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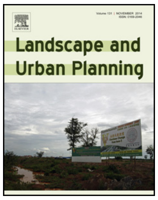

Landscape and Urban Planning

Research Paper

Millipede (Diplopoda) assemblages alter drastically by urbanisation

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HIGHLIGHTS

- We studied the effects of urbanisation on millipede assemblages in lowland forests.
- Highest millipede abundance, species richness and diversity in the suburban area.
- Our results support the intermediate disturbance hypothesis.
- Forest specialist millipedes decreased along the rural–suburban–urban gradient.

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ABSTRACT

Urban areas are radically growing worldwide, causing changes in biodiversity and natural habitats. We studied the effects of urbanisation on millipede (Diplopoda) assemblages along a forested rural–suburban–urban gradient in Hungary. We tested four hypotheses: (1) intermediate disturbance hypothesis, suggesting that millipedes are the most diverse in the suburban area; (2) habitat specialist hypothesis, assuming that the number of forest specialist species decline along the rural–suburban–urban gradient; (3) synanthropic species hypothesis, suggesting that the number of synanthropic species increase along the rural–suburban–urban gradient; and (4) mean body size hypothesis, assuming that average millipede size is decreasing from the rural area towards the urban one. We studied the effects of relevant environmental factors on the abundance of millipedes. The number of millipede individuals, species richness and diversity were significantly higher in the suburban area than in the rural and urban ones, supporting the intermediate disturbance hypothesis. The ratio of forest specialist millipede individuals and species decreased significantly along the rural–urban gradient, while the ratio of synanthropic millipede individuals and species increased significantly along the gradient. The average body size of millipedes was significantly lower in the urban area compared to the rural and suburban ones. Multivariate methods revealed changes in species composition along the rural–urban gradient. Canonical correspondence analysis demonstrated that temperature, amount of decaying wood, concentration of zinc and calcium and pH explained significant proportion of the variation in millipedes' abundance. Our results confirmed that the environmental factors and the composition of the millipede assemblages changed remarkably along the rural–suburban–urban gradient.

1. Introduction

Urban areas are radically growing worldwide causing changes in biodiversity and natural habitats (McDonald, Kareiva, & Forman, 2008). Urbanisation has a strong negative effect on species richness, mainly in urban core areas, however the effects of moderate levels of urbanisation in suburban areas has a significant variation among different taxonomic groups (McKinney, 2008). The study of McKinney (2006) showed, that cities homogenise the physical environment and natural environment as well. Biological homogenisation increases with the growth of urban areas, where the same "urban-adaptable" species become widespread and abundant.

Almost all the studies on the effects of urbanisation on arthropods are focused on predators: ground beetles (Croci, Butet, Georges, Aguejdad, & Clergeau, 2008; Magura, Lövei, & Tóthmérész, 2010; Niemelä & Kotze, 2009), ground-dwelling spiders (Magura, Horváth, & Tóthmérész, 2010), rove beetles (Magura, Nagy, &

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Tóthmérész, 2013), ground beetles and rove beetles (Deichsel, 2006), ground beetles, spiders and rove beetles (Vergnes, Le Viol, & Clergeau, 2012; Vergnes, Pellisier, Lemperiere, Rollard, & Clergeau, 2014). Much less attention was paid to decomposers, except woodlice (Hornung, Tóthmérész, Magura, & Vilisics, 2007; Vilisics, Elek, Lövei, & Hornung, 2007) and rove beetles associated with decaying organic materials (Magura et al., 2013). Millipedes are used in environmental assessment for ranking protected areas (Borges et al., 2005), habitat quality evaluation (Tuf & Tufová, 2008), and landscape stress indications (Paoletti et al., 2007). Papers dealing with urban millipedes reports mostly faunistical aspects (Enghoff, 1973; Korsós, Hornung, Szlávecz, & Kontschán, 2002; Stoev, 2004; Vilisics, Bogyó, Sattler, & Moretti, 2012) or mass migrations (Voigtländer, 2005).

Millipedes are one of the most diverse groups of terrestrial arthropod decomposers in temperate and tropical areas. The number of described millipede (Myriapoda: Diplopoda) species are over 12,000, nevertheless there are more than 1500 millipede species recorded from Europe and the estimated diversity ranks up to 80,000 species worldwide (Enghoff, 2013; Sierwald & Bond, 2007). Millipedes are vital organisms in habitats covered with wooded vegetation and shrub by consuming leaf litter (Hopkin & Read, 1992). The main effect of millipedes on soil processes is the fragmentation, mineralisation and redistribution of the organic matter, however millipedes have an influence on soil elements and soil aeriation as well (Cárcamo, Abe, Prescott, Holl, & Chanway, 2000; Hopkin & Read, 1992; Smit & Van Aarde, 2001). Soil animals, including millipedes enhance decomposition rates in temperate areas (Wall et al., 2008), such as in Hungary. According to different authors, millipedes are responsible for ingesting about 5–15%, or more of the annual litter fall (Cárcamo et al., 2000; David & Gillon, 2002; Hopkin & Read, 1992). Faecal pellets of millipedes form a rich substrate for fungi and bacteria and offer food source for other soil organisms, like earthworms (Hopkin & Read, 1992). Millipedes are not forming a distinct trophic level, rather they belong to a gradient from primary to secondary decomposers in forest decomposer communities (Scheu, 2002). Global changes in temperature, atmospheric CO_2 level and land cover could affect the abundance and diversity of decomposer invertebrates (David & Handa, 2010). Moreover, millipedes are providing important ecosystem services and affecting soil ecosystems (Brussaard et al., 1997; Lavelle et al., 2006). Changes in decomposer's diversity or abundance could affect changes in soil texture, soil elements and in soil ecosystems. As decomposers are a component of the diet of some carnivorous invertebrates, such as ground beetles, rove beetles and ants (Brunke, Bahlai, Sears, & Hallett, 2009; Hopkin & Read, 1992), the changes in decomposer assemblages may influence the upper trophic levels.

