the urban-to-rural disturbance gradient, and provide future research directions.

2. The GLOBENET protocol

The standard GLOBENET protocol is as follows (Niemelä et al., 2000): (1) select three urban disturbance regimes; highly disturbed urban, less disturbed suburban, and least disturbed rural, (2) within each disturbance regime select four replicate sites (a total of 12 sites), (3) within each site place 10 pitfall traps in a random arrangement, at least 10 m apart, to ensure independent sampling (a total of 120 traps installed across the urban–rural gradient), (4) traps are plastic collecting cups, 65 mm in diameter, with an alcohol–glycerol mixture as collecting fluid, and (5) the trapping period covering the whole growing season is recommended. Some deviations to this protocol exist (as in Birmingham, Sadler et al., 2006), but the effects of such deviations are likely to be small at the level of analyses in this review. As beetle catches in pitfall traps reflect the activity of the species, trap catches are not directly related to population size of the species captured. Thus, we use the term 'activity density' (e.g. Thomas et al., 1998) to refer to beetle catches in the traps.

3. Results

3.1. Geographical extent of GLOBENET studies

To date the GLOBENET approach has been employed in at least eight cities in the boreal and temporal zones in Europe, North America and Asia; Brussels (Belgium), Sofia (Bulgaria), Edmonton

