

Millipedes (Myriapoda: Diplopoda) in human-modified landscapes

Egyetemi doktori (PhD) értekezés

Bogyó Dávid

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1. Introduction

1.1. Biology and ecology of millipedes (Myriapoda: Diplopoda)

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 12000. More than 1500 millipede species recorded from Europe and the estimated diversity ranks up to 50000-80000 species worldwide (Sierwald & Bond, 2007; Golovatch & Kime, 2009; Enghoff, 2013; Minelli & Golovatch, 2013).

Millipedes (Diplopoda) represent one of the four classes of Myriapoda, together with Chilopoda (centipedes), Symphyla and (Paurapoda). The main difference from these taxonomical groups is, that millipedes have diplosegments (carrying two leg pairs per segments). The first millipede fossil record is originated from the Upper Silurian (ca. 422-420 million years ago), but the expansion of this animals expanded during the Devonian and Carboniferous periods (from 419 to 299 million years ago) (Hopkin & Read, 1992). The Class Diplopoda has 16 recent orders, for whom 7 (Polyxenida, Glomerida, Polyzoniida, Julida, Callipodida, Chordeumatida, Polydesmida) is presented in Hungary (Korsós, 2008).

Millipedes mainly have an elongated and cylindrical body structure and a calcified cuticle. The head capsule is usually strongly calcified to help moving the animal in the soil, between dead wood and leaf litter. The millipede body usually consist from numerous segments, up to 192 (Hopkin & Read, 1992; Marek & Bond, 2006). The “leggiest” millipede species - *Illacme plenipes* - has a leg number of 750 pairs (Marek & Bond, 2006), but most millipedes have fewer than 50 leg pairs. Except Penicillata and Glomerida, male millipedes have modified limbs on the seventh body ring, called gonopods. The most important female sexual organs, called vulvae are internal structures, but sometimes visible during copulation behind the second pair of legs. Millipede vulvae and male gonopods are unique to each species and do have a major importance in species identification. Millipedes are well known about chemical defence, which is the most important

defence system except the usually hard exoskeleton. Majority of the millipedes have defense glands, usually one per segment, producing a wide range of chemicals (hydrogen cyanide, benzoquinone, quinazolinones etc.) (Hopkin & Read, 1992). In spite of possible toxic effects, some people from Burkina Faso regularly eat millipedes, benefiting the high percentage of protein content in millipede body and possible antimalarial value (Enghoff et al., 2014).

Millipedes are vital organisms in habitats covered with trees and shrub by consuming leaf litter (Hopkin & Read, 1992); typical micro-habitats are the followings: leaf litter, litter/soil interface, the uppermost soil, and dead wood (Golovatch & Kime, 2009). On the other hand millipedes can dwell in extreme habitats as well: alpine ecosystems, deserts, caves or even areas close to the Arctic circle (Hopkin & Read, 1992; Mikhajlova, 2004; Mock & Tajovsky, 2008; Golovatch & Kime, 2009; Minelli & Golovatch, 2013). The main effect of millipedes on soil processes is fragmentation, mineralisation and redistribution of the organic matter, however millipedes have an influence on soil elements and soil aeration as well (Cárcamo et al., 2000; Hopkin & Read, 1992; Smit & Van Aarde, 2001). The main food source of millipedes is leaf litter, thus millipedes are responsible for ingesting about 5-15 %, or more of the annual litter fall (Cárcamo et al., 2000; David & Gillon, 2002; Golovatch & Kime, 2009). 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 & Falca, 2000; Scheu 2002). Millipedes are providing important ecosystem services and affecting soil ecosystems (Brussaard et al., 1997; Lavelle et al., 2006). On the other hand, millipedes are well known about more or less harmful, but sometimes shocking mass migrations and some species can act as pests of different crops (Blower, 1985; Hopkin & Read, 1992; Kania & Tracz, 2005; Voigtländer, 2005). Millipedes were used as indicator species in some studies: Borges et al. (2005) used them to rank protected areas, Paoletti et al. (2007) suggested them as landscape stress indicators, Synder and Hendrix (2008) used millipedes as bioindicators of ecological restoration, while Tuf & Tufová (2008) recommended them to use in habitat quality evaluation.

1.2. Millipedes in European cities

The distribution of millipedes is generally limited because of their low natural dispersal capabilities. Human activities strongly affect the distribution of several millipede species, in some cases reshaping their natural dispersion to a considerable extent. Half of the species occurring in the British Isles was introduced into North America (Hopkin & Read, 1992). Cosmopolitan and Holarctic species of millipedes and other soil animals are known to inhabit European urban habitats (Smith et al., 2006; Riedel et al., 2009; Vilisics et al., 2012). Human activities, such as gardening, transportation of soil, and cultivation of ornamental plants are likely the most important factors for species exchanges of less mobile organisms such as millipedes. At the same time other studies (Bogyó & Korsós, 2009; Riedel et al., 2009; Kocourek, 2014; Bogyó et al., 2015) shows that the native species pool has an effect on urban soil fauna: native species typical in natural and semi-natural habitats do occur within and around cities. Particular urban habitats, such as botanical and private gardens and parks, however, harbour established populations of alien soil arthropods (Korsós et al., 2002; Mock, 2006; Riedel et al., 2009; Stoev et al., 2010; Bogyó & Korsós, 2010), too.

Reviewing the literature on the millipede fauna of 17 European cities (Bratislava, Budapest, Bucharest, Copenhagen, Debrecen, Kiel, London, Lublin, Lugano, Lucerne, Moscow, Olomouc, Prague, Sofia, Vienna, Warsaw and Zürich) we have found 90 species of millipedes living in and around this cities (see Table 1, based on the works of Lokshina, 1960; Bielak, 1964; Strasser, 1966; Enghoff, 1973; Davis, 1979; Tischler, 1980; Jedryczkowski, 1982; Korsós, 1992; Jedryczkowski, 1996; Korsós et al., 2002; Stoev, 2004; Giurginca, 2006; Smith et al., 2006; Bogyó & Korsós, 2009; Reidel et al., 2009; Kania, 2011; Holecová et al.; 2012; Vilisics et al., 2012; Giurginca et al., 2014; Kocourek, 2014; Bogyó et al., 2015; Bogyó et al. (unpublished)). Some cities have a very poor fauna, but on the other hand some well studied and big, heterogenous cities show high species number (Prague 50 species, Warsaw 34 species, Budapest 33 species). The average millipede species number of the above discussed cities is ~19.5. The most widespread urban millipede species in Europe are as it follows: *Brachydesmus superus* (found in 14 cities), *Ophiulus pilosus* (found in 13

cities), *Blaniulus guttulatus*, *Kryphioiulus occultus*, *Polydesmus complanatus*, *Proteroiulus fuscus* (all of them found in 10 cities). This species are mainly reported as eurytopic species with synanthropic preference and often preferring xeric and/or open landscapes (Blower, 1985; Tuf & Tufová, 2008; Voigtländer, 2011). All of this species were listed by Szlávecz et al. (2008, unpublished) as homogenizing millipede species in Europe. Many of this studies reported alien and invasive millipede species, in some cases with expanding ranges (Korsós, 1992; Korsós et al., 2002; Bogyó & Korsós, 2010; Kania, 2011). The alien millipede, *Oxidus gracilis* occurred in the half of the cities described above.

1.3. Urbanization and ground dwelling invertebrates

Urban areas are radically growing worldwide causing changes in biodiversity and natural habitats (McDonald et al., 2008). Urbanization has a strong negative effect on species richness, mainly in urban core areas. However, the effects of moderate levels of urbanization in suburban areas has a substantial variation among different taxonomic groups (McKinney, 2008). The study of McKinney (2006) showed, that cities homogenise the physical environment and natural environment, biotic homogenisation increases with the growth of urban areas, where the same urban-adaptable species become widespread and abundant.