The aim of the present paper was to study the effects of urbanisation on millipede assemblages along a rural–suburban–urban gradient. We tested the following hypotheses for millipedes: (1) intermediate disturbance hypothesis (IDH) predicts that diversity should be the highest in habitat with moderate levels of disturbance (Connell, 1978; Vilisics et al., 2007). (2) Habitat specialist hypothesis supposes that the abundance and the species richness of forest specialist species decline along the rural–suburban–urban gradient (Magura, Tóthmérész, & Molnár, 2004). (3) Synantrophic species hypothesis predicts that the abundance and the species richness of synanhropic species increase along the rural–suburban–urban gradient (Magura et al., 2004; Magura, Hornung, & Tóthmérész, 2008). (4) Mean body size hypothesis supposes that average millipede size is decreasing from the rural area towards the urban one (Magura, Tóthmérész, & Lövei, 2006). We also investigated the changes of the millipede assemblages along the urbanisation gradient, identified the characteristic and/or key species across this gradient. Temperature, soil-moisture, heavy metal content of soils and vegetation heterogeneity can be modified by urban environments (Pickett et al., 2011). We studied the effects of the most relevant environmental factors on the abundance of millipedes, and we hypothesised that environmental factors like temperature, humidity, pH, heavy metals and the amount of decaying wood have a major influence on the distribution of millipede species (Hopkin & Read, 1992; Riedel, Navrátil, Tuf, & Tufová, 2009; Smith, Chapman, & Eggleton, 2006).

2. Materials and methods

2.1. Study area and sampling methods

Millipedes were studied in and around the city of Debrecen, which is the second largest city in Hungary. The city is located in the Great Hungarian Plain and has more than 204,000 inhabitants with a mean population density of 442.5 inhabitants/km^2. The typical forest of the region is a lowland oak forest; the soil of these oak forests is sandy soil with different level of humus. Three forested sampling areas were selected along the rural–suburban–urban gradient within the boundaries of the city and in the surrounding forest reserve (Magura et al., 2004) (Fig. 1). The rural–suburban–urban gradient extended over a distance of approximately 6 km, from the city centre through the suburbs to the neighbouring Nagyerdő Forest Reserve. This Forest Reserve is a protected area since 1939. The level of urbanisation was expressed by the amount of built-up area (buildings, roads and asphalt covered paths), measured by the ArcView GIS 10.0 programme using an aerial photograph in a square of 1 km^2 size. In the rural area there was no built-up area was 0%; in the suburban area it was approximately 30%, while in the urban area the built-up area exceeded 60%. In the rural area there were no forestry and other management activities and no surface modification. In the suburban area there was a moderate management activity, the fallen trees were regularly removed. In the urban area there were many pathways covered with asphalt, gravel or dirt and the management activities were intense (removing fallen trees, trunks and branches, thinning the shrub layer, mowing, planting exotic species). The studied forest patches had an extension of 6 ha at least each. They are located in an old, closed oak forest (more than 100 years *Convallario-Quercetum* association).

According to the GlobeNet protocol (Niemelä et al., 2000), four sampling sites, at least 50 m from each other, were selected within each sampling area (rural, suburban and urban). Millipedes were collected at each site using pitfall traps, randomly placing ten traps at least 10 m apart from each other. This resulted in a total of 120 traps along the gradient. The pitfall traps were unbaited, consisting of 500 ml plastic cups (65 mm diameter) containing about 100 ml 75% ethylene-glycol. Traps were covered with bark pieces to protect them from litter, rain and small animals. Trapped millipedes were collected every two weeks from the end of March to the end of November. We measured soil pH, ground temperature (in 2 cm depth), air temperature on the surface, relative humidity on the soil surface nearby the traps (Table 1). For pH measurement soil solution was prepared from 6.0 g wet soil. Soil samples were put into plastic beakers and after it filled with 50 ml deionised water. The pH was measured with a digital type Testo 206 (Testo AG, Germany). Other parameters, such as ground temperature, air temperature, and humidity were measured with field instrument Voltcraft DT-8820. We used the average of three measurements (Spring, Summer, Autumn). We also estimated the percentage cover of leaf litter, decaying wood, herbs, shrub and canopy within a circle of 100 cm radius around the pitfall traps (Table 1). Soil samples were collected along the rural–urban gradient. At each site, one bulk soil samples were collected ($n = 12$). For elemental analysis 0.2 g of soil samples were digested using 4.5 ml

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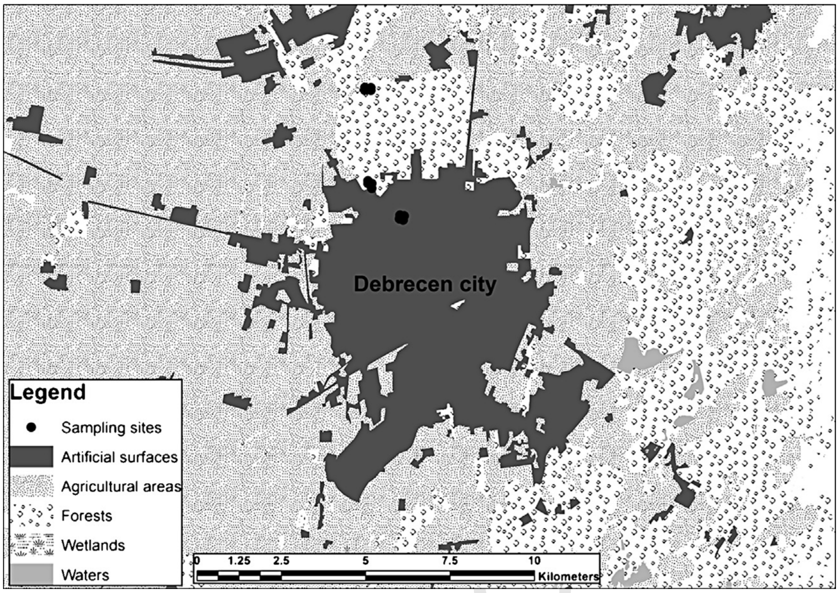

Fig. 1. Land use and the location of the sampling sites in the city of Debrecen.