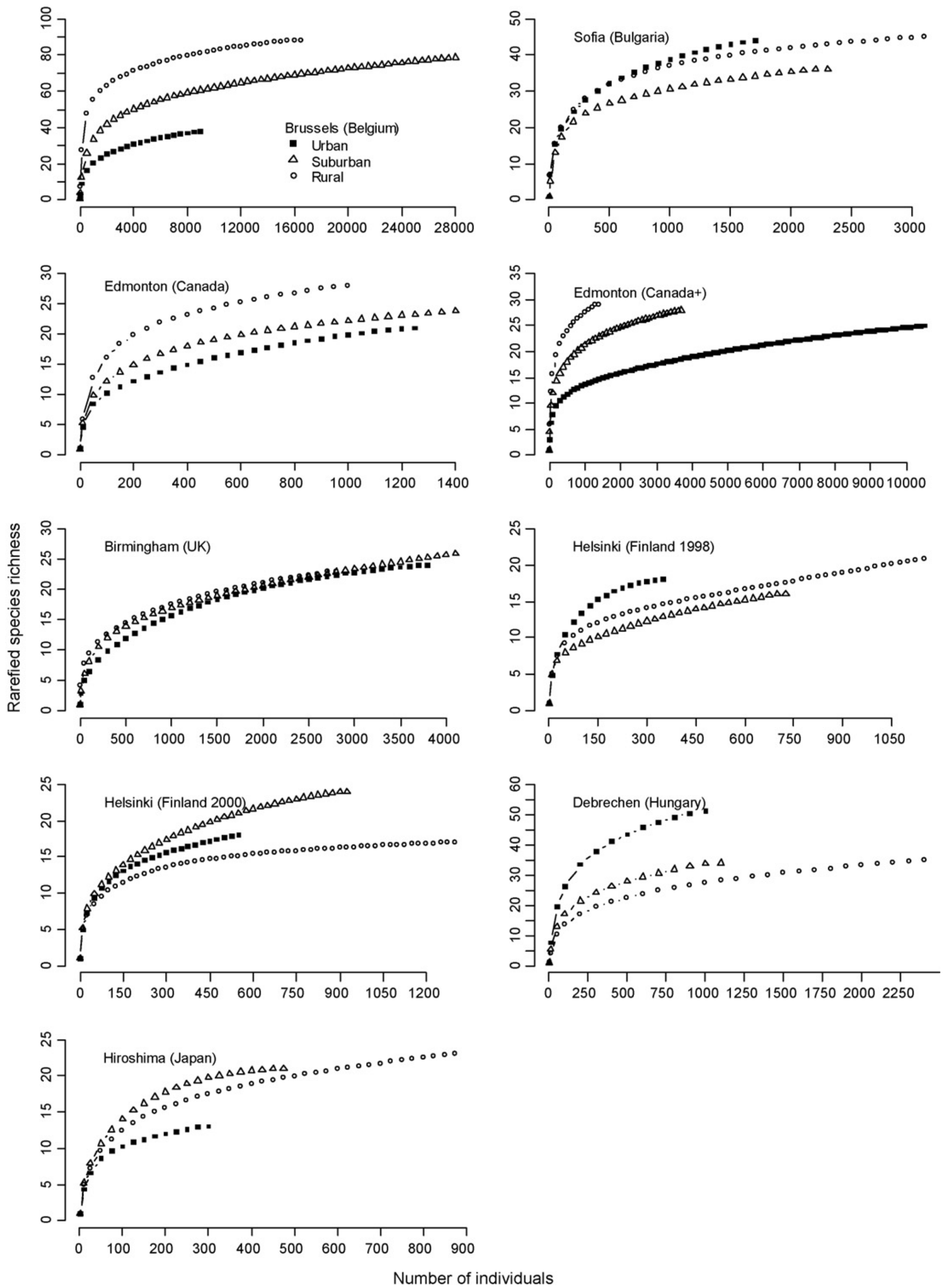

Fig. 1. Rarefaction curves for carabid beetle assemblages collected from urban, suburban and rural sites in various GLOBENET cities.

