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Original article

Changes of isopod assemblages along an urban–suburban–rural gradient in Hungary

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Abstract

Responses of isopod assemblages to urbanisation were studied along an urban–suburban–rural gradient representing a decrease in the intensity of human disturbance. Pitfall trapping collected six species (*Armadillidium vulgare*, *Porcellio scaber*, *Porcellium collicola*, *Trachelipus ratzeburgii*, *Cylisticus convexus*, and *Trachelipus rathkii*). *A. vulgare* occurred abundantly in all sites reflecting the broad tolerance and invasive nature of this species. Indicator species analysis demonstrated that *P. scaber* and *T. rathkii* were significant quantitative character species for the urban site, while *T. ratzeburgii* was characteristic for the natural habitats (suburban and rural sites). CANOCO revealed that ground and air temperature show positive correlation with the distribution of *P. scaber* and *T. rathkii*, and negative correlation with *T. ratzeburgii*. Nested ANOVA on trap level showed that there were no significant differences between the number of isopod species and individuals, and the diversity of isopod assemblages in the three studied areas. Significant differences were observed at site level. The results did not support the hypothesis that diversity should decrease in response to habitat disturbance. They also contradicted the intermediate disturbance hypothesis; species richness was not the highest in the moderately disturbed suburban area. Multivariate methods detected that the isopod assemblages of the rural and suburban areas were relatively similar, while that of the urban area was relatively separated.

Keywords: Oniscidea; Globenet; Increased disturbance hypothesis; Intermediate disturbance hypothesis; Species richness; Diversity; Urbanisation

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1. Introduction

The effects of urbanisation can be explored through investigations of biotic and abiotic changes along urban-to-rural gradients [27,29]. Such gradients, from densely built inner cities to increasingly rural surroundings, reflect diminishing intensities of human influence. Urban forests are exposed to unique features compared to suburban and rural forests, including higher air pollution and disturbance intensity, the heat island phenomenon and the presence or greater abundance of exotic species [34,41]. The floristic richness of many urban habitats frequently exceeds that of less urbanised areas [45], reflecting the diverse, and mosaic nature of urban habitats and the presence of introduced plants. The city–forest ecotone also plays an important role in maintaining this diversity [5].

Recently, a multi-national research framework has been initiated to assess and compare the influence of

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urbanisation using invertebrates and standardised field methods (Globenet) [30]. Carabids were selected as the focal taxon, but other taxa (ants, and spiders) have also been studied recently within the Globenet framework [1]. According to the Globenet protocol, we involved in our research three kinds of forested habitats (urban park, suburban forested area, and rural forest), representing different levels of human disturbance [31]. The target taxon was the terrestrial, surface active woodlouse assemblage. Isopods are regarded as a useful and reliable monitoring group. They are widespread, easily identified and in most cases dominant components of the macrodecomposer guild in temperate regions [32]. Isopods belong to the saprophagous components of the soil macrofauna. These organisms process the majority of dead organic material and so influence the rate of nutrient release, an important ecosystem function. The urban fauna can be very diverse, often due to introduced, exotic species [18,20]. In this paper, we tested the following predictions for isopods in urban environments: (1) diversity should be highest in the suburban area (IDH – intermediate disturbance hypothesis); and (2) diversity should decrease from a high value in the rural area to a low one in the urban area (increasing disturbance hypothesis). We also investigated the changes in the isopod assemblages along the urbanisation gradient, identified the characteristic and/or key species across this gradient, and correlated certain environmental variables with the observed pattern of isopod abundance and species richness.

2. Material and methods

2.1. Study area

The study areas were situated in and around the city of Debrecen (Eastern Hungary), the second largest city of the country. Three forested sampling areas – each covering an area of at least 6 ha – were selected along an urbanisation gradient [16]; this represented urban, suburban and rural areas, according to the Globenet protocol [30]. All sampling sites were in forest stands dominated by English oak (*Quercus robur*); distance among the studied areas was at least 1 km [24]. In the urban park area, there were several asphalt-covered paths and the shrub layer was strongly thinned, while in the suburban area the fallen trees were removed, while in the rural area forest management was only occasional at a low-intensity level. The urban–rural gradient extended over a distance of approximately 6 km, from the city centre (47° 32′ N 21° 38′ E), through the suburbs to the neighbouring Nagyerdő Forest Reserve (47° 35′ N 21° 37′ E). The criteria for distinguishing urban, suburban and rural area were the ratio of the built-up area to the natural habitats. Disturbance was estimated based on a 1 × 1 km unit around the centre of the investigated area. In the urban area the built-up area exceeded 60%, in the suburban area it was approximately 30%, while in the rural area the built-up area was 0%. The area of the built-up environment and the natural habitats was measured by the ArcView GIS program using an aerial photograph.