During the last decades, studies of animal taxa along urbanization gradients were popular research topic around the world. Many of the published papers focused on predators, such as carabid beetles: Niemelä et al. (2002), Ishitani et al. (2003), Venn et al. (2003), Magura et al. (2004), Sadler et al. (2006), Elek & Lövei (2007), Croci et al. (2008), Magura et al. (2008), Tóthmérész et al. (2011), reviewed by Niemelä & Kotze (2009) and Magura et al. (2010). Spiders along urbanization gradients were investigated by Alaruikka et al. (2002), Magura et al. (2008), Horváth et al. (2012). Rove beetles were studied by Magura et al. (2013), Protura were studied by Christian & Szeptycki (2004). Multi taxa approaches on the same topic were published by Deichsel (2006), Vergnes et al. (2012) and Vergnes et al. (2014).

For decomposers the number of published papers is rather limited. Isopods were studied by Hornung et al. (2007), Vilisics et al. (2007) and Magura et al. (2008). Millipede assemblages along urbanization gradients were studied by Bogyó & Korsós (2009) and Bogyó et al. (2015) as well as partially by Enghoff (1973), and Mwabvu (2006). Other Myriapoda studies were carried out by Lesniewska et al. (2008) and Papastefanou et al. (2014) on Chilopoda assemblages along urbanization gradients.

1.4. Aim of the study

1.4.1. Millipedes in selected cities of Switzerland

- urban millipede fauna and assemblage composition in three cities of Switzerland in the framework of the BiodiverCity project (Vilisics et al., 2012);
- here we hypothesised that urban habitats are suitable for cosmopolitan, holarctic, and non-native millipedes.

1.4.2. A new urban millipede species in Hungary: *Cylindroiulus caeruleocinctus*

- we described a new anthropogenic millipede species from Hungary from the city of Debrecen partially through the GlobeNet Project (Bogyó & Korsós, 2009, 2010);
- we summarized the ecology, biology and European distribution of *Cylindroiulus caeruleocinctus*.

1.4.3. Millipedes and urbanization

- we studied the effects of urbanization on millipede assemblages along a rural-suburban-urban gradient in Debrecen (Hungary) (Bogyó et al., 2015). We tested several hypotheses for millipedes:
- intermediate disturbance hypothesis (IDH) predicts that diversity should be the highest in habitat with moderate levels of disturbance

(Connel, 1978). According to Wootton (1998), basal species in the food web tended to follow the IDH, therefore we hypothesised that millipede diversity will be the highest in the suburban area. (2) habitat specialist hypothesis supposes that the abundance and the species richness of forest specialist species decline along the rural-suburban-urban gradient (Magura et al., 2004);

- synantrophic species hypothesis predicts that the abundance and the species richness of synantrophic species increase along the rural-suburban-urban gradient (Magura et al., 2004; Magura et al., 2008);
- mean body size hypothesis supposes that average millipede size is decreasing from the rural area toward the urban one (Magura et al., 2006);
- we also investigated the changes of the millipede assemblages along the urbanization 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 some environmental factors (temperature, humidity, pH, heavy metals and the amount of decaying wood) have major influence on the distribution of millipede species (Hopkin & Read, 1992; Riedel et al., 2009; Smith et al., 2006).

2. Materials and methods

2.1. Millipedes in selected cities of Switzerland

2.1.1. Study area

The research discussed firstly took place in three Swiss cities, namely Zürich (371,000 inhabitants /92 km²), Lucerne (59,000 /24 km²) and Lugano (49,000/26 km²), which represent small to medium sized cities. These cities lay on a north to south gradient (ca. 200 km, with Lugano south of the Alps) and all are bordered by a lake and mountains. There were 36 sampling sites in each city but only 106 could be used for the analyses: 36 in Zürich and Lugano, 34 in Lucerne. The three cities share common features like historical

centres, residential areas, business quarters, public green areas, parks and cemeteries, and former industrial areas.

The three cities are characterized by continental climate, moderate temperature (North: average January temperature 1°C, July 17°C; South: January 3°C, July 20°C) with an annual precipitation of 1000 mm for Zürich, 1150 mm for Lucerne and 1600 mm for Lugano. Within each of the three cities sampling points were selected along a continuous urbanization gradient, which was measured as the fraction of sealed and built area in the 50m radius around the sampling points. The selection of the individual sampling points followed a reasoned choice sampling strategy to cover the entire urbanization gradient (3% to 92% sealed and built area). A wide range of urban habitat types (private gardens, semi-public spaces of apartment buildings, public parks and courtyards of industrial buildings) was included into the study which represents a high degree of urbanization. A minimal distance of 250 metres was kept between sampling sites and the city fringe. Exact locations of the study sites is given in the work of Germann et al. (2008).

2.1.2. Sampling method

Millipedes (and isopods (belonging to the same functional guild)) were sampled through pitfall traps, consisting of 3 plastic cups (opening diameter 75 mm) per trap site recessed into the soil and arranged in an isosceles triangle with a distance of one meter. Traps were emptied weekly during 7 weeks from June to August 2006 (Sattler et al., 2010), which corresponds to the period with highest arthropod activity in Switzerland (Duelli et al., 1999; Obrist & Duelli, 2010). Valid nomenclature follows Enghoff (2013). The reference collection is deposited at the Natural History Museum in Lugano (Switzerland).

2.1.3. Data analysis

For data analysis we used species richness (number of species) as the most common measure to quantify biodiversity (Tóthmérész, 1998;

Magurran, 2004). Incidence is the frequency with which the species occurs at all in the study sites of a city. This value was used to assess steadiness of a species in the three cities. This value is indicative to the regularity of a species' occurrence which does not necessarily correlate with abundance. We regarded incidence rate high when it was over 50%, and low when it did not reach 10%.

Similarity of the selected decomposer assemblages (Diplopoda and Isopoda combined) among cities was assessed using the Sørensen index (Legendre & Legendre, 1998) obtained from the species-abundance matrices of the three cities. For these analyses we used data of specimens identified to species level only.

2.2. A new urban species in Hungary: *Cylindroiulus caeruleocinctus*

2.2.1. Study area and sampling

The second research was part of the GlobeNet project in 2004 in the town of Debrecen, Eastern Hungary (for research sites see Magura et al., 2004; Bogyó et al., 2015). The study site was a forested urban park (Nagyerdei Park) with asphalt covered paths and abundant non-native plants (see Figure 1). The site is the urban part of an urban-rural gradient (Magura et al., 2004). The specimens were collected by pitfall trapping (pitfall traps contained 75% ethylene glycol and were covered with bark). Besides pitfall trapping there was a hand collection also carried out in the city center in and around a high school building (N 47°31' 32"E 21°37'44") of Debrecen. The specimens were preserved into 70% ethanol. The material has been deposited in the Myriapoda Collection of the Hungarian Natural History Museum, Budapest and in the author's private collection.

2.3. Millipedes and urbanization

2.3.1. Study area

In the third research millipedes were studied in and around the city of Debrecen, which is the second largest city of Hungary. The city is located in the Great Hungarian Plain and has more than 204.000 inhabitants with a

mean population density of 443 individuals/km². The typical forest of the region is a lowland oak forest (English oak (*Quercus robur*)); 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) (Figure 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. The level of urbanization was expressed by the amount of built-up area (buildings, roads and asphalt covered paths), measured by the ArcView GIS program using an aerial photograph in a square of 1 km² size. In the rural area there was no built-up area; 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 almost all 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 (more than 100 years), closed oak forest (*Convallario-Quercetum* association).

2.3.2. Sampling protocol

Following 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 areas). Millipedes were collected at each site using pitfall traps, randomly placing ten traps at least 10 m apart from each other. This resulted a total of 120 traps along the gradient. The pitfall traps were unbaited, consisting of 500 ml plastic cups (65 mm diameter) containing ca. 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 2). 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 device, Testo 206 (Testo AG, Germany). Other parameters, such as ground temperature, air temperature, and humidity were measured with the field instrument Voltcraft DT-8820. We used the average of three measurements through the year (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 2). Soil samples were collected along the studied 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 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 (Ca), or millipedes can accumulate them (Cd, Mg, Pb, Zc) (Hopkin & Read, 1992) (Table 2).

2.3.3. Data analyses

To test differences in the millipede abundance, species richness, standardized number of species and the average body size among the three sampling areas (rural-suburban-urban) and among the 12 sites, mixed Generalized Linear Model (GLMM) was used (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, standardized number of species and body size) were defined as a quasi-Poisson distribution with log link function (Zuur et al., 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 standardized for every trap using species rarefaction or ES(m) diversity (Heck et al., 1975; Tóthmérész et al., 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 3) 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 the works of Blower (1985), Korsós (1994), Tuf & Tufová (2008) and Voigtländer (2011).