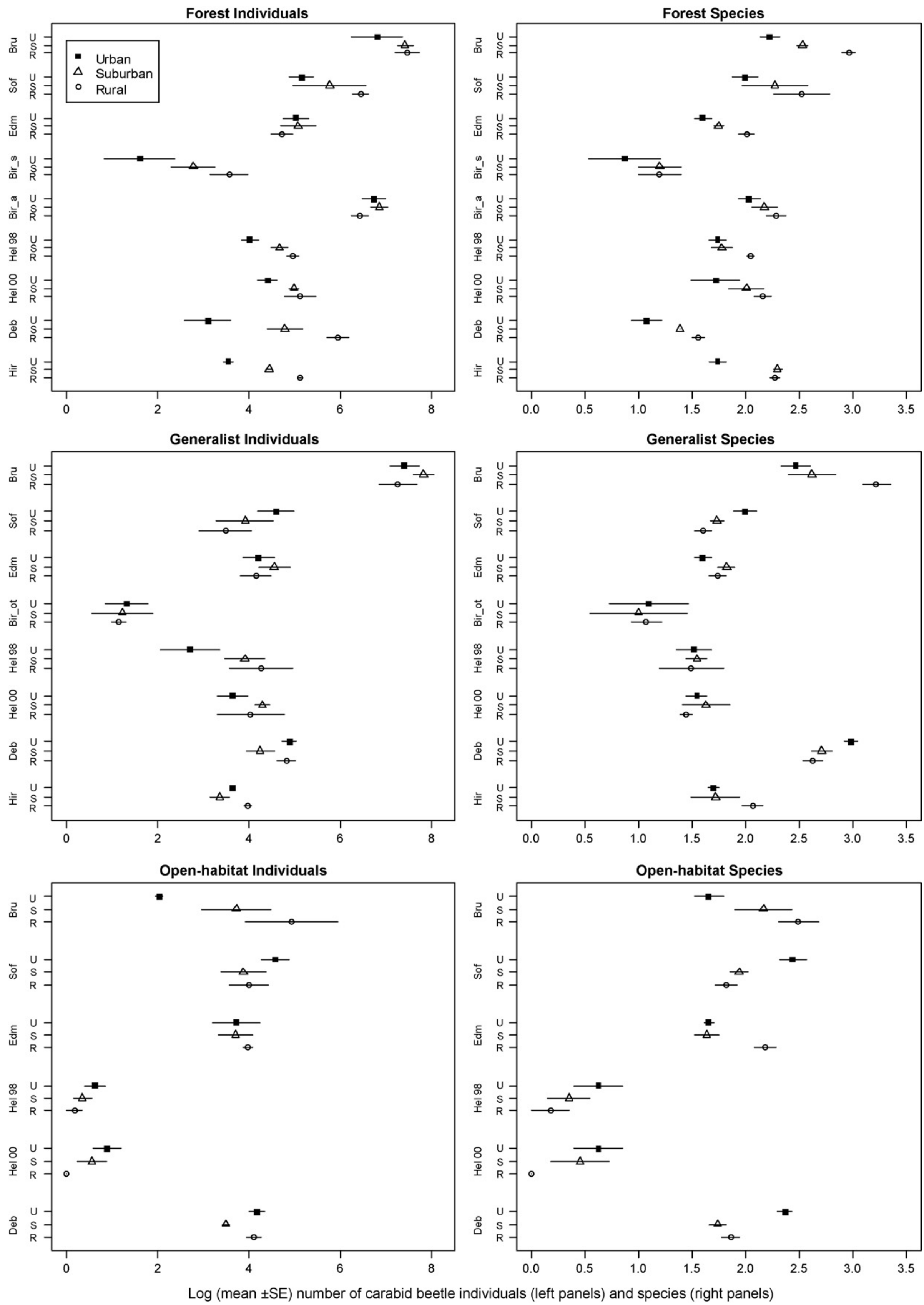

Fig. 2. Log (mean ± SE) number of forest, generalist and open habitat ground beetle individuals (left panels) and species (right panels) collected from the various GLOBENET cities. U = urban, S = suburban, R = rural. Bru = Brussels, Sof = Sofia, Edm = Edmonton, Bir_s = Birmingham-wood specialist species, Bir_a = Birmingham-wood associated species, Bir_ot = Birmingham-species associated with other habitats, Hel 98 = Helsinki-1998 dataset, Hel 00 = Helsinki-2000 dataset, Deb = Debrechen, Hir = Hiroshima.

(Canada), Sorø (Denmark), Birmingham (England), Helsinki (Finland), Debrecen (Hungary) and Hiroshima (Japan) (Alaruikka et al., 2002; Niemelä et al., 2002; Ishitani et al., 2003; Venn et al., 2003; Magura et al., 2004, 2008; Gaublomme et al., 2005, 2008; Sadler et al., 2006; Sapia et al., 2006; Elek and Lövei, 2007).

3.2. Carabid abundance, species richness and diversity along urban-to-rural gradients

Generally, carabid beetles collected in forests in the abovementioned cities showed evidence of an increase in overall activity density from the city centres to suburbia and the rural surroundings (Debrecen, Helsinki, Hiroshima, Sofia, Brussels) (see also Table 1). In Edmonton, carabid beetle catches were significantly higher in suburbia, and lowest in the rural surroundings. Edmonton was characterised by a number of exotic carabid species mainly occurring in urban areas, and when these were included in the analysis, activity density decreased significantly from urban to suburban to rural. In Birmingham, carabid catches did not change significantly across the gradient, but as in Edmonton was highest in suburbia, and lowest in the rural surroundings. In contrast, carabid activity density was lowest in the suburbs of Sorø compared to urban and rural sites.

The number of carabid species mainly increased from urban to rural in many cities (Birmingham, Brussels, Edmonton, Helsinki, Hiroshima, Sofia) (see also Table 1). However, in another data set collected from Helsinki, there was no significant difference in number of species along the urban–rural gradient (Alaruikka et al., 2002). In Debrecen, there were significantly more species in the urban and rural zones compared to the suburban zone, while in a study combining two sampling years from Debrecen there was no difference in the number of species along the gradient (Magura et al., 2008). In Sorø (Denmark), there was no difference in the number of species along the gradient (Elek and Lövei, 2007).