65% (m/m) nitric acid and 0.5 ml 30% (m/m) hydrogen-peroxide in a microwave digestion unit (Milestone 1200 Mega) for 5 min at 300 W and for 5 min at 600 W. Digested samples were diluted to 25 ml with deionised water. Elements were analysed by inductively coupled plasma optical emission spectrometry (ICP-OES). Major elements were chosen which are useful for the mineralised millipede exoskeleton (calcium), or millipedes can accumulate them (cadmium, magnesium, lead, zinc) (Hopkin & Read, 1992) (Table 1).

2.2. Data analyses

To test differences in the millipede abundance, species richness, standardised number of species and the average body size among the three sampling areas (rural, suburban, urban) and among the 12 sites, mixed Generalised Linear Model (GLMM) was used (software: STATISTICA for Windows 7.0 (StatSoft Inc., 2010)) Data from the individual traps and nested design was used (sites were nested within the sampling areas). The response variables (abundance, species richness, standardised number of species and body size) were defined as a quasi-Poisson distribution with log link function (Zuur, Ieno, Walker, Saveiliev, & Smith, 2009). When GLM revealed a significant difference between the means, a Tukey's test was performed for multiple comparisons among means. To eliminate the effect of sample size, species richness was standardised for every trap using species rarefaction or ES(m) diversity (Heck, van Belle, & Simberloff, 1975; Tóthmérész, Máthé, Balázs, & Magura, 2011). The ES(m) diversity of millipede assemblages in a trap was estimated for 10 individuals.

Dominance of the millipedes with different habitat preference (forest specialist species and synanthropic species, see Table 2) in the given assemblage was expressed as the ratio of species in different classes. Habitat preference (forest specialist species, synanthropic species) of millipedes was determined based on recent literature (Blower, 1985; Korsós, 1994; Tuf & Tufová, 2008; Voigtländer, 2011). The synanthropic millipede species with mainly eurytopic general habitat preference, but sometimes stenotopic habitat preference as well have adapted to prefer disturbed and often man made habitats instead of natural ones (Golovatch & Kime, 2009; Korsós, 1992; Riedel et al., 2009; Voigtländer, 2011). Body size was based on the average of the adult body size (average of male and female length diameter/width) given in the literature (Blower, 1985; David, 1995; Schubart, 1934; Tadler & Taler, 1993).

The composition of millipede assemblages was compared at trap level along the rural–suburban–urban gradient by multidimensional scaling based on the abundance of millipedes using the Bray-Curtis index of dissimilarity (Legendre & Legendre, 1998). Quantitative character species of rural, suburban and urban areas were identified using the indicator value (IndVal) method. Indicator species are defined as the most characteristic species of each group, found mostly in a single group and present in the

Table 1
Average values (±SD) of the environmental variables in the study areas.

Environmental variables	Rural	Suburban	Urban
Ca (mg/kg)	1805.00 ± 769.00	1318.00 ± 478.00	2756.00 ± 293.00
Cd (mg/kg)	0.40 ± 0.10	0.20 ± 0.10	0.40 ± 0.10
Mg (mg/kg)	1078.00 ± 83.00	603.00 ± 110.00	1086.00 ± 210.00
Pb (mg/kg)	17.70 ± 3.10	14.00 ± 4.10	18.90 ± 3.20
Zn (mg/kg)	16.70 ± 1.20	12.40 ± 2.70	20.80 ± 2.40
pH	5.86 ± 0.24	4.73 ± 0.25	6.41 ± 0.28
Relative humidity (%)	57.26 ± 2.13	75.52 ± 2.83	60.01 ± 3.63
Ground temperature (°C)	20.32 ± 1.34	21.19 ± 0.32	24.75 ± 0.38
Air temperature (°C)	26.15 ± 1.37	25.80 ± 0.41	30.89 ± 0.69
Canopy cover (%)	51.74 ± 16.75	47.45 ± 3.20	54.73 ± 5.80
Cover of shrubs (%)	10.95 ± 6.59	54.07 ± 12.40	23.89 ± 7.30
Cover of herbs (%)	66.88 ± 12.24	31.11 ± 17.88	45.95 ± 24.68
Cover of decaying wood (%)	10.70 ± 3.87	4.33 ± 1.45	3.61 ± 1.85
Cover of leaf litter (%)	20.53 ± 13.25	56.15 ± 12.39	20.02 ± 22.38

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Table 2
Habitat preference and quantitative character values of the millipede species. The IndVal column shows the species character value for the corresponding cluster level.