Body size was based on the average of the adult body size (average of male and female length x diameter/width) given in the literature (Blower, 1985; David, 1995; Schubart, 1934; Tadler & Thaler, 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. (Dufrene & Legendre, 1997; Elek et al., 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

3.1. Millipedes in selected cities of Switzerland

3.1.1. Faunistical results

Species level identifications resulted a number of 8 millipede species (and 17 species of isopods), while two millipedes were identified to genus level. The total number of captured millipede individuals was 105.

Among millipedes, seven species are widely distributed across Europe (Enghoff, 2013), six of which are known to occur in areas under human influence: *Brachydesmus superus*, *Cylindroiulus caeruleocinctus*, *Ophiulus pilosus*, *Oxidus gracilis*, *Polydesmus angustus*, and *Propolydesmus testaceus* (Blower, 1985; Kime 1990; Pedroli-Christen, 1993; Tadler & Thaler, 1993).

Nemasoma varicorne is also described as a stenotopic species, without clear preferences (Voigtländer, 2011). *Cylindroiulus verhoeffi*, on the contrary, is restricted in Northern Italy, Southern Switzerland and adjacent areas in France (Pedroli-Christen, 1993).

3.1.2. Species richness, composition and incidence

We found seven millipede species in Zürich, four in Lugano, and three in Lucerne. The species *Ophiulus pilosus* was the only one occurring in all three cities. Two other species (*Brachydesmus superus* and *Oxidus gracilis*) were found in two cities, i. e. Zürich and Lucerne (Table 4). *Ophiulus pilosus* dominated the assemblages with 20 individuals in both Zürich (62.5%) and Lugano (42.5%), while *Polydesmus angustus* was dominant in Lucerne (23 ind., 85%) (Table 4).

Millipedes show a different occurrence patterns than isopods, for which the differences among the three cities seem to be greater. Overall, 50% of all millipede and isopod species were observed in only one city. The mean number of individuals for millipedes and isopods combined (per site) varied substantially in the three cities, i.e. Lucerne [mean 159.7 (SE: 75.3)], Lugano [mean 45 (SE: 12.56)], and Zürich [mean 221.7 (SE: 77.22)]. Sørensen similarity in species compositions between cities (considering millipedes and isopods combined) was highest between Zürich and Lucerne (0.67) and lowest between Zürich and Lugano (0.40) Similarity between Lucerne and Lugano was 0.58.

Incidences of millipede and isopod species per city were generally low, i.e. below 10% of the total number of traps. The only millipede with an incidence over 25% (out of 36 traps) was *Ophiulus pilosus* in Lugano, while the rest of millipede species of our study occurred with incidences < 10% (Figure 2).

3.2. A new urban species in Hungary: *Cylindroiulus caeruleocinctus*

Using pitfall trapping we have found 4 specimens of *Cylindroiulus caeruleocinctus* in the Nagyerdei Park, Debrecen, Hungary: 06.09.2004, 1 male; 11.10.2004, 3 females. Between mid September and October 2008 we have collected 25 additional specimens by hand. 10 males and 15 females were found dead in the basement on stairs in the Péchy Mihály High School, which is in the centre of Debrecen (Hungary), 2.5 km away from the urban park mentioned above. Surrounded by the school building there is a small yard, and the millipedes may have looked for some warmer place to move in and died on the concrete ground of the basement.

3.3. Millipedes and urbanization

Fourteen millipede species was identified along the rural-suburban-urban gradient belonging to three millipede orders (Julida, Chordeumatida, Polydesmida) (Table 3). 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 lower number of 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 millipede abundance. In the urban area *Ophiulus pilosus* and *Megaphyllum unilineatum* were the most abundant species, while in the suburban area *Megaphyllum projectum* was highly the most abundant species. In the rural area *Megaphyllum projectum* represented more than 80% of the total number of trapped millipedes.

The overall number of individuals and species number was significantly higher in the suburban area than in the rural and urban areas ($\text{Chi}^2=264,26$; $\text{df}=2, 9$; $p<0.0001$; $\text{Chi}^2=209,15$; $\text{df}=2, 9$; $p<0.0001$ Figure 3a-b). The standardized number of species was also significantly higher in the suburban area than in the other areas ($\text{Chi}^2=158,85$; $\text{df}=2, 9$; $p<0.0001$ Figure 3c). The ratio of forest specialist millipede individuals and the ratio of forest specialist species was decreased significantly along the rural-suburban-urban gradient

($\text{Chi}^2=914,98$; $\text{df}=2, 9$; $p<0.0001$; $\text{Chi}^2=239,01$; $\text{df}=2, 9$; $p<0.0001$; Figure 4a-b). The ratio of synanthropic millipede individuals and the ratio of synanthropic species was increased significantly along the gradient ($\text{Chi}^2=1458,36$; $\text{df}=2, 9$; $p<0.0001$; $\text{Chi}^2=232,62$; $\text{df}=2, 9$; $p<0.0001$; Figure 5a-b). The average body size of the millipedes was significantly lower in the urban area compared to the rural or suburban ones ($\text{Chi}^2=54,47$; $\text{df}=2, 9$; $p<0.0001$; Figure 6). 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 *Kriphoiulus occultus*, *Megaphyllum unilineatum* and *Ophiulus 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 *Megaphyllum projectum* were characteristic to the suburban and rural sites. However *Mastigona bosniensis* favored the rural sites with lower percentage of canopy cover (Figure 7). 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 (Figure 8). We identified five groups of quantitative character species by the IndVal method for the compared areas (Table 3): (1) species preferring the urban area, either recorded exclusively or being most abundant in the urban area (*Cylindroiulus caeruleocinctus*, *Cylindroiulus latestriatus*, *Kriphoiulus occultus*); (2) species characteristic of urban and suburban area (*Ophiulus pilosus*, *Megaphyllum unilineatum*); (3) species preferring the suburban area (*Cylindroiulus boleti*, *Leptoiulus proximus*, *Polydesmus schaessburgensis*); (4) species characteristic of the suburban and rural areas (*Megaphyllum projectum*, *Polydesmus complanatus*); and (5) species preferring the rural area (*Mastigona bosniensis*).

4. Discussion

4.1. Millipedes in selected cities of Switzerland

4.1.1. Species compositions, abundances and incidence

Our survey in three Swiss cities resulted in a low species richness and abundance of millipedes, while the similar detritivorous isopods were captured in higher number of species and individuals. In the light of total numbers of the known millipede fauna of Switzerland (7.9 % of the 127 species) (Pedroli-Christen, 1993) the number of 10 millipede species seems to be low, as well as millipede species number per city. The average urban species numbers is around 22 in temperate Europe (excluding the three cities investigated here), but a lower species numbers (6-14, e.g. Bucharest, London, Sofia) are also known (see literature in Table 1).

Reports on urban millipede (and isopod) fauna show relatively high species richnesses as compared to known native, local faunas (see literature of Table 1). Such reports are, however, hardly comparable due to differences in sampled habitats, sampling efforts and methodology. Pitfall trapping resulted 19% (14 species) of known millipede fauna of Hungary from parks of the city Debrecen (Hungary) (Bogyó & Korsós, 2009). A similar method showed ca. 14% (11 species) of the known millipede fauna of Czechia from parks of the city Olomouc in the Czech Republic (Riedel et al., 2009). Pitfall trapping resulted Isopoda species richness of 6 from parks and nearby rural forested areas in Debrecen and Sorø, Denmark (Hornung et al., 2007; Vilisics et al., 2007), comprising 11% of Hungarian, and ca. 27% of known Danish Isopoda fauna (Meinertz, 1964).

Pooled abundances of isopods and millipedes were well over 1000 in each above mentioned studies. As total millipede catch was less than 100, the question arises why abundances were so low? In his review David (2009) has pinpointed the negative effects of habitat loss and low food quality on millipede assemblages, and demography. Furthermore, management practices altering microhabitats (like coarse woody debris) has great effect on soil macro-invertebrates, including isopods and millipedes, too. (Kappes et al., 2009; Topp et al., 2006). The low activity density values, thus may be a result

of the intensive management such as mowing and removal of plant litter. In this study, the chosen habitats show a high degree of urbanisation: private gardens, semi-public spaces of apartment buildings, public parks and courtyards of industrial buildings. This kind of public spaces are disturbed habitats with regular gardening, trampling and do have a high percentage of artificial surface.