We used rarefaction analysis (Simberloff, 1979) to examine species richness from a standard number of individuals collected in each city. In most cities, these results are similar to those presented above for species richness (Table 1, Fig. 1). In Brussels, Edmonton, and to some degree in Helsinki (2000 dataset), rarefied species richness was higher in the rural sites than elsewhere along the gradient, while in Sofia, Helsinki (1998 dataset), and Debrechen, urban sites appear to be species richer (Fig. 1).

Carabid diversity, when calculated, was lowest in the urban, and highest in the rural environment in Birmingham (Sadler et al., 2006), Helsinki (Venn et al., 2003) and Sorø (Elek and Lövei, 2007).

3.3. Species dominance along urban-to-rural gradients

As per Gray's (1989) prediction, the highly disturbed urban environments were generally characterised by a few dominant species, more so than in the suburban and rural sites. The urban zones in Birmingham, Edmonton, Helsinki and Hiroshima were, respectively, characterised by high single-species dominance; *Pterostichus madidus* (74%), *Calathus ingrates* (48%), *Calathus micropterus* (46%) and *Lesticus magnus* (42%). In Birmingham, dominance (Berger Parker index) was higher in the urban and suburban zones as compared to the rural zone, which was primarily caused by the increasing catches of *Pterostichus madidus* from a rural low of <10% to 60–85% at the most urban sites (Sadler et al., 2006). In Debrecen, the proportion of opportunistic species (i.e. habitat generalists) was significantly higher in urban sites compared to suburban and rural sites (Magura et al., 2004, 2008) (see also Fig. 2), and in Sorø the abundance of generalist species was significantly higher in urban areas than in suburban or rural areas, although dominance was higher in the rural sites (Elek and Lövei, 2007). In Brussels, the prediction of increasing dominance of opportunistic species did not receive unequivocal support. *Nebria brevicollis* and *Pterostichus madidus* made up about 68% of the total catch, and there was a significant positive correlation (at the 5% level) between the proportion of *N. brevicollis* and the degree of urbanisation among the sampling sites but for *P. madidus* there was no such correlation (Gaublomme et al., 2008).

3.4. Carabid assemblage structure along the urbanisation gradient

The different studies used somewhat different, mainly multivariate techniques, in analysing carabid assemblage structure changes along the gradients. In general, urban, suburban and rural zones separated out to varying degrees in terms of carabid beetle assemblage structure. For example, urban sites separated from suburban and rural sites in both Hiroshima (Ishitani et al., 2003) and Debrecen (Magura et al., 2004, 2008). In Hiroshima, this is to a great extent caused by the difference in the identities of the two most abundant species, which were the same in the suburban and rural sites but different in the urban sites. In Debrecen – based on the indicator value (IndVal) procedure (see Dufrêne and Legendre, 1997) – the urban environment was characterised by open habitat and generalist species while the rural environment was mainly characterised by forest and generalist species (Magura et al., 2004). Alternatively, in Birmingham, the rural zone separated from the urban and suburban zones. In Helsinki and Sorø, the carabid assemblage showed clustering of sites according to the intensity of urbanisation (Alaruikka et al., 2002; Venn et al., 2003; Elek and Lövei, 2007). The carabid assemblages of Sofia, Edmonton and Brussels did not separate into distinct clusters (Niemelä et al., 2002; Gaublomme et al., 2005).

3.5. Species traits along urban-to-rural gradients

The proportion of large-sized carabid beetles of the total catch usually increased towards the rural environment, e.g. in Helsinki, Sofia and Brussels (Niemelä et al., 2002; Gaublomme et al., 2005), as predicted by the stress hypothesis of Gray (1989). Also in Birmingham, the number of large-sized species increased from the urban sites through suburban sites to the rural ones, while the number of small-sized species was highest in the suburban zone (Sadler et al., 2006). Interestingly, however, body sizes of specimens of *P. madidus* and *Abax parallelepipedus* increased with increasing urban cover (Sadler et al., 2006). In Sorø, the number of small and medium-sized species was higher in the urban sites as compared to suburban and rural sites, while the number of large-sized species was highest in the rural sites (Elek and Lövei, 2007). However, in another Helsinki study, large and medium-sized carabids were somewhat more likely to be collected from rural sites than from suburban or urban sites but no such difference was found for species richness (Alaruikka et al., 2002).