2.2. Sampling design

Four sites, at least 50 m apart, were selected within each sampling area (urban, suburban, and rural). Isopods were collected at each site using pitfall traps, randomly placing 10 traps at least 10 m apart from each other at each site. This resulted in a total of 120 traps scattered along the urban–rural gradient (3 area × 4 sites × 10 traps). The pitfall traps were unbaited, consisting of plastic cups (diameter 65 mm, volume 250 ml) containing 75% ethylene glycol as a killing-preserving solution. The traps were covered with bark pieces to protect them from litter and rain. Trapped isopods were collected from the end of March to the end of November 2001. For the purpose of analysis, we pooled samples from the whole year.

Ground temperature at 2 cm depth, and air temperature and relative humidity at the soil surface were measured adjacent to each trap monthly on the morning of a typical sunny day. The statistical analyses were based on averages. We also estimated the percentage cover of leaf litter, decaying wood material, herbs, shrubs and the canopy within a radius of 1 m around each trap (see Table 1).

Table 1

Average values (±SE) of the studied environmental factors in the study areas

	Urban	Suburban	Rural
Ground temperature	24.9 ± 0.249^a	22.3 ± 0.100^b	21.6 ± 0.249^c
Air temperature	31.2 ± 0.146^a	27.3 ± 0.076^b	27.8 ± 0.220^c
Relative humidity	60.4 ± 0.744^a	76.6 ± 0.495^b	58.9 ± 0.503^c
Cover of leaf litter	21.1 ± 4.152^a	57.1 ± 4.181^b	21.1 ± 3.207^a
Cover of decaying wood material	3.8 ± 0.495^a	4.2 ± 0.557^a	11.0 ± 1.442^b
Cover of herbs	46.5 ± 5.243^a	29.1 ± 4.108^b	68.6 ± 3.348^c
Cover of shrubs	25.7 ± 3.570^a	55.1 ± 3.602^b	11.6 ± 2.183^c
Canopy cover	55.7 ± 3.577^a	49.2 ± 3.035^a	52.5 ± 3.331^a

Different letters indicate significant ($p < 0.05$) differences by ANOVA using the Tukey's post hoc test.

2.3. Data analyses

To test differences in the overall isopod abundance, species richness, and diversity (Shannon, Simpson, Berger–Parker; see [40]) among the three sampling areas (urban, suburban and rural), and among the 12 sites, nested analyses of variance (ANOVA) were performed using data from the individual traps (sites nested within the sampling areas). The distribution of data used in the ANOVA models was normal (tested by the Kolmogorov–Smirnov test [39]).

The composition of the isopod assemblages along the urban–rural gradient was compared at trap level by multidimensional scaling (MDS) based on the number of individuals using the Bray–Curtis index of dissimilarity [19].

Characteristic species of the urban, suburban and rural areas were identified using the IndVal (indicator value) procedure [3]. This method identifies quantitatively the characteristic species of the studied habitat types, and generates a significance value (p-value) for the strength of association using a randomised computerised resampling technique. The characteristic value (IndVal) of a species is expressed as a product of the specificity and fidelity measures. It receives its maximum (100) when all individuals of a species are found in a single habitat type (high specificity) and when the species occurs at all sites of that type (high fidelity) [3]. The characteristic species is defined as the most characteristic species of each habitat type, found mostly in that habitat and present in the majority of sites belonging to that habitat. This proved to be a useful method to identify the characteristic invertebrate species in several habitats [4,22,23].

The relationships between the environmental factors and the abundance and species richness of isopods were examined using the CANOCO package [43,44]. The CANOCO algorithms perform ordinations of traps and species data, and arrange the ordination according to the environmental variables that accompany the trap data [19].