Species	Habitat preference	IndVal	*p*	Urban area		Suburban area		Rural area	
				A	*B*	*A*	*B*	*A*	*B*
Rural									
Mastigona bosniensis	Forest	51	*	4	3	66	18	198	24
Suburban and Rural									
Megaphyllum projectum	Forest	99.6	*	9	4	2921	40	1546	40
Polydesmus complanatus	Forest	85.9	*	4	4	338	40	79	30
Suburban									
Polydesmus schaessburgensis	Forest	85.2	*	5	4	244	37	16	9
Cylindroiulus boleti	Forest	65.3	*	12	8	81	30	0	0
Leptoiulus proximus	Forest	10	*	0	0	5	4	0	0
Choneiulus palmatus	Synanthropic	5.6	ns	1	1	3	3	0	0
Proteroiulus fuscus	Synanthropic	2.5	ns	0	0	1	1	0	0
Urban and Suburban									
Ophyiulus pilosus	Synanthropic	97.5	*	465	40	397	38	0	0
Megaphyllum unilineatum	Synanthropic	59.9	*	366	13	561	37	20	10
Urban									
Kryphioiulus occultus	Synanthropic	51.1	*	58	25	23	12	3	3
Cylindroiulus latestriatus	Synanthropic	15	*	10	6	0	0	0	0
Cylindroiulus caeruleocinctus	Synanthropic	10	*	4	4	0	0	0	0
Enantiulus nanus	Forest	2.5	ns	2	1	0	0	0	0

Notations: ns, not significant; *A*: the number of specimens present; *B*: the number of traps where the species is present in the sample group.
* $p < 0.05$.

majority of sites belonging to that group. The method derives indicators from any hierarchical or non-hierarchical site classification. The indicator value (IndVal) of a species is expressed as a product of the specificity and fidelity measure. The specificity measure (A_{ij}) is defined in the following way:

$$A_{ij} = \frac{N\text{individuals}_{ij}}{N\text{individuals}_{i.}},$$

where Nindividulas$_{ij}$ is the mean number of individuals of species *i* across sites of group *j*, while Nindividuals$_{i}$ is the sum of the mean numbers of individuals of species *i* over all groups. The fidelity of the species is measured by B_{ij}:

$$B_{ij} = \frac{N\text{sites}_{ij}}{N\text{sites}_{.j}},$$

where Nsites$_{ij}$ is the number of sites in cluster *j* where species *i* is present, while Nsites$_{j}$ is the total number of sites in that cluster. Therefore, the Indicator Value (IndVal$_{ij}$) is as follows:

$$\text{IndVal}_{ij} = A_{ij} \times B_{ij} \times 100.$$

The indicator value of a species *i* is the largest value of IndVal$_{ij}$ observed over all groups *j*.

The indicator value is maximum (100) when all individuals of a species are found in a single group of sites (high specificity) and when the species occurs in all sites of that group (high fidelity) (Dufrêne & Legendre, 1997; Elek, Magura, & Tóthmérész, 2001). Relationships between environmental factors and the abundance of millipedes were examined using the detrended canonical correspondence analysis (DCCA) by second order polynomials calculated by the CANOCO package. Triplot scaling in the ordination was symmetric (ter Braak & Smilauer, 1998).

3. Results

Fourteen millipede species were identified along the rural–suburban–urban gradient belonging to three millipede orders (Julida, Chordeumatida, Polydesmida) (Table 2). In the rural site there were 6, in the suburban site 11, in the urban site 12 millipede species. The highest number of millipede individuals was caught in the suburban area (4660 individuals). We trapped fewer individuals in the rural (1842 individuals) and in the urban area (940 individuals). The most abundant species was *Megaphyllum projectum*, presenting in all of the investigated areas, made up about 60% of the total catch. In the urban area *Ophyiulus pilosus* and *Megaphyllum unilineatum* were the most abundant species, while in the suburban area *M. projectum* was by far the most abundant species. In the rural area *M. projectum* represented more than 80% of the total number of trapped millipedes.

The overall number of individuals and species number were significantly higher in the suburban area than in the rural and urban areas ($\text{Chi}^2 = 264.26$; df = 2, 9; $p < 0.0001$; $\text{Chi}^2 = 209.15$; df = 2, 9; $p < 0.0001$ Fig. 2a and b). The standardised number of species was also significantly higher in the suburban area than in the other areas ($\text{Chi}^2 = 158.85$; df = 2, 9; $p < 0.0001$; Fig. 2c). The ratio of forest specialist millipede individuals and the ratio of forest specialist species was decreased significantly along the rural–suburban–urban gradient ($\text{Chi}^2 = 914.98$; df = 2, 9; $p < 0.0001$; $\text{Chi}^2 = 239.01$; df = 2, 9; $p < 0.0001$; Fig. 3a and b). The ratio of synanthropic millipede individuals and the ratio of synanthropic species was increased significantly along the gradient ($\text{Chi}^2 = 1458.36$; df = 2, 9; $p < 0.0001$; $\text{Chi}^2 = 232.62$; df = 2, 9; $p < 0.0001$; Fig. 4a and b). The average body size of the millipedes was significantly lower in the urban area compared to the rural or suburban ones ($\text{Chi}^2 = 54.47$; df = 2, 9; $p < 0.0001$; Fig. 5). The DCCA triplot showed that there was a separation among the sites along the rural–suburban–urban gradient based on the abundance of species. The urban sites differed from the suburban and rural sites, which were more similar to each other. The urban sites are located on the right part, whereas the suburban sites on the centre and the rural sites on the left part of the ordination scatter-plot. The urban sites were characterised by higher ground and air temperature, higher pH values, lower amount of decaying wood and by higher concentration of calcium and zinc in the soil. The suburban sites disposed of higher relative humidity and cover of herbs. The rural sites had higher amount of decaying wood, lower pH values and lower ground and air temperature. The triplot graph also demonstrated that *Kriphyoiulus occultus*, *M. unilineatum* and *O. pilosus* were associated with the urban sites of higher ground and air temperature, higher pH values and lower amount of decaying wood. The results showed that *Polydesmus complanatus* and *M. projectum* were characteristic to the suburban and rural sites. However *Mastigona bosniensis* favoured the rural sites with lower percentage of canopy cover (Fig. 6).