In Hiroshima, the proportion of small, medium and large-sized species of the total number of species found in urban, suburban and rural sites did not differ (Ishitani et al., 2003), and no differences were found in the body-size distribution across the gradient in Edmonton (Niemelä et al., 2002). However, the proportion of small-sized individuals was somewhat higher in urban Hiroshima than in the suburban or rural sites. Large-sized forest specialists were absent from urban Hiroshima (Ishitani et al., 2003).

Magura et al. (2006) examined the performance of body size inequality indices and demonstrated that one of them (the Lorenz asymmetry coefficient) indicated a significant difference in inequality and/or asymmetry of body size across the urbanization gradient. This difference was primarily due to more individuals with larger body size in rural areas as compared to suburban and urban areas.

Most of the GLOBENET studies have been conducted in forested environments, and consequently, it is of interest to examine the distribution of forest-associated species along the urbanisation gradient. In Birmingham and in Sorø, for instance, the number of forest and forest associated species were significantly higher at the rural end of the gradient (Sadler et al., 2006; Elek and Lövei, 2007). Similarly, in Debrecen the number of forest specialist individuals and species were significantly higher at the rural end of the gradient, while open-habitat carabids were significantly more abundant and species rich at the urban end of the gradient (Magura et al., 2004, 2008). In Sorø, generalist and open-habitat species were more frequently captured in urban sites than in suburban or rural sites (Elek and Lövei, 2007). In Brussels, the number of forest specialists decreased and the number of generalist species increased from rural to urban sites (Gaublomme et al., 2005, 2008), and in Helsinki, forest specialist carabids were somewhat more likely (but statistically non-significantly) to be caught in suburban and rural sites. Generalists were more likely to be collected from rural sites in Helsinki (Alaruikka et al., 2002). In Hiroshima, carabid beetle habitat specialisation interacted significantly with body size. Urban environments were mainly characterised by small-sized forest specialists and medium-sized generalists while suburban and rural sites were characterised by medium-sized forest specialists and small-sized generalists (Ishitani et al., 2003). In general terms, the number of forest species and their activity density was higher in rural than in suburban and especially urban sites (Fig. 2). Activity density and number of generalist species was not clearly associated with location along the gradient. In contrast to expectations, open-habitat species were not strongly associated with the gradient either (Fig. 2).

In terms of flight capability, urban and/or suburban environments were mainly characterised by species capable of flight, whereas flightless species were more common in rural and/or suburban environments, in Helsinki, Brussels and Birmingham (Venn et al., 2003; Gaublomme et al., 2005; Sadler et al., 2006). In Birmingham, the number of wing dimorphic species did not vary along the urbanisation gradient (Sadler et al., 2006).

4. Discussion and future prospects

Results from the eight cities indicate that, generally, activity density and species richness of carabid beetles increased from city centres to the rural environment (see Table 1). Furthermore, the highly disturbed urban environments were generally characterised by a few dominant species, more so than the suburban and rural sites. In terms of body size, the proportion of large-sized carabid beetles usually decreased towards the city centres. Forest specialists tended to be more common in the suburban and rural sites as compared to the urban ones where forests are small and isolated (see Fig. 2). In terms of dispersal ability, urban and/or suburban environments were mainly characterised by species capable of flight, whereas flightless species were more common in rural and/or suburban environments. As such, the GLOBENET project will benefit greatly from a more detailed analysis on the responses of individual species or habitat affinity groups (i.e. open habitat species, forest specialist species, forest generalist species, true generalist species) to the urbanisation gradient (Magura et al., 2008). Some studies have shown that open habitat species are more likely to be found in urban environments, while forest specialists and forest associated carabid species are mainly limited to the rural and suburban zones (see also Fig. 2).