In our study we found introduced species to show low incidences, regardless to their abundances. The introduced millipede *Oxidus gracilis* (Stoev et al., 2010) showed low incidences, as it appeared in only 3% of the sites in Lucerne, and 12% of Lugano. On the other hand, the outdoor survival of this species in European conditions seems to be a rarity (Blower 1985; Pedroli-Christen, 1993). It is likely that these species survive in sites which provide special environmental conditions, such as higher annual average temperature, so they may aggregate in higher numbers at certain spots of a city, while never establish in others.

The three millipedes occurring in two or more cities (*Ophiulus pilosus*, *Brachydesmus superus*, *Oxidus gracilis*) are widespread in Europe and occupy rural and urban settlements, but all of them have a high preference for anthropogenic habitats (Blower 1985; Pedroli-Christen 1993; Enghoff 2013). *Ophiulus pilosus* in Lugano showed the highest incidence of occurrences among the millipedes. We found a somewhat similar trend at isopods, as species of wide distribution showed the greatest incidences. Moreover, this result is consistent with Kime (1990) and Voigtländer (2011), who suggested that this species might profit from human disturbance.

4.1.2. Geographic effects

As European biodiversity hot-spots are found in the Mediterranean Basin and the central mountain zones, species richness of invertebrates generally show great contrasts between south and north of Europe. As with many other invertebrate taxa (Lepidoptera and Mollusca in IUCN 2011 European Red List), geographic patterns of European millipedes and isopods show a decrease in species richness from southern biodiversity hot-spots to the north. The available literature on millipede and isopod faunas suggests species

diversity to decrease roughly by half from Southern Europe to Central Europe, and it further halves towards Fennoscandia (Diplopoda Italy: Stoch, 2004; Czech Republic: Tajovský, 2001; Scandinavia: Andersson et al., 2005; Isopoda: Italy: Stoch, 2004; Hungary: Vilisics & Hornung, 2009; Scandinavia: Meinertz, 1964). The Alps are also rich in millipede species, endemic millipedes of Switzerland are known almost exclusively from alpine or subalpine ecosystems (Pedroli-Christen, 1993). Similarities between species compositions hint at the impact of geographical location and distance between cities: the two northern cities (Zürich and Lucerne), which share more species than any other combination of two cities, are only 60 km apart. Lugano is located 170 km south of Lucerne and 210 km south of Zürich, from which it is additionally separated by the Alps. Lugano is already under the influence of Mediterranean climate, which affects the regional flora and fauna. Some xerophilic millipedes (like *Brachydesmus superus*) show synanthropic trends in their northern range of distribution as well (Voigtländer, 2011). One possible reason for this finding is the so-called heat island effect (Andreev, 2004) which describes a higher average annual temperature in the city core in comparison with the surrounding areas. Introduced isopod and millipede species often find shelter in private and botanical gardens, but their occurrence is typically aggregated to a restricted area within the city (Vilisics & Hornung, 2009; Stoev et al., 2010)

The findings of *Oxidus gracilis* and *Cylindroiulus verhoeffi* are interesting from a biogeographical perspective: *Oxidus gracilis* is a species of tropical Eastern-Asian origin, introduced by human activities into European greenhouses (Blower, 1985) and seldom survives outdoors in Europe (Pedroli-Christen, 1993). The species was only known at four locations in Switzerland so far (Pedroli-Christen, 1993), while we found one individual in Lucerne and 16 individuals in 4 ruderal sites of Lugano. *Cylindroiulus verhoeffi* is considered as an endemic species (“Lombardo-Venetian endemism”) with a very restricted distribution (Attems, 1949; Pedroli-Christen, 1993; Enghoff, 2013).

4.1.3. Biotic homogenization

Biotic homogenization has been described earlier (McKinney, 2006, 2008) as an ongoing process characterized by extinction of local faunal elements and dominance of tolerant species, resulting in increasing similarities in species compositions among cities. Szilávecz et al. (2008; unpublished) in their presentation at URBIO2008 (Urban Biodiversity & Design, Erfurt, Germany) pinpointed a biotic homogenization process on soil dwelling macro-invertebrates (Annelids, Diplopods, Isopods) in major European cities. Based on European literature data from the past 50 years (from e.g. Czech Republic, Hungary, Poland, Romania) the list includes 10 millipede species (*Blaniulus guttulatus*, *Brachydesmus superus*, *Brachyiulus pusillus*, *Cylindroiulus britannicus*, *Cylindroiulus caeruleocinctus*, *Cylindroiulus latestriatus*, *Cylindroiulus truncorum*, *Kryphioiulus occultus*, *Nemasoma varicorne*, *Nopoiulus kochii*, *Ophiulus pilosus*, *Oxidus gracilis*, *Polydesmus complanatus*, *Polydesmus inconstans*, *Proteroiulus fuscus*, *Strongylosoma stigmatosum*) regarded as homogenizing in Europe. These species are widespread throughout temperate Europe, and several of them were introduced to many parts of the world (Blower, 1985; Kime, 1990; Enghoff 2013).

As the list and analysis haven't been published yet, we cannot build hypotheses on this approach. Nevertheless, it is interesting, that our samplings from three Swiss cities resulted 62.5% of millipedes regarded as homogenizing for temperate Europe, as described by Szilávecz et al. (2008; unpublished). Following this list, we found such „homogenizing” isopods and millipedes (combined) taking 81.5% of the fully identified catch in Zürich, 69% in Lucerne and 70% in Lugano.

Our study found that urban millipede (and isopod) assemblages in Switzerland are dominated by species widely distributed in temperate Europe. However their incidence and abundance in urban habitats might be different compared to other ecosystems. The high incidence values of common synanthropic (species living in habitats created by humans), as well as locally distributed species within cities, may point at the special urban feature of high habitat heterogeneity in closer spatial distance than in (semi-)

natural ecosystems. In this way, urban areas offer suitable habitats for species with wide ecological requirements and possibly host species assemblages not found outside the cities.

4.2. A new urban species in Hungary: *Cylindroiulus caeruleocinctus*

Cylindroiulus caeruleocinctus (Wood, 1864) (syn. *Cylindroiulus teutonicus* (Pocock, 1900)) was considered as a variety of *C. londinensis* (Leach, 1815) (Brade-Birks, 1922; Blower, 1958), until Mauriès (1964) separated them into two species. Former records of the species distribution in Western Europe should be handled with care, as it was pointed out by Kime (1990) and David (1995), because they can refer to both *Cylindroiulus caeruleocinctus* and *Cylindroiulus londinensis*. However, according to Blower (1985), *C. caeruleocinctus* occurs mostly on calcareous soil under cultivation, and also prefers leaves with higher calcium content (Lynford, 1943). A high degree of correlation with calcareous basic soil is probably not true in the strict sense, because most of the occurrences in various synanthropic habitats blur such a tendency (Kime, 2004). The species is usually found in open habitats (Schubart 1934), and often in synanthropic circumstances, as a result of human-mediated dispersion. In many countries it does not occur at all in natural habitats (Golovatch, 1984; Jedryczkowski 1992; Kocourek 2004; Mock, 2006). Schaefer (1982) found the species in gardens of London very common in pitfall traps, but rarely in soil and litter samples. Haacker (1968) described the species as hygrophilous with activity peaks in spring; Pedroli-Christen (1993) reported a smaller peak in autumn.

The species is widely distributed in Europe and in North America (Blower, 1985). Its European range mainly occupies the western and northern part of the continent, completed by scattered Central European records (Enghoff, 2013). Kime (1999) describes *Cylindroiulus caeruleocinctus* as an Atlantic species. The majority of the data from Eastern and Central Europe comes from synanthropic localities. We reviewed all the available literature to provide a current European distribution (Table 5).

Cylindroiulus caeruleocinctus is common in the southern and central part of the United Kingdom and in some parts of Ireland (Blower, 1985).