3. Results

3.1. Isopod diversity along the urban–rural gradient

3.1.1. Abundance

The total isopod sample consisted of 9115 individuals representing six species; 3548 individuals belonging to six species were captured in the urban area [*Armadillidium vulgare* (Latreille, 1804), *Porcellio scaber* Latreille, 1804, *Porcellium collicola* (Verhoeff, 1907), *Trachelipus rathkii* (Brandt, 1833), *Trachelipus ratzeburgii* (Brandt, 1833), *Cylisticus convexus* (De Geer, 1778)], five species and 2720 individuals in the suburban area (*A. vulgare*, *P. collicola*, *T. rathkii*, *T. ratzeburgii*, *C. convexus*), and four species and 2847 individuals in the rural area (*A. vulgare*, *P. collicola*, *T. rathkii*, *T. ratzeburgii*). Analysing the trap-level data (number of individuals) by ANOVA we found no significant difference in overall isopod abundance (Table 2; Fig. 1A) at the gradient level, but there were significant differences at site level.

3.1.2. Number of species and diversity indices

The general pattern of changes in species richness along the gradient is similar to the changes in abundance (Table 2; Fig. 1B). We found no significant difference in overall isopod species richness. There was no significant difference in the Shannon-, Simpson- and Berger–Parker diversity along the gradient (Table 2; Fig. 2). Significant differences were observed at site level for both the Shannon and Simpson diversity indices.

3.2. Isopod assemblage composition along the urban–rural gradient

There was no marked separation among the sites along the urban–rural gradient. The MDS ordination based on the abundance data revealed that the urban assemblage was separated from the suburban and rural

Table 2
Nested ANOVA showing differences in isopod diversity, abundance and species richness along the urban–suburban–rural gradient and among the 12 sites

	Source of variation	df	MS	F	p
Shannon diversity	Gradient	2	0.0678	1.3230	ns
	Sites	9	0.0512	3.5755	<0.01
	Error	108	0.0143		
Simpson diversity	Gradient	2	1.3796	1.5376	ns
	Sites	9	0.8972	2.2529	<0.05
	Error	108	0.3983		
Berger–Parker diversity	Gradient	2	0.6152	1.7406	ns
	Sites	9	0.3534	1.6312	ns
	Error	108	0.2167		
All species, number of species	Gradient	2	0.0089	0.6306	ns
	Sites	9	0.0141	0.6205	ns
	Error	108	0.0228		
All species, number of individuals	Gradient	2	0.2479	0.4858	ns
	Sites	9	0.5102	2.2880	<0.05
	Error	108	0.2230		

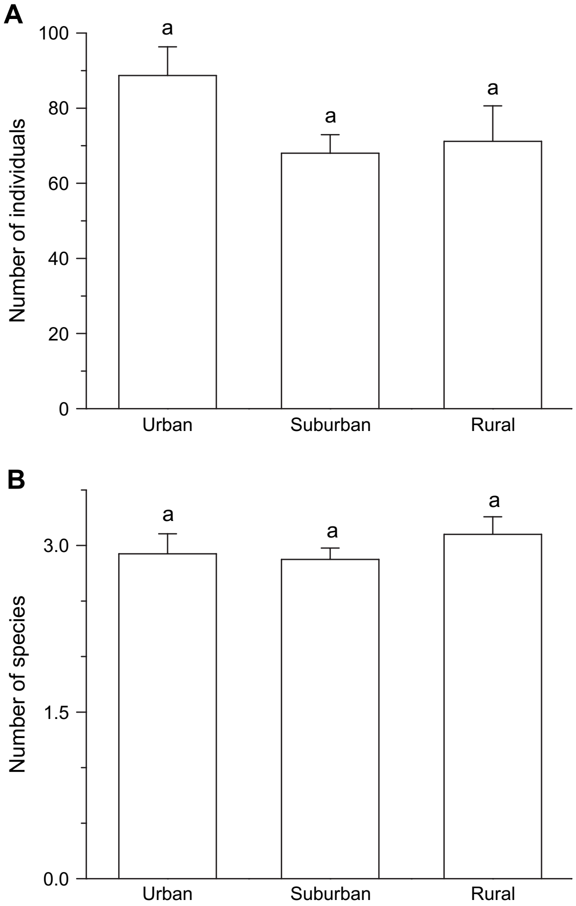

Fig. 1. Mean values (±SE) of overall isopod abundance (A) and overall isopod species richness (B) per trap along the urban–suburban–rural gradient. Different letters indicate significant ($p < 0.05$) differences based on the LSD (least significant difference) multiple comparison.

assemblage and the assemblage of the suburban and urban areas was similar to each other (Fig. 3).