These results support our expectations on the kinds of effects urbanisation has on carabid communities. However, there are exceptions to these generalities. For instance, species richness and activity density did not always increase from city centres to the rural surroundings. Furthermore, there are interesting local peculiarities that affect the patterns. For example, in Edmonton, Canada, the higher number of introduced species in urban sites resulted in the loss of statistical significance in species richness across the gradient.

The GLOBENET results so far suggest that there are some generalities in the response of carabid beetles to urbanisation in different cities. The challenge now is to infer process from these patterns. Sadler et al. (2006) suggested that changes in carabid assemblage structure were related to woodland fragmentation, which led to variations in woodland size, location and site disturbance due to trampling. The importance of forest fragment size was also evident in Brussels where large forest fragments were favoured by forest specialists while generalists dominated smaller fragments (Gaublomme et al., 2008). Furthermore, studies on the genetic structure of populations along urban–rural gradients suggest that fragmentation and isolation of urban habitat patches has an effect on beetle populations. The study of the genetic structure of populations of *P. madidus* and *Abax parallelepipedus* along urban–rural gradients revealed that genetic differentiation among sites was higher in Birmingham as compared to Brussels, corresponding to the more severe fragmentation and isolation among study sites in Birmingham (Desender et al., 2005).

Magura et al. (2008) related the occurrence of different species groups (forest species, open-habitat species, etc.) to habitat variables along the gradient. They concluded that species differ in their response to urbanization. From this and other studies it can be inferred that large, flightless and specialist woodland species are susceptible to changes associated with urbanization (e.g. fragmentation and disturbance), presumably due to their longer life spans, lower reproductive rates, specialized niches and limited dispersal potential. Yet, other species, such as *Pterostichus melanarius* may become very dominant in heavily trampled urban woodlands in Helsinki (Grandchamp et al., 2000), and is a successful invasive species in North America (Spence and Spence, 1988; Niemelä and Spence, 1991), with well established populations in urban environments (see Niemelä et al., 2002). This suggests that some species favour urban environments and can become dominant in the species community even outside their original distribution range.

It is important to direct future studies on the processes and mechanisms which affect urban species assemblages. Such mechanistic questions include, for example, why certain species or habitat affinity groups respond in a particular way to urbanisation and the subsequent fragmentation of habitats (Sadler et al., 2006). Fragmentation leads to increased patchiness, isolation and edge effects. Consequences of fragmentation on carabids have been studied (e.g. Niemelä, 2001), and studies done in urban areas show that carabid species are sensitive to the effects of fragmentation (e.g. Croci et al., 2008). However, to address such questions in more detail, the urban–rural gradient needs to be operationalised, i.e. disturbance and urbanisation features along the urban–rural gradient need to be quantified. For example, the selected sites could be defined in terms of the percentages area covered by buildings, pavements, lawns, grasslands, and trees and shrubs, by the number of moving vehicles and pedestrians, by climatic variables such as temperature and relative humidity, by pollution of the air and soil, and by direct human effects such as trampling and waste (see Blair, 1996; Lehvävirta, 1999). Interesting prospects include the use of body size inequality by Magura et al. (2006) as a quantification of the gradient or the use of the effects of heavy metal contamination in urban environments on carabid beetle body size, energetic reserves and development (Maryański et al., 2002), and fluctuating asymmetry (Weller and Ganzhorn, 2004), which has been linked to habitat quality.

Although relating carabid beetles to these variables would still be correlative, such work will undoubtedly begin to pinpoint the more important urbanisation factors affecting individual carabid species and habitat affinity groups. For instance, the use of such common measure could enable us to examine the non-linear and threshold-like nature of assemblage metrics between rural and suburban as reported by Sadler et al. (2006).