Among the Scandinavian countries, it is absent from Iceland, it occurs in Norway along the southwestern and southernmost shoreline (Andersson et al., 2005), both in pine and mixed deciduous forests (Djursvoll et al., 2006); in Sweden it was found only in the south (Andersson et al., 2005); in Denmark the species is present in the entire country and it is able to live outdoor, but without doubt it is an introduced species (Enghoff, 1974). In Finland, there is only one record from a city park of Helsinki (Palmén, 1949).

In the Netherlands it is by far the most common millipede species, which occurs in gardens but may even enter houses (Jeekel, 2000; Berg et al., 2008). In Belgium it is also widespread; there are many records throughout the country (Kime, 2004). Kime (1992) found it in high population densities in calcareous grasslands, and also in oak/beech forests. Specimens have been caught in open sites and have rarely turned up in closed woodland. In Luxemburg the species is common in open habitats and in synanthropic localities as well (Kime, 1996, 1999).

Cylindroiulus caeruleocinctus is widespread in France and in the Mediterranean region (Geoffroy, 1996; David, 1995, in litt., 2008). In Spain the species was not found in Cataluña, south of the Pyrenees (Vicente, 1985), but it was mentioned from Northern Spain (Serra et al., 1996; Read, 2007). It was reported from the mainland of Portugal, too (as *Cylindroiulus teutonicus*, by Machado, 1946). Despite their possible confusion with *Cylindroiulus londinensis* (see above), these former records can still be considered valid for *Cylindroiulus caeruleocinctus*, because *Cylindroiulus londinensis* is a forest species of the warmer and wetter parts of the Atlantic zone (Kime, in litt, 2009). In contrast we questionmark the record by Ceuca (1972), because his *Cylindroiulus londinensis* data are from further east in open country. In Italy *Cylindroiulus caeruleocinctus* occurs only in the extremely northern part of the country (Foddai et al., 1995).

In Switzerland it is widespread (Pedroli-Christen, 1993). In Germany it is also widely distributed and was found in different biotopes (Schubart, 1934; Blower, 1985; Kime, 1990; Spelda, 2006). In Poland the species is a cosmopolitan element, occurring in synanthropic habitats, such as gardens, parks and houses (Jedryczkowski, 1992). It is also present in the Baltic countries (Estonia, Latvia and Lithuania) (Enghoff, 2013). In some Central

European countries, *Cylindroiulus caeruleocinctus* has isolated occurrences. Occasionally, mass appearances have been reported from Austria in the cities of Innsbruck and Kufstein, probably due to human introduction (Thaler, 1988). In the Czech Republic in some cities such as Prague it can be very abundant (Kocourek, 2004; Mock, 2006), as well as in some of the vineyards of Moravia (Tajovsky & Ríhová, 2014). In Slovakia the species was found only in the gardens of Kosice (Mock, 2006). From the former Yugoslavia it has been mentioned by Blower (1985), but it is stated as absent in the Fauna Europaea database (Enghoff, 2013). In the former USSR it occurs on the European plain, but it is restricted only to synanthropic habitats (Lokshina, 1969; Golovatch, 1992; Chorny & Golovatch, 1993).

In the neighbourhood of Debrecen, Hungary, the nearest data are from the cities of Kosice (Slovakia, distance ca. 130 km) (Mock, 2006) and Lvov (Ukraine, distance ca. 310 km) (Lokshina, 1969; Chorny & Golovatch, 1993). By massive increasing of human activities, and maybe also due to natural processes, it seems that the range of *Cylindroiulus caeruleocinctus* is slowly expanding towards the southern and eastern parts of the European continent as it is observed in case of some chilopod species (Lindner, 2007). At present, it is only missing from Romania, Bulgaria, Greece, and mainly from the Mediterranean territories.

4.3. Millipedes and urbanization

We studied the effects of urbanization on millipede assemblages along a forested rural-suburban-urban gradient in Debrecen (NE Hungary) (Bogyó et al., 2015). 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 (14 species) was 14% of the Hungarian millipede fauna. Other papers dealing with millipedes in urban areas of temperate Europe showed similar millipede diversity (8-26 species in urban areas) (Vilisics et al., 2012). The most abundant species, *Megaphyllum projectum* is a characteristic and widespread species in Central-European natural woodlands (Voigtländer, 2011). It was 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 standardized number of species were significantly higher in the suburban area than in the other areas. These results support the IDH (Connel, 1978) and the predictions of Wootton (1998): the IDH has generally been supported for basal species in a food web, in spite of top consumers. A few urbanization studies on invertebrates supported the IDH in case of other detritivorous arthropods: woodlice (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, 2006). In general, several studies showed a decline in animal species richness toward 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 urbanization. The high diversity and density in suburban forest remnants can be explained 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 et al.(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 big 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 urbanization gradient (Magura et al. 2008, 2010a, b; McKinney, 2006; McKinney, 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.

Urbanization causes several types of disturbance. From the rural area toward 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 et al., 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 activities). 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 detritivores. 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 (*Cylindroiulus latestriatus*, *Kryphioidius occultus*, *Megaphyllum 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, *Cylindroiulus boleti* preferred the urban and suburban sites, though it was mentioned in the earlier literature as a forest specialist species. *Cylindroiulus boleti* is probably a more generalist species, as it was suggested by Tuf and Tufová (2008). We found that *Polydesmus complanatus* and *Megaphyllum 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 holartic, globally widespread and exotic millipede species. *Cylindroiulus 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, 2009). 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 tree species has a major effect on millipede communities (Stašiov et al., 2012).

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.

Summary

Millipedes are one of the most diverse groups of terrestrial arthropod decomposers in temperate and tropical areas. Millipedes are abundant organisms in habitats covered with trees and shrub by consuming leaf litter, providing important ecosystem services and affecting soil ecosystems. Urban areas are radically growing worldwide causing changes in biodiversity and natural habitats. Urbanization has a strong negative effect on species richness, mainly in urban core areas, however the effects of moderate levels of urbanization in suburban areas has a significant variation among different taxonomic groups. The aim of my dissertation was to investigate the overall effect of urbanization on the millipede species, fauna and assemblages, summarizing the results of three different studies.

(i) During our studies we investigated urban millipede fauna and assemblage composition in three cities (Lugano, Lucerne, Zürich) of Switzerland in the framework of the BiodiverCity project. A wide range of urban habitat types (private gardens, semi-public spaces of apartment buildings, public parks and courtyards of industrial buildings) was included into the study which represents a high degree of urbanization. Millipedes were sampled through pitfall traps, consisting of 3 plastic cups (diameter 75 mm) per trap site recessed into the soil and arranged in an isosceles triangle with a distance of one meter. Traps were emptied weekly during 7 weeks from June to August 2006.

Species level identifications resulted a number of 8 millipede species, while two millipedes were identified to genus level. The total number of captured millipede individuals was 105. We found seven millipede species in Zürich, four in Lugano, and three in Lucerne. The species *Ophyiulus pilosus* was the only one occurring in all three cities. *Ophyiulus pilosus* dominated the assemblages with 20 individuals in both Zürich (62.5%) and Lugano (42.5%), while *Polydesmus angustus* was dominant in Lucerne (23 ind., 85%). Incidences of millipede species per city were generally low, i.e. below 10% of the total number of traps. The only millipede with an incidence over 25% was *Ophyiulus pilosus* in Lugano, while the rest of millipede species of our study occurred with incidences < 10%. The findings of *Oxidus gracilis* and *Cylindroiulus verhoeffi* are interesting from a biogeographical perspective: *Oxidus gracilis* is a species of tropical Eastern-Asian origin, introduced by human activities into European greenhouses and was only known at four locations in Switzerland so far. On the other hand *Cylindroiulus verhoeffi* is considered as an endemic species (“Lombardo-Venetian endemism”) with a very restricted distribution. Our study found that urban millipede assemblages in Switzerland are dominated by species widely distributed in temperate Europe. However their incidence and abundance in urban habitats might be different compared to other ecosystems. The high incidence values of common synanthropic (species living in habitats created by humans), as well as locally distributed species within cities, may point at the special urban feature of high habitat heterogeneity in closer spatial distance than in (semi-) natural ecosystems. In this way, urban areas offer suitable habitats for species with wide ecological requirements and possibly

host species assemblages not found outside the cities. Our results overlap with former findings on invertebrates and biotic homogenization. We found, that the studied urban habitats of Switzerland are suitable for cosmopolitan, holarctic, and non-native millipedes, but they have a poor millipede fauna with limited number of species and low abundance.