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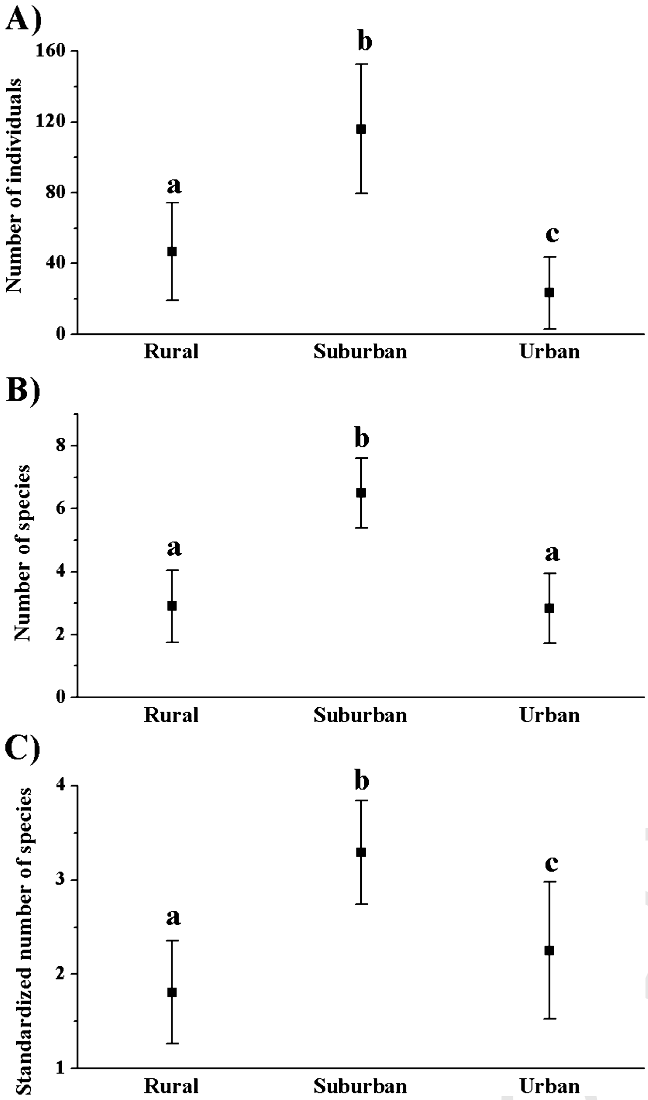

Fig. 2. Mean values (±SD) of the overall millipede abundance (A), species richness (B) and standardised number of millipede species for 10 individuals (C) per trap along the rural–suburban–urban gradient. Different letters indicate significant differences by Tukey test.

There was a marked separation among the sites along the rural–urban gradient by the hierarchical cluster analysis. Urban sites formed a distinct cluster based on the millipede abundances, while rural and suburban sites formed an other cluster (Fig. 7). We identified five groups of quantitative character species by the IndVal method for the compared areas (Table 2): (1) species preferring the urban area, either recorded exclusively or being most abundant in the urban area (*Cylindroiulus caeruleocinctus*, *Cylindroiulus latestriatus*, *Kryphioiulus occultus*); (2) species characteristic of urban and suburban area (*O. pilosus*, *M. unilineatum*); (3) species preferring the suburban area (*Cylindroiulus boleti*, *Leptoiulus proximus*, *Polydesmus schaessburgensis*); (4) species characteristic of the suburban and rural areas (*M. projectum*, *P. complanatus*); and (5) species preferring the rural area (*M. bosniensis*).

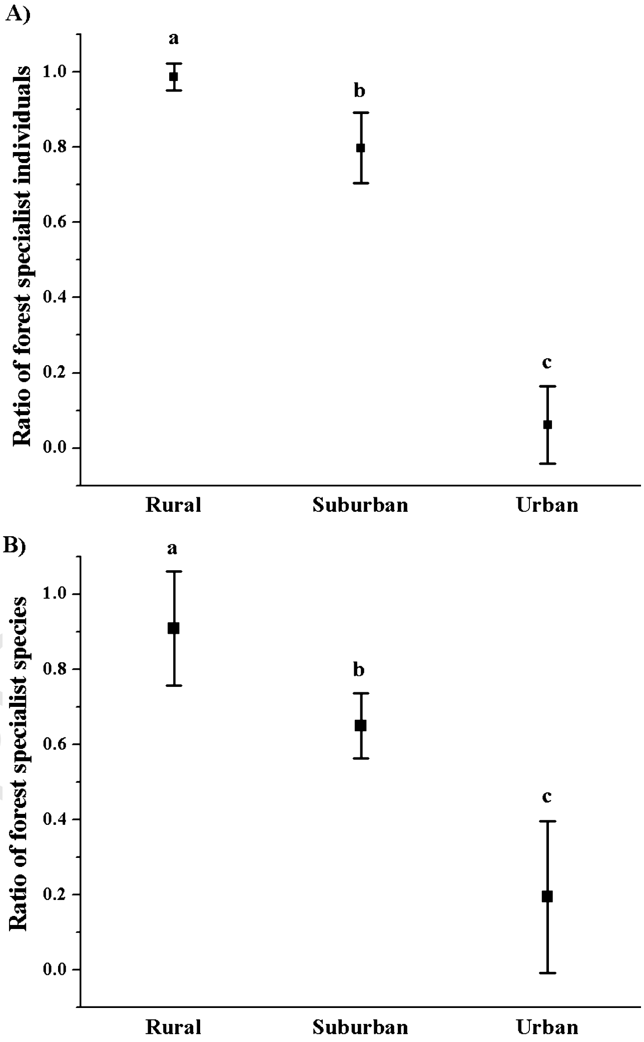

Fig. 3. Mean value of the ratio (±SD) of the forest specialist millipede individuals (A) and the forest specialist millipede species (B) per trap along the rural–suburban–urban gradient. Different letters indicate significant differences by Tukey test.