The use of various landscape indices to characterise the urban environment would improve our understanding of how the landscape affects carabid distribution. For instance, Sadler et al. (2006) reported that forest remnants as small as 8 ha were able to support populations of large-bodied woodland carabids. For the maintenance of urban biodiversity, it would be useful to know the generality of such an observation. Also habitat isolation resulting from urbanisation appears to be significant in structuring urban carabid assemblages (Sadler et al., 2006), but again there are no comparative studies using the same metrics to estimate habitat isolation.

Taken together the GLOBENET studies show some consistent patterns among cities from various parts of the world. Identification of the patterns enables us to start focusing on unravelling the mechanisms affecting species distribution in response to urbanisation. However, we still have a limited set of studies at hand, and expanding studies on carabids along urbanisation gradients to other biogeographical regions, especially tropical, other types of habitats and other taxa would enhance our understanding of the generalities of the patterns. Ultimately, in order to have an impact on urban planning and management of green areas, the information gained from such studies must feed into decision-making processes in the cities.

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References

Alaruikka, D., Kotze, D.J., Matveinen, K., Niemelä, J., 2002. Carabid beetle and spider assemblages along a forested urban–rural gradient in southern Finland. Journal of Insect Conservation 6, 195–206.

Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. Ecological Applications 6, 506–519.

Blake, S., Foster, G.N., Eyre, M.D., Luff, M.L., 1994. Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. Pedobiologia 38, 502–512.

Blake, S., Foster, G.N., Fisher, G.E.J., Ligertwood, G.L., 1996. Effects of management practices on the carabid faunas of newly established wildflower meadows in southern Scotland. Annales Zoologici Fennici 33, 139–147.

Croci, S., Butet, A., Georges, A., Aguejdad, R., Clergeau, P., 2008. Small urban woodlands as biodiversity conservation hot-spot: a multi-taxon approach. Landscape Ecology 23, 1171–1186.

Desender, K., Small, E., Gaublomme, E., Verdyck, P., 2005. Rural–urban gradients and the population genetic structure of woodland ground beetles. Conservation Genetics 6, 51–62.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecological Monographs 67, 345–366.

Elek, Z., Lövei, G., 2007. Patterns in ground beetle (Coleoptera: Carabidae) assemblages along an urbanisation gradient in Denmark. Acta Oecologia 32, 104–111.

Gaublomme, E., Dhuyvetter, H., Verdyck, P., Desender, K., 2005. Effects of urbanisation on carabid beetles in old beech forests. In: Lövei, G.L., Toft, S. (Eds.), European Carabidology 2003. Proceedings of the 11th European Carabidologists' Meeting, DIAS Report, vol. 114, pp. 111–123.

Gaublomme, E., Hendrickx, F., Dhuyvetter, H., Desender, K., 2008. The effects of forest patch size and matrix type on changes in carabid beetle assemblages in an urbanized landscape. Biological Conservation 141, 2585–2596.

Grandchamp, A.-C., Niemelä, J., Kotze, J., 2000. The effects of trampling on assemblages of ground beetles (Coleoptera, Carabidae) in urban forests in Helsinki, Finland. Urban Ecosystems 4, 321–332.

Gray, J.S., 1989. Effects of environmental stress on species rich assemblages. Biological Journal of the Linnean Society 37, 19–32.

Ishitani, M., Kotze, D.J., Niemelä, J., 2003. Changes in carabid beetle assemblages across an urban–rural gradient in Japan. Ecography 26, 481–489.

Lehvävirta, S., 1999. Structural elements as barriers against wear in urban woodlands. Urban Ecosystems 3, 45–56.

Lövei, G.L., Sunderland, K.D., 1996. Ecology and behaviour of ground beetles (Coleoptera: Carabidae). Annual Review of Entomology 41, 231–256.

Magura, T., Tóthmérész, B., Molnár, T., 2004. Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. Landscape Ecology 19, 747–759.

Magura, T., Tóthmérész, B., Lövei, G.L., 2006. Body size inequality of carabids along an urbanisation gradient. Basic and Applied Ecology 7, 472–482.