(ii) We described a new anthropogenic millipede species from Hungary from the city of Debrecen, partially through the GlobeNet Project. In our study we summarized the ecology, biology and European distribution of *Cylindroiulus caeruleocinctus*. Our study site was mainly a forested urban park of Debrecen (Nagyerdei Park) with asphalt covered paths and abundant non-native plants. We collected specimens of *Cylindroiulus caeruleocinctus* by pitfall trapping (pitfall traps contained 75% ethylene glycol and were covered with bark). Besides pitfall trapping there was a hand collection also carried out in the city center in and around a high school building of Debrecen. Using pitfall trapping we have found 4 specimens of *Cylindroiulus caeruleocinctus* in the Nagyerdei Park, Debrecen, Hungary in 2004 and 25 specimens of the same species in the basement on stairs in the Péchy Mihály High School, which is in the centre of Debrecen (Hungary). In our study we gave an up-to-date picture of the European distribution of *Cylindroiulus caeruleocinctus*. The occurrences of the species are largely synanthropic, while the current European distribution of the species suggests an anthropogenic expansion towards East and Southeast Europe. The species has not yet been reported from Romania, Bulgaria, Greece, Albania, and it is also missing from the territories of former Yugoslavia.

(iii) We studied the effects of urbanisation on millipede (Diplopoda) assemblages along a forested rural-suburban-urban gradient in Hungary. we studied the effects of urbanization on millipede assemblages along a rural-suburban-urban gradient in Debrecen (Hungary), in the framework of the GlobeNet Project. We tested several hypotheses for millipedes:

- intermediate disturbance hypothesis (IDH) predicts that diversity should be the highest in habitat with moderate levels of disturbance (Connell, 1978; Wootton, 1998);

- habitat specialist hypothesis supposes that the abundance and the species richness of forest specialist species decline along the rural-suburban-urban gradient (Magura et al., 2004);
- synanthropic species hypothesis predicts that the abundance and the species richness of synanthropic species increase along the rural-suburban-urban gradient (Magura et al., 2004; Magura et al., 2008);
- mean body size hypothesis supposes that average millipede size is decreasing from the rural area toward the urban one (Magura et al., 2006);

We also investigated the changes of the millipede assemblages along the urbanization gradient, identified the characteristic and/or key species across this gradient. We studied the effects of the most relevant environmental factors on the abundance of millipedes, and we hypothesised that some environmental factors (temperature, humidity, pH, heavy metals and the amount of decaying wood) have major influence on the distribution of millipede species.

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.

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.

Összefoglalás

Az ikerszelvényesek (Myriapoda: Diplopoda) fontos szerepet töltenek be a talajban zajló lebontási folyamatokban. Jelenleg mintegy 12000 ikerszelvényes faj ismert világszerte. A leíratlan fajok számát ennek négyhatszerezésére teszik, így a taxon az egyik legdiverzebb teresztris gerinctelen csoport a mérsékelt és a trópusi övben. Európában hozzávetőlegesen 1500, Magyarországon 103 faj előfordulása ismert (Sierwald & Bond 2007; Bogyó et al. 2012; Enghoff 2013; Minelli & Golovatch 2013). Az ikerszelvényesek legnagyobb faj és egyedszámban az erdővel borított élőhelyeken fordulnak elő, ahol a lombavar felaprózásával és lebontásával fontos ökoszisztéma szolgáltatásokat nyújtanak (Hopkin & Read 1992; Lavelle et al. 2006).

Az urbanizáció napjaink egyik legjelentősebb környezet és természetátalakító tevékenysége. A városi és városiasodó területek aránya és területfoglalása évről évre nő, ezáltal számos természetes élőhely alakul át. A városiasodásnak összességében negatív hatása van a biodiverzításra, mindenekelőtt a városok központi részein. Ettől eltérően a kertvárosi területeken tapasztalható mérsékelt szintű zavarás hatása igen széles skálán mozog a különböző vizsgált élőlénycsoportok esetében (McKinney 2008).

Európa városi területeinek talajlakó gerinctelen faunáját elsősorban kozmopolita és holarktikus fajok dominálják, melyek között nem ritka az inváziós, vagy egzotikus fajok megjelenése sem (Smith et al. 2006; Riedel et al. 2009; Stoev et al. 2010; Vilisics et al. 2012). Az urbanizáció jelentősen elősegíti a kevésbé mozgékony ikerszelvényes fajok terjedését, a helyi fauna átalakulását. Ilyenek például a kertészeti tevékenységek, a talajszállítás, vagy a fűrészaruk transzportja (Hopkin & Read 1992). Más kutatások kimutatták, hogy az őshonos, helyi faunaelemeknek is jelentős hatása lehet a városok ikerszelvényes faunájára. Ezek a fajok tipikusan a városokban és azok közelében elhelyezkedő természetes élőhelyeken, valamint a városszéli, kevésbé zavart élőhelyeken fordulnak elő elsősorban (Bogyó & Korsós 2009; Riedel et al. 2009; Kocourek 2014; Bogyó et al. 2015). Egyes speciálisan városokra jellemző élőhelytípusok (pl. botanikus kertek, melegházak, közparkok, magánkertek) behurcolt, exóta ikerszelvényes fajok

populációinak adnak otthont (Korsós et al. 2002; Mock 2006; Bogyó & Korsós 2010).

Az utóbbi évtizedekben az urbanizáció hatását különböző élőlénycsoportokra nézve számos tanulmány taglalta. A talajlakó ízeltlábúak közül elsősorban a futóbogarak (Coleoptera: Carabidae) kutatása volt jelentős (Niemelä & Kotze 2009; Magura et al. 2010), de más taxonok kutatottsága is számottevő, például a pókoké (Araneae) (Alaruikka et al. 2002; Horváth et al. 2012). A soklábúak közül a százlábúakra (Chilopoda) vonatkozóan csupán két tanulmány készült (Lesniewska et al. 2008; Papastefanou et al. 2014). A lebontó életmódú, talajlakó ízeltlábúak közül a szárazföldi ászkarák (Isopoda) terén végeztek kutatásokat (Hornung et al. 2007; Vilisics et al. 2007; Magura et al. 2008). A disszertáció célja az, hogy három kutatási projekt kapcsán a doktorjelölt kutatásának eredményeit összegezve képet adjon az urbanizáció általános hatásairól az ikerszelvényes fajokra, a helyi ikerszelvényes faunára és az ikerszelvényes közösségekre nézve (Bogyó & Korsós 2010; Vilisics et al. 2012; Bogyó et al. 2015).

(i) Dél- és Kelet-Svájc három városának (Lugano, Lucerne, Zürich) ikerszelvényes faunáját és az ikerszelvényes közösségeket vizsgáltuk a BiodiverCity projekt keretében (Vilisics et al. 2012). A kutatás során ezeknek a városoknak az erősen urbanizálódott élőhelyein (kertek, társasházak udvarai, közparkok, ipari létesítmények területe) gyűjtöttük a talajlakó, lebontó ízeltlábúakat (Diplopoda, Isopoda) talajcspadázással, 2006. júniustól augusztusig terjedő időszakában.