We identified the quantitative character species of the studied habitat types by the IndVal procedure (Table 3): (1) habitat generalists, numerous in all areas (*A. vulgare*, *P. collicola*); (2) synantropic species (preferring the urban area) or species with broad tolerance, either recorded exclusively (*P. scaber*) or most abundant in the urban area (*T. rathkii*); (3) species characteristic of the suburban area (*C. convexus*); and (4) species characteristic for the suburban and rural areas (*T. ratzeburgii*).

3.3. Environmental factors and isopods

A Canonical Correspondence Analysis (CANOCO) revealed that ground and air temperatures showed positive correlations with the abundance distributions of *P. scaber* and *T. rathkii*, and correlated negatively with *T. ratzeburgii* (Fig. 4).

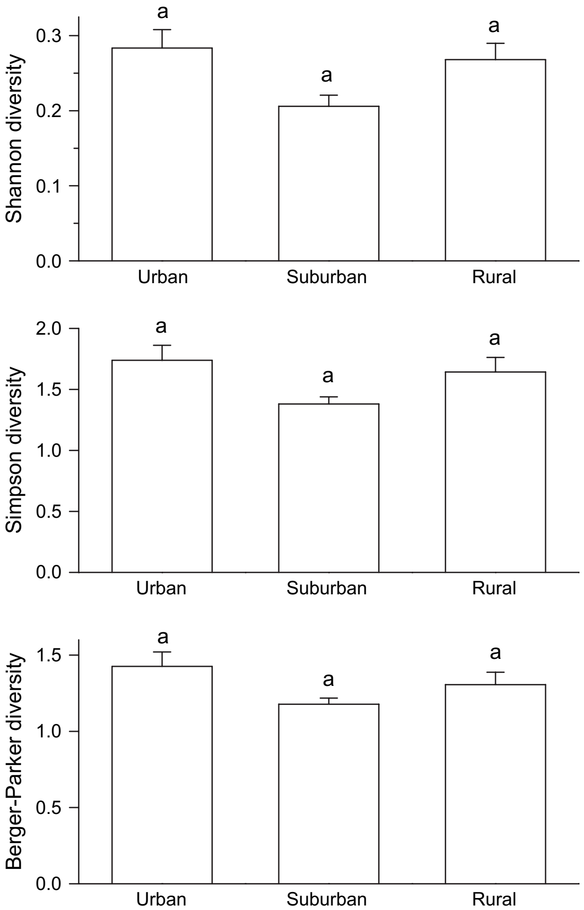

Fig. 2. Mean values (±SE) of overall isopod diversity per trap along the urban–suburban–rural gradient. Different letters indicate significant ($p < 0.05$) differences based on the LSD (least significant difference) multiple comparison.

4. Discussion

4.1. Diversity

Urbanisation causes several forms of disturbance, such as alteration, fragmentation and isolation of indigenous habitats, changes in temperature, moisture and edaphic conditions, and pollution [29]. Gray [6] hypothesised that in habitats influenced by disturbance, overall diversity should decrease. Our results did not support this hypothesis. The overall species richness and diversity of isopods were almost as high in the urban area as in the rural one. Overall diversity changes along the disturbance gradient (urban–rural gradient) can be complex, because in a group of taxa, species richness may

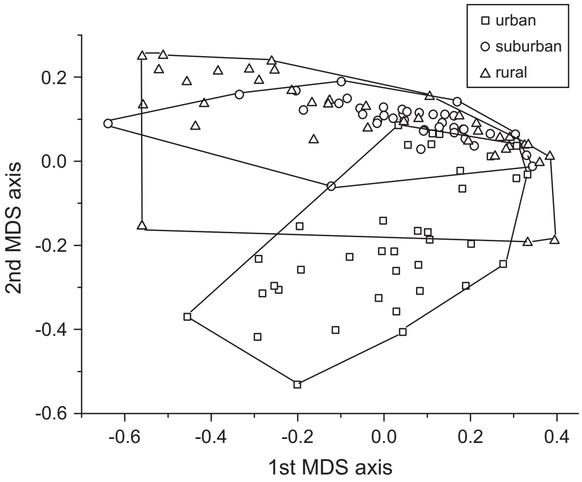

Fig. 3. Ordination of the isopod assemblages along the studied urban–rural gradient using the Bray–Curtis index of dissimilarity and MDS ordination.