4. Discussion

We studied the effects of urbanisation on millipede assemblages along a forested rural–suburban–urban gradient in Debrecen (NE Hungary). The total number of millipede individuals, species richness and diversity were significantly higher in the suburban area than in the rural and urban ones as predicted by the intermediate disturbance hypothesis. According to the habitat specialist hypothesis we found a significant decrease of forest specialist millipedes along the rural–urban gradient. On the other hand a significant increase of synanthropic millipede species was observed along the same gradient as predicted by the synanthropic species hypothesis. The average body size of the millipedes was significantly lower in the urban area compared to the rural and suburban ones, supporting the mean body size hypothesis.

The number of collected millipede species in our study (14 species) is 14% of the Hungarian millipede fauna. Other papers dealing with millipedes in urban areas of temperate Europe – summarised by Vilisics et al. (2012) – showed similar millipede diversity (8–26 species in urban areas). In our study the most abundant species, *M. projectum* is a characteristic and widespread species in Central-European natural woodlands (Voigtländer, 2011). It is the most abundant litter-dwelling millipede species in Hungary in oak and mixed forests (Korsós, 1994).

The overall number of individuals and species, and the standardised number of species was significantly higher in the suburban area than in the other areas. These results support the IDH described by Connell (1978). A few urbanisation studies on invertebrates supported the IDH in case of other detritivorous arthropods: woodlice

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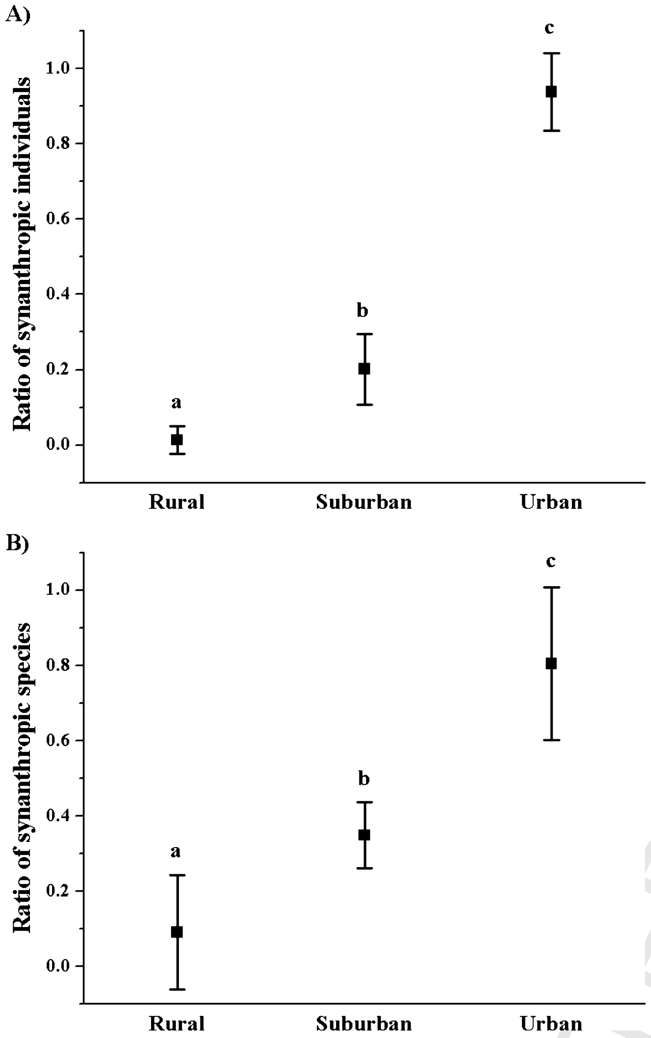

Fig. 4. Mean value of the ratio (±SD) of the synanthropic millipede individuals (A) and the synanthropic millipede species (B) per trap along the rural–suburban–urban gradient. Different letters indicate significant differences by Tukey test.

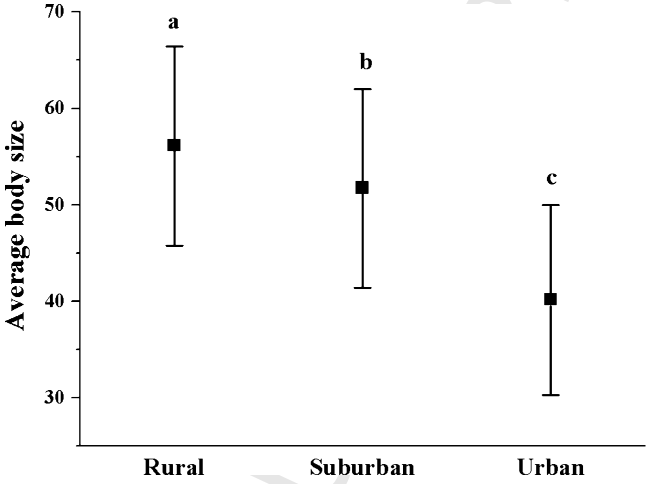

Fig. 5. Mean values (±SD) of the millipede body size (average of the adult body size = average of male and female length × diameter/width) per trap along the rural–suburban–urban gradient. Different letters indicate significant differences by Tukey test.