Vizsgálataink során összesen 10 ikerszelvényes fajt fogtunk, összesen 105 egyeddel. Zürichben 7, Luganóban 4, Lucerne-ben pedig 3 fajt fogtunk. Az ikerszelvényes fajok közül kizárólag az *Ophiulus pilosus* fordult elő mindhárom vizsgált városban. Lucerne-ben ez a faj volt a leggyakoribb, egyaránt 20 egyede került elő Zürichben (az itt fogott egyedek 63%-a) és Luganóban (az itt fogott egyedek 43%-a). Lucerne leggyakoribb ikerszelvényes faja a *Polydesmus angustus* volt 23 egyeddel, amely több mint 80%-át tette ki az itt előkerült ikerszelvényeseknek. A vizsgált városok teljes csapdaszámához viszonyítva az egyes ikerszelvényes fajokat általában igen alacsony számú csapdában fogtuk meg (városonként kevesebb, mint a csapdák 10%-ában). Egyedül a közismerten szünantróp *Ophiulus pilosus*

fordult elő a csapdák több mint 25%-ban, Lucerne városában. Biogeográfiai és faunisztikai szempontból két faj emelhető ki: az *Oxidus gracilis* és a *Cylindroiulus verhoeffi*. Előbbi Kelet-Ázsia trópusi részéről származó faj, melyet az amerikai és európai kontinensre is behurcoltak. Az *Oxidus gracilis*-t Európában döntően melegházakban és azok környékén mutatták ki, korábban csak Svájc négy lelőhelyéről volt ismert (Stoev et al. 2010; Pedroli-Christen 1993), ahol kültéren ritka. A kutatás során Lugano városából előkerült egy másik kiemelt figyelmet érdemlő faj, a *Cylindroiulus verhoeffi*, melyet az irodalom rendkívül szűk elterjedésű, endemikus fajként említ (“lombardiai-velencei” endemizmus: Pedroli-Christen 1993). Kutatásunk során azt találtuk, hogy a vizsgált svájci városokban elsősorban az Európában széles elterjedésű, tág tűrőképességű ikerszelvényes fajok élnek. Eredményeink azt mutatják, hogy a gyakori szünantróp fajok és a ritka helyi faunaelemek egyaránt előfordulnak a városokban; így a városi területek, mint heterogén élőhelyek kis területen is diverz faunának adhatnak otthont. Mindemellett kiemelendő, hogy a városi élőhelyek elsősorban a tág tűrőképességű ikerszelvényes fajoknak kedveznek, amely eredmény a biotikus homogenizáció elméletét igazolja (McKinney, 2006). Eredményeink aqlapján elmondható, hogy összességében a svájci városok ikerszelvényes közösségeit kozmopolita, holarktikus, és sok esetben behurcolt fajok alkotják. A vizsgált területek általában alacsony egyedszámmal jellemezhetők, illetve bizonyos antropogén élőhelyeken az ikerszelvényesek szinte teljesen eltűnnek.

(ii) A hazai faunára nézve új ikerszelvényes fajt írtunk le Debrecenből. A *Cylindroiulus caeruleocinctus* nevű fajt először a Magyarországon is futó GlobeNet projekt kutatásai során gyűjtöttük (Bogyó & Korsós 2010). A faj egyik lelőhelye a debreceni Nagyerdei Park volt, mely kocsányos tölgyes erdőből keletkezett erősen urbanizált városi park, melyet aszfaltozott úthálózat és betelepített, idegenhonos növények jellemeznek. Ezen a területen talajcsapdázással gyűjtöttük a faj 4 példányát 2004 folyamán. Ezt követően kézi egyeléssel további 25 példány került elő debrecen központjából, a Péchy Mihály Építőipari Szakközépiskola udvaráról és lépcsőházából 2008 során. Tanulmányunkban irodalmi adatok szisztematikus áttekintésével összegeztük a *Cylindroiulus caeruleocinctus* ökológiai igényeit, biológiáját és európai elterjedési mintázatát. Ezek alapján a faj Európában döntően szünantróp, de eredetileg természetese módon az atlantikus területek nyílt élőhelyeit kedvelő

faj. A faj Dél- és Kelet-Európa irányába terjeszkedik részben természetes, döntően azonban emberi hatásra. Számos európai nagyvárosban jelentős, szigetszerű populációja van a behurcolásnak köszönhetően (Bogyó & Korsós 2010; Enghoff 2013).

(iii) Az urbanizáció hatását vizsgáltuk ikerszelvényes közösségeken egy városon kívüli-városszéli-városi élőhelygrádiens mentén, a nemzetközi GlobeNet protokoll szerint (Magura et al. 2004; Bogyó et al. 2015). A kutatás Debrecenben és a várost körülvevő Nagyerdőben zajlott. A városon kívüli mintavételi területen nem voltak mesterséges létesítmények, a beépítettség aránya a városszéli élőhelyen 30%, míg a városi mintavételi területen minimum 60% volt. A mintavételi területek mindegyike kocsányos tölgyes erdő (*Convallario-Quercetum roboris* társulás), illetve annak maradványa volt. Kutatásunk sorána a GlobeNet projekt mintavételi protokollját követtük (Niemelä et al. 2000): a mintavételi területeken (városon kívüli, városszéli, városi) belül négy mintavételi helyet jelöltünk ki, melyek területén 10-10 talacsapdát helyeztünk el random módon. Ennek megfelelően összesen 120 etilén-glikollal feltöltött talajcsapdával (3×4×10) dolgoztunk a vizsgált élőhelygrádiens mentén. A talajcsapdákat kéthetente ürítettük 2004. március végétől novemberig.

Az ikerszelvényesekre vonatkozó kutatási hipotéziseink az alábbiak voltak:

- a köztes zavarási hipotézis szerint a diverzitás növekszik az enyhén (mérsékelten) zavart élőhelyeken (Connell 1978; Wootton 1998);
- a habitat-specialista hipotézis szerint az eredeti (természetközeli) élőhelyekhez kötődő élőlények sokfélesége csökken az erősen zavart élőhelyek felé haladva (Magura et al. 2004);
- a szünantróp faj hipotézis szerint az ember által módosított élőhelyeket preferáló élőlények sokfélesége nő az erősen zavart élőhelyek felé haladva (Magura et al. 2004, 2008);
- az átlagos testméret hipotézis szerint egyes élőlények átlagos testmérete csökken a városon kívüli (természetközeli) élőhely felől a városi élőhely felé haladva (Magura et al. 2006).

Vizsgáltuk továbbá az ikerszelvényesek közösségi szintű változásait az urbanizációs grádiens mentén és az egyes élőhelyekre vonatkozóan azonosítottuk az ikerszelvényesek karakterfajait. Vizsgáltuk a releváns környezeti tényezők ikerszelvényesekre gyakorolt hatásait, feltételezve, hogy az irodalomban is dokumentált hatótényezőknek (hőmérséklet, talajnedvesség, pH, nehézfémek mennyisége, holt fa mennyisége) kutatási területeinken is jelentős hatása lesz az ikerszelvényesek térbeli eloszlására (Hopkin & Read 1992; Riedel et al. 2009; Smith et al. 2006).

A vizsgált élőhelygrádiens mentén összesen három rend 14 ikerszelvényes fajt azonosítottuk, mely a hazai faunának hozzávetőlegesen 14%-a. Az ikerszelvényesek egyedszáma a városszéli élőhelyen volt a legmagasabb (4660 egyed). Ennél jelentősen alacsonyabb egyedszámban fogtunk ikerszelvényeseket a városon kívüli (1842 egyed) és a városi (940 egyed) élőhelyen. A leggyakoribb ikerszelvényes faj az élőhelygrádiens mentén a *Megaphyllum projectum* volt, amely az összes fogott egyed 60%-át tette ki, illetve a városon kívüli, természetközeli élőhely teljes egyedszámának mintegy 80%-át adta. A városi élőhelyen az *Ophiulus pilosus* és a *Megaphyllum unilineatum* volt a leggyakoribb faj, míg a városszéli élőhelyen a korábban említett *Megaphyllum projectum* volt a leginkább tömeges.

Az ikerszelvényesek átlagos egyedszáma és fajszáma szignifikánsan magasabb volt a városszéli élőhelyen a városon kívüli és városi élőhelyekkel összehasonlítva. Az ikerszelvényesek diverzitása (várható fajszáma) szintén szignifikánsan nagyobb volt a városszéli élőhelyen a városon kívüli és városi élőhelyekkel összehasonlítva. Mindezen eredmények a köztes zavarási hipotézist igazolják (Connell 1978), és megerősítik Wootton (1998) érvelését, miszerint a tápláléklánc alsó szintjein lévő élőlények diverzitása nagyobb a mérsékelt zavarású élőhelyeken. A köztes zavarási hipotézist mindeztől kezdve kevésszer írták le urbanizációs grádiens mentén; a lebontó életmódot folytató szárazföldi ászkarák (Vilicsics et al. 2007) és a soklábúak másik osztálya esetében (Chilopoda: Papastefanou et al. 2014) is hasonló mintázatot találtak.