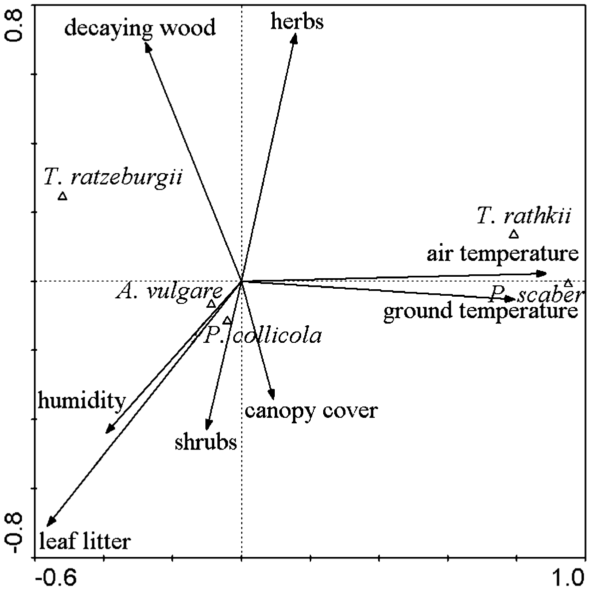

Fig. 4. Canonical Correspondence Analysis of the abundance data of isopods and the measured environmental variables. *Cylisticus convexus* was omitted because it was represented by only three individuals.

increase or decrease with disturbance depending on their habitat preference. Our findings also contradict the IDH [2]. Species richness and/or diversity were not highest in the moderately disturbed suburban area as the IDH predicts. This may be because basal species in food webs probably conform to this hypothesis, but isopods, considered as decomposers do not [49].

Moreover, urban areas do support important pools of biodiversity. Within many urban areas studied in the United States and Europe, there are places with levels of biodiversity that are comparable to the surrounding native habitats (e.g. [28,8,37]). The average isopod species richness in Hungarian deciduous forests is around 5–6 [21]. It is argued that differences in the landscapes (here: urban, suburban, and rural area) might affect species abundance[13]. However, differences in overall Oniscidea abundance between areas were not observed.

Table 3
Two-way indicator table showing the species indicator power for the habitat clustering hierarchy

	IndVal	Urban	Suburban	Rural
All habitat				
Armadillidium vulgare	95.83 ns	2088/37	2280/39	2218/39
Porcellium collicola	80.83 ns	272/31	245/35	226/31
Suburban and rural				
Trachelipus ratzeburgii	83.62*	16/3	183/36	339/35
Urban				
Trachelipus rathkii	75.07*	1143/31	10/3	64/19
Porcellio scaber	35.00*	28/14	0/0	0/0
Suburban				
Cylisticus convexus	3.33 ns	1/1	2/2	0/0

The IndVal column indicates the species indicator value for the corresponding clustering level, which is the maximum indicator value observed in all the clustering hierarchy. ns, not significant; $*p < 0.05$. In the columns for each species, the first value indicates the number of specimens present and the second value corresponds to the number of traps where the species is present, in this sample group.

4.2. Isopod assemblage composition along the urban–rural gradient

Few studies have been published on the ecological characteristics of urban isopod assemblages (community structure, diversity and abundance relations) [18,20]. Similar urban–rural forest surveys, focusing on the soil macro fauna (earthworms, isopods, and millipedes) are in progress in the framework of the Baltimore Ecosystem Studies Long Term Ecological Project, in the United States [7,15,33]. In the Baltimore metropolitan area, the abundance of isopods in the rural forest was extremely low. Most of the isopod species and specimens were collected in city parks. Two isopod species (*C. convexus* and *T. rathkii*) dominated these samples. *C. convexus* in Hungary occurred always in low numbers in human influenced habitats. It was also introduced to North America, where it became one of the most common oniscid species especially in the urban forests of the North-eastern United States [14].

A surprisingly large fraction of the regional fauna may be found in cities [18,20]. In a previous study in Budapest we found altogether 18 isopod species, of which five (27%) were introduced. Three species represented rural, forest characteristic ones [*Orthometopon planum* (Budde-Lund, 1885), *T. ratzeburgii* and *Protracheoniscus politus* (C. Koch, 1841)]. *A. vulgare* and *P. collicola* are generalist and expansive in Hungary. They were present in planted, moderately disturbed forests. The species distribution among localities reflected the degree of anthropogenic impact. *C. convexus* and *Porcellionides pruinosus* (Brandt, 1833) indicated strong human influence [20]. Urban habitats are often considered to be hotspots of species introductions [26,42]. Exotic species can easily colonize these heavily disturbed areas. Once established they can grow in number and begin to expand their range, occasionally becoming invasive by the generalized statistical "tens rule" [48].