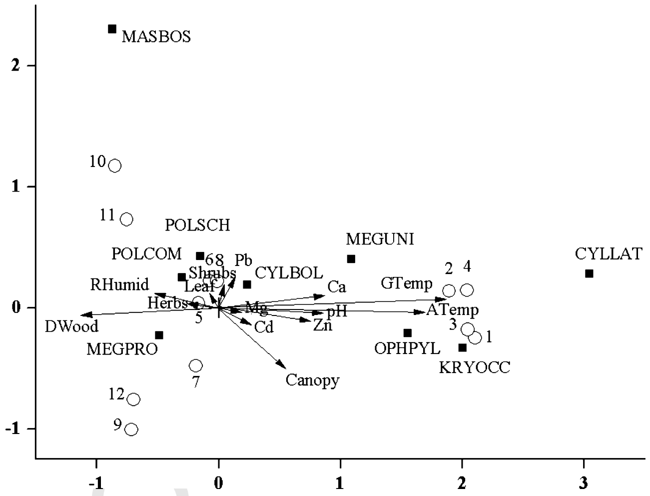

Fig. 6. DCCA for the nine frequent millipede species where the number of individuals made up at least 1% of the total catch. Empty circles represent the sampling sites (1–4: urban sites, 5–8: suburban sites, 9–12: rural sites). The arrows denote the increase of the value of the environmental variables and the concentration of macroelements and heavy metals (ATemp: air temperature on the surface; Canopy: canopy cover; DWood: cover of decaying wood material; GTemp: ground temperature at 2 cm depth; Herbs: cover of herbs; Leaf: cover of leaf litter; RHumid: relative humidity on the surface; Shrubs: cover of shrubs; Ca: calcium; Cd: cadmium; Mg: magnesium, Pb: lead, pH: pH of the soil, Zn: zinc). Filled squares and the six-letter abbreviations indicate the millipede species (CYLBOL: *Cylindroiulus boleti*; CYLLAT: *Cylindroiulus latestriatus*; KRYOCC: *Kryphioiulus occultus*; MASBOS: *Mastigona bosniensis*; MEGPRO: *Megaphyllum projectum*; MEGUNI: *Megaphyllum unilineatum*; OPHPIL: *Ophyiulus pilosus*; POLCOM: *Polydesmus complanatus*; POLSCH: *Polydesmus schaessburgensis*).

(Vilisics et al., 2007), ground beetles (Tóthmérész et al., 2011) and rove beetles (Vergnes et al., 2014) so far. In some studies high suburban millipede species richness were shown (Enghoff, 1973), but other ones showed negative effect of urban disturbance on millipede species richness together with higher diversity in peri-urban habitats (Mwabvu, 2007). In general, several studies showed a decline in animal species richness towards the rural–suburban–urban gradient, but sometimes species richness was high in suburban habitats which are more similar to natural areas (McKinney, 2006). In one third of the investigated invertebrate studies McKinney (2008) showed increasing species richness in suburban areas with moderate level of urbanisation. The high diversity and density in suburban forest remnants can be explained

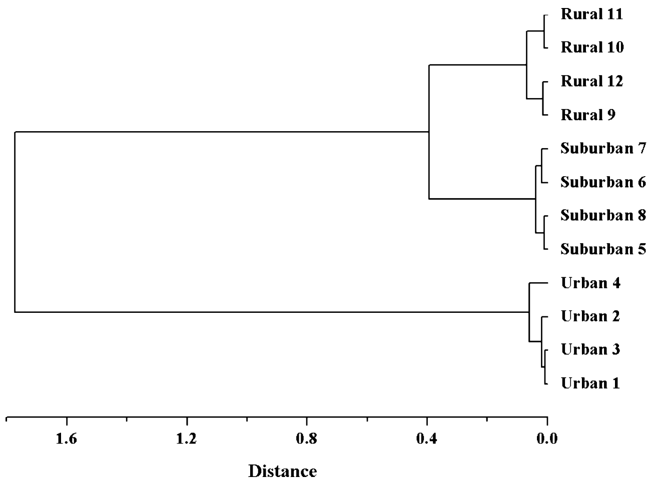

Fig. 7. Hierarchical cluster analysis of the millipede assemblages along the studied rural–suburban–urban gradient using Bray–Curtis index of dissimilarity and Ward fusion method.

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with the land cover changes in urban areas, which may critical for habitat specialist saprophagous macroarthropods in Europe (David & Handa, 2010). Higher habitat heterogeneity in and around cities can support higher diversity than in stable natural forest ecosystems (Smith et al., 2006). David, Devernay, Loucougaray, and Le Floc'h (1999) also showed that millipede species diversity and population density were lower at closed wooded sites than in more opened ones. The degree of land cover heterogeneity is more important for millipede diversity than large uniform natural habitats (David & Handa, 2010). In our situation, the higher habitat heterogeneity of the suburban area may have a positive effect on millipede diversity. In the suburban area, habitat patches with closed canopy co-occur with patches of moderate closure because of the moderate management activity. This patchiness contributed to the higher habitat heterogeneity and facilitated the survival and persistence of both the forest specialist species and the synanthropic species in the suburban area.

Both the ratio of forest specialist millipede species and the ratio of forest specialist millipede individuals were decreased significantly along the rural–suburban–urban gradient. However, both the ratio of synanthropic millipede species and the ratio of synanthropic millipede individuals were increased significantly along the gradient. These results are consistent with the previous findings showing decline of forest specialist species and increase of synanthropic species along the urbanisation gradient (Magura et al., 2008; Magura, Horváth, et al., 2010; Magura, Lövei, et al., 2010; McKinney, 2006, 2008; Tóthmérész et al., 2011). High number of synanthropic and non-native millipede species in urban and suburban areas along Europe was previously shown by some authors (Korsós et al., 2002; Riedel et al., 2009; Smith et al., 2006). In Switzerland high number of widespread and synanthropic millipede species and low millipede density was observed in urban areas, possibly as a result of biotic homogenisation (Vilisics et al., 2012). Habitat loss may result in the drastic decline of forest specialist species (David & Handa, 2010). In our situation, in the urban area asphalt covered pathways fragment the habitat into even smaller patches. The division of the original forests into smaller, isolated patches causes a loss of forest specialist species through a reduction in the habitat area and limited dispersal (Didham, Ghazoul, Stork, & Davis, 1996; Didham, Kapos, & Ewers, 2012).