Magura, T., Lövei, G.L., Tóthmérész, B., 2008. Time-consistent rearrangement of carabid beetle assemblages by an urbanisation gradient in Hungary. Acta Oecologia 34, 233–243.

Maryański, M., Kramarz, P., Laskowski, R., Niklińska, M., 2002. Decreased energetic reserves, morphological changes and accumulation of metals in carabid beetles (*Poecilus cupreus* L.) exposed to zinc- or cadmium-contaminated food. Ecotoxicology 11, 127–139.

McDonnell, M.J., Pickett, S.T.A., 1990. Ecosystem structure and function along urban–rural gradients: an unexploited opportunity for ecology. Ecology 71, 1232–1237.

McDonnell, M.J., Pickett, S.T.A., Groffman, P., Bohlen, P., Pouyat, R.V., Zipperer, W.C., et al., 1997. Ecosystem processes along an urban-to-rural gradient. Urban Ecosystems 1, 21–36.

Niemelä, J., 1999. Is there a need for a theory of urban ecology? Urban Ecosystems 3, 57–65.

Niemelä, J., 2000. Biodiversity monitoring for decision-making. Annales Zoologici Fennici 37, 307–317.

Niemelä, J., 2001. Carabid beetles (Coleoptera, Carabidae) indicating habitat fragmentation: a review. European Journal of Entomology 98, 127–132.

Niemelä, J., Spence, J.R., 1991. Distribution and abundance of an exotic ground-beetle (Carabidae): a test of community impact. Oikos 62, 351–359.

Niemelä, J., Kotze, J., Ashworth, A., Brandmayr, P., Desender, K., New, T., et al., 2000. The search for common anthropogenic impacts on biodiversity: a global network. Journal of Insect Conservation 4, 3–9.

Niemelä, J., Kotze, D.J., Venn, S., Penev, L., Stoyanov, I., Spence, J., et al., 2002. Carabid beetle assemblages (Coleoptera, Carabidae) across urban–rural gradients: an international comparison. Landscape Ecology 17, 387–401.

R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN: 3-900051-07-0 http://www.R-project.org.

Rainio, J., Niemelä, J., 2003. Ground beetles (Coleoptera: Carabidae) as bioindicators. Biodiversity and Conservation 12, 489–506.

Sadler, J.P., Small, E.C., Fiszpan, H., Telfer, M.G., Niemelä, J., 2006. Investigating environmental variation and landscape characteristics of an urban–rural gradient using woodland carabid assemblages. Journal of Biogeography 33, 1126–1138.

Sapia, M., Lövei, G.L., Elek, Z., 2006. Effects of varying sampling effort on the observed diversity of carabid (Coleoptera: Carabidae) assemblages in the Danglobe Project, Denmark. Entomologica Fennica 17, 345–350.

Simberloff, D., 1979. Rarefaction as a distribution-free method of expressing and estimating diversity. In: Grassle, J.F., Patil, G.P., Smith, W.K., Taillie, C. (Eds.), Ecological Diversity in Theory and Practice. International Cooperative Publishing, Burtonsville, MA, pp. 159–176.

Spence, J.R., Spence, D.H., 1988. Of ground beetles and men: introduced species and the synanthropic fauna of western Canada. Memoirs of the Entomological Society of Canada 144, 151–168.

Thomas, C.F.G., Parkinson, L., Marshall, E.J.P., 1998. Isolating the components of activity-density for the carabid beetle *Pterostichus melanarius* in farmland. Oecologia 116, 103–112.

Venn, S.J., Kotze, D.J., Niemelä, J., 2003. Urbanization effects on carabid diversity in boreal forests. European Journal of Entomology 100, 73–80.

Weller, B., Ganzhorn, J., 2004. Carabid beetle community composition, body size, and fluctuating asymmetry along an urban–rural gradient. Basic and Applied Ecology 5, 193–201.