The exclusive appearance of *P. scaber* in the urban park is in accordance with this species' habitat preference. Contrary to the Atlantic and Mediterranean areas of Europe, in Hungary this species can be found only in human settlements, and in and around houses (its Hungarian name, "cellar bug" refers to its most frequent occurrence) where heat island effect succeeds, while it is a species of ubiquitous, eurotopic nature in Britain [10]. Habitat preferences of species may depend on the biogeographical region. For example the originally East- and Middle-European *C. convexus* inhabits natural coastal and different human sites in Britain [9]. *T. rathkii*, similarly to *A. vulgare* has a wide range of habitats in whole Europe which are mainly different grasslands and synantropic places. *P. collicola* is distributed from northern Greece through Hungary to south-east Germany [38]. In Hungary it has a broad tolerance living both in humid grasslands and moderately dry forests, from occasionally inundated gallery forests to urban parks.

The relatively stronger separation of the urban area from the suburban and rural ones in our study was likely caused by the higher abundances of the generalist species. Furthermore, *T. ratzeburgii* was sensitive to changes in environmental conditions in the urban area, and it was only abundant in the suburban and rural sites.

4.3. Environmental factors and isopods

Although terrestrial isopods are dependent first of all on soil moisture and humidity, here we could use the values of indirect factors measured: ground temperature at 2 cm depth and the air temperature on the surface were higher in the urban area, which appeared to be favoured by *T. rathkii* and *P. scaber*. These species preferred the urban habitats, which is usually characterised by higher average temperature (heat islands). The negative correlation of *T. ratzeburgii* to these factors is explained by the fact that this species prefers unmanaged habitats, which are usually characterised by lower ground and air temperature.

Species distribution, spatial and temporal pattern, abundance of isopods may depend on disturbance, on food quality and shelter site availability. Proportion of dicotyledonous plants as good quality food may play an important regulating factor in isopod abundance [35,36]. The quality of leaf litter did not influence microhabitat selection of *A. vulgare* although it had significant affects on its growth and survival. Soil texture and the overall fluctuation of yearly climate had an influence on the species' spatial distribution [11]. The abundance of *Trachelipus nodulosus* C.L. Koch and *A. vulgare* proved to be correlated with soil parameters and vegetation composition, respectively [12].

4.4. Findings of other Globenet projects

There are published papers about the results of the Globenet project concerning carabid beetles in five countries, including Finland, Canada, Bulgaria, Japan and Hungary. The average number of individuals and species were compared in each project along an urban–suburban–rural gradient. In Finland both the number of individuals and the number of species increased significantly from the urban area towards the rural area [31]. Another study in Finland reported no significant difference in the number of individuals, while the number of species increased significantly from the urban towards the rural area [47]. In a third study no significant difference was found neither in the number of individuals nor in the number of species [1]. In Canada the number of individuals was the highest in the suburban area, while the number of species was the highest in the rural area [31]. In Bulgaria there were no significant differences neither in the number of individuals nor in the number of species [31]. In Japan both the number of individuals and the number of species increased from the urban area towards the rural area [17]. In Hungary the number of individuals was significantly higher in the rural area than in the suburban and urban areas, but the number of species was significantly lower in the suburban area than in the urban and rural areas during 2001. There were no differences in the number of species between the urban and rural area [24]. However, there was no significant difference in the number of species along the urbanisation gradient in Hungary during 2002 [25]. In spite of that the number of species was not different, the number of forest specialist species increased significantly from the urban towards the rural area in both years [24,25].

In Finland spider species were also studied in the Globenet project. There were no significant differences neither in the number of individuals nor in the species richness [1].

The outcome of these studies is rather diverse. It is likely, that the number of individuals and the number of species are not the most appropriate measures characterising the effect of urbanisation. Groups of species with different ecological characteristics (forest specialists, open habitat species, generalists, etc.) influenced in a strikingly different way by the urbanisation. These subtle differences in the ecological behaviour and/or habitat preference of the species should be considered during the studies. The habitat affinity indices may provide a useful way to quantify these ecological characteristics of the assemblages [46].

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