Eredményeink azt mutatják, hogy az erdei specialista ikerszelvényes fajok számának és egyedszámának aránya szignifikánsan csökkent az

urbanizációs grádiens mentén a természetközeli, városon kívüli erdőtől a városi élőhely felé haladva. A szünantróp ikerszelvényes fajok számának és egyedszámának aránya szignifikánsan csökkent az urbanizációs grádiens mentén a városi élőhelytől a városon kívüli élőhely felé haladva. Más taxonok esetében is hasonló eredményekről számoltak be: az erdei specialista fajok csökkenését (habitat-specialista hipotézis) és a szünantróp fajok növekedését (szünantróp faj hipotézis) is leírták urbanizációs grádiensek mentén (Magura et al. 2008, 2010a, b; McKinney 2006, 2008; Tóthmérész et al. 2011).

Az ikerszelvényesek átlagos testmérete szignifikánsan kisebb volt a városi élőhelyen, mint a városszéli és városon kívüli élőhelyeken, ami az átlagos testméret hipotézist igazolja. A kisebb testméretű fajok dominanciáját városi területeken magyarázhatja az elérhető táplálék alacsonyabb minősége, mely szintén befolyásolja az ikerszelvényesek testméretét (Enghoff 1992). A kapott eredmények hasonlóak Magura és munkatársai (2006) eredményeihez: kutatásuk során kisebb testméretű futóbogarakat találtak a városi élőhelyen, mint a városszéli és városon kívüli élőhelyeken.

A kanonikus korrespondencia analízis eredményei alapján a mért környezeti változók és az ikerszelvényes közösségek határozott változást mutattak a városon kívüli-városszéli-városi élőhelygrádiens mentén. A városi élőhely ikerszelvényes közössége határozottan elkülönült a városszéli és városon kívüli élőhely közösségeitől, melyek hasonlóbbak voltak egymáshoz. A mért környezeti változók alapján a városi élőhely magas talaj- és levegőhőmérséklettel, magas pH-val, a Ca és Zn talajban mért magas koncentrációjával, valamint kisebb holt fa mennyiséggel volt jellemezhető. Hasonló eredményekről számoltak be Pickett és munkatársai (2011) városi élőhelyekre vonatkozó kutatásaik során. Az irodalmi adatok szerint a levegőből származó Zn, Cd és Pb szennyező hatása csökkentheti az ikerszelvényesek abundanciáját (Hopkin & Read 1992). A városszéli élőhelyen magasabb relatív páratartalmat és magasabb avarborítást regisztráltunk. A városon kívüli, természetközeli erdő magas holt fa mennyiséggel, alacsony pH-val, valamint alacsony talaj- és levegőhőmérséklettel volt jellemezhető. Eredményeink igazolták, hogy a magas hőmérséklettel, magas pH-val és alacsony holt fa mennyiséggel jellemezhető városi élőhelyhez főleg a *Kriphyoius occultus*, *Megaphyllum*

unilineatum és *Ophiulus pilosus* fajok kötődtek, míg a városszéli és városon kívüli élőhelyek környezeti viszonyai leginkább a *Polydesmus complanatus* és *Megaphyllum projectum* fajoknak feleltek meg. Kimutattuk, hogy a *Mastigona bosniensis* elsősorban a városon kívüli élőhely alacsonyabb borítottságú erdeinek karakterfaja.

Az ikerszelvényesek öt karakterfaj-csoportját azonosítottuk és az IndVal módszer segítségével vizsgáltuk, hogy melyek a szignifikáns karakterfajok: (1) kizárólag a városi élőhelyen, vagy legnagyobb egyedszámban a városi élőhelyen előforduló fajok: (*Cylindroiulus caeruleocinctus*, *Cylindroiulus latestriatus*, *Kryphioidius occultus*); (2) a városi és városszéli élőhelyek karakterfajai: (*Ophiulus pilosus*, *Megaphyllum unilineatum*); (3) a városszéli élőhely karakterfajai: (*Cylindroiulus boleti*, *Leptoiulus proximus*, *Polydesmus schaessburgensis*); (4) a városszéli és városon kívüli élőhely karakterfajai (*Megaphyllum projectum*, *Polydesmus complanatus*); (5) a városon kívüli, természetközeli élőhely karakterfaja (*Mastigona bosniensis*)

Eredményeink igazolták, hogy mind a mért környezeti változók, mind pedig a vizsgált élőhelyek ikerszelvényes közösségei jól detektálható változást mutatnak az urbanizációs grádiens mentén. A természetes és szünantróp élőhelyek együttes előfordulása magas ikerszelvényes diverzitást eredményezett a városszéli élőhelyen, összehasonlítva azt a városi és városon kívüli élőhelyekkel. A vizsgált városi élőhely alkalmasnak bizonyult a melegkedvelő és szárazságtűrő, valamint a szünantróp, behurcolt és idegenhonos fajok számára is. Ezzel egyidejűleg ugyanezen városi élőhelyen a természetes élőhelyek arányának csökkenése, a feldarabolódás, valamint a táplálék minőségének megváltozása szignifikánsan csökkentette az erdei specialista fajok előfordulását.

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Table 1. Occurrence of millipede species in and around the cities of Europe

City	Referencee	Species list	Species no.
Budapest	Korsós 1992, Korsós et al. 2002	<i>Amphitomeus attemsii</i> (Schubart, 1934), <i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Brachydesmus superus</i> Latzel, 1884, <i>Brachydesmus dadayi</i> Verhoeff, 1895, <i>Brachyiulus bagnalli</i> (Brolemann, 1924), <i>Cibiniulus phlepsii</i> (Verhoeff, 1897), <i>Choneiulus palmatus</i> (Nemec, 1895), <i>Craspedosoma rawlinsii</i> Leach, 1814, <i>Cylindroiulus arborum</i> Verhoeff, 1928, <i>Cylindroiulus boleti</i> (C.L.Koch, 1847), <i>Cylindroiulus horvathi</i> (Verhoeff, 1897), <i>Cylindroiulus latestriatus</i> (Curtis, 1845), <i>Cylindroiulus parisiiorum</i> (Brolemann & Verhoeff, 1896), <i>Cylindroiulus truncorum</i> (Silvestri, 1896), <i>Cynedesmus formicola</i> Cook, 1896, <i>Dorypetalum degenerans</i> (Latzel, 1884), <i>Glomeris hexasticha</i> Brandt, 1833, <i>Kryphioidulus ocellatus</i> (C.L. Koch, 1847), <i>Megaphyllum projectum</i> Verhoeff, 1894, <i>Megaphyllum unilineatum</i> (C.L. Koch, 1838), <i>Mesoiulus paradoxus</i> Berlese, 1886, <i>Nemasoma varicornis</i> C.L.Koch, 1847, <i>Nopiulus kochii</i> (Gervais, 1847), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Ommatiulus sabulosus</i> (Linnaeus 1758), <i>Oxidus gracilis</i> (C.L. Koch 1847), <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus denticulatus</i> C.L. Koch, 1847, <i>Polyxenus lagurus</i> (Linnaeus, 1758), <i>Poratia digitata</i> (Porat, 1889), <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Strongylosoma stigmatosum</i> (Eichwald, 1830), <i>Xestoiulus laeticollis</i> (Porat, 1889)	33
Bucharest	Giurginca 2006, Giurginca et al. 2014	<i>Brachydesmus superus</i> Latzel, 1884, <i>Bulgardicus bucarestensis</i> Tabacaru & Giurginca, 2005, <i>Cylindroiulus arborum</i> Verhoeff, 1928, <i>Cylindroiulus boleti</i> (C.L.Koch, 1847), <i>Megaphyllum transsylvanicum</i> (Verhoeff, 1897), <i>Megaphyllum unilineatum</i> (C.L. Koch, 1838)	6
Bratislava	Holecová et al. 2012	<i>Brachydesmus superus</i> Latzel, 1884, <i>Brachyiulus bagnalli</i> (Brolemann, 1924), <i>Craspedosoma rawlinsii</i> Leach, 1814, <i>Cylindroiulus boleti</i> (C.L.Koch, 1847), <i>