Millipede body size is usually higher in habitats with higher temperature (Enghoff, 1992; Golovatch & Kime, 2009). However, our study showed that the average millipede body size in urban area with higher ground and air temperature was smaller than in rural and suburban ones. The smaller average body size in the urban area may be a result of the lower food quality, which is also affecting the body size of the millipedes (Enghoff, 1992). The studied urban area offers higher amount of non-native and exotic plant material, which can cause lower food quality. Magura et al. (2006), studying ground beetles, also reported that small individuals were more frequent in the urban areas than in suburban and rural ones. Based on the abundance of the species, both the DCCA analysis and the hierarchical cluster analysis showed higher similarity of the assemblages of rural and suburban sites, while the assemblages of urban sites were notably separated. These results can be explained by the facts that forest specialist species preferred mainly the rural and suburban sites, while synanthropic species preferred the urban sites.

Urbanisation causes several types of disturbance. From the rural area towards the urban one the number and density of human inhabitants increases. These processes result in higher coverage of artificially created surfaces, air and soil pollution, urban heat island effect as well as variations in litter decomposition and ecosystem processes (Carreiro & Tripler, 2005; Rizwan, Denis, & Liu, 2008). The radical changes in environmental conditions in urban areas can act as a filter, removing all the species lacking specific combinations of traits, as described by Keddy (1992). Forest specialist species are less adaptable to an environment with high temperature, low humidity and lower food quality. In suburban sites, at moderate level of disturbance even these species can find suitable environment. In urban landscapes modifications affect the dispersal of the organisms through fragmentation, on the other hand the modification of the environment at the local scale modifies the niche of organisms (Vergnes et al., 2012). All these alterations in the urban area may cause the decrease of forest specialist millipede species and the increase of synanthropic species.

Similarly to previous study of Pickett et al. (2011) in our study the urban area was also characterised by higher temperatures (both air and ground temperatures), lower relative humidity, higher pH values, lower amount of decaying wood and leaf litter and higher concentration of studied heavy metals and calcium concentration in soils. Heavy metal deposition may affect decomposition in terrestrial ecosystems, moreover millipedes can accumulate heavy metals. The aerial fallout of zinc, cadmium and lead may lead to the decrease of millipede abundance (Hopkin & Read, 1992). Higher concentration of heavy metals in urban soils may correlate with the lower amount of leaf litter in urban areas (usually removed by management activties). Higher amount of leaf litter may act as barrier for heavy metals, preventing them to reach the soil (Smith et al., 2006). However, Santorufo et al. (2014) showed that the presence of heavy metal in plants may affect the characteristic of leaves that are more difficult to eat by medium sized detritivors. High concentrations of heavy metal lead to the accumulation of leaf litter by reducing its quality.

As in other urban studies (Smith et al., 2006), high calcium concentrations in the studied urban area also positively correlated with soil pH. Millipedes need calcium to build up their calcified exoskeleton. In the urban area the high calcium concentration was not resulted in increase of the number of millipede individuals. Other effects, like habitat loss may override the positive effect of elevated calcium concentration. Four synanthropic species (*C. latestriatus, K. occultus, M. unilineatum* and *Ophyilus pilosus*) showed positive correlation with the concentration of zinc, calcium and pH values. These, mainly xerothermic and synanthropic species may tolerate this habitat with higher concentration of heavy metals and pH value. Expansion of xerothermic millipede species in other European cities was also reported (Stoev, 2004). These xerothermic species prefer more opened habitats and some of them are today widespread urban generalist species (Riedel et al., 2009; Smith et al., 2006; Voigtländer, 2011). The millipede species, *C. boleti* preferred the urban and suburban sites, though it was mentioned in the earlier literature as a forest specialist species. *C. boleti* is probably a more generalist species, as it was suggested by Tuf and Tufová (2008).

We found that *P. complanatus* and *M. projectum* were characteristic species of the suburban and rural sites, whereas *Mastigona bosniense* was most abundant in the rural sites with lower canopy cover. These results are similar to earlier findings (Korsós, 1994; Riedel et al., 2009; Voigtländer, 2011). Urban sites may offer suitable environment for xerothermic and tolerant species, but forest specialist species seem to decline. Urban sites are also suitable for holarctic, globally widespread and exotic millipede species. *C. caeruleocinctus*, which was recorded exclusively in the urban sites in our study, is a good example of the millipede introduction into urban habitats around Europe (Bogyó & Korsós, 2010; Mock, 2006). Change of the composition of millipede assemblages may be a result of the alteration of the food (leaf litter) quality. In urban sites invasive and exotic plant species can overrun native species and adversely affect native habitats (David & Handa, 2010; Vitousek, D'Antonio, Loope, & Westbrooks, 1996). Due to their aggressive growth habits, invasive species may prevent regeneration of the native forest ecosystems. The altered composition of the

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tree species has a major effect on millipede communities (Stašiov et al., 2012).

5. Conclusions

According to our results the intermediate disturbance hypothesis was proved, as the total number of millipede individuals, species richness and diversity were significantly higher in the suburban area than in the rural and urban ones. The mixture of the urban habitat types and natural habitat types, as well as higher openness in suburban areas seems to support higher millipede diversity than in rural and urban areas. Urban sites were suitable habitats for xerothermic, tolerant and invasive millipede species. However, alteration of food quality, habitat loss and fragmentation had significant negative effect on forest specialist species. To protect forest specialist soil invertebrates it is essential to prevent habitat loss and fragmentation of natural habitats. It is very important to create and manage urban parks and suburban forests in a way which supports natural forest fragments. Specialist litter-dwelling macroarthropods can survive in even very small habitat fragments (David & Handa, 2010). It is recommended to leave forest patches in undisturbed conditions, leaving fallen trees, trunks and leaf litter on the ground. Creation of new (asphalted) pathways increases fragmentation and should be neglected as well as building of new public utilities and buildings supporting urban heat island effect. Reducing the percentage of big uniform open habitats in urban parks is also recommended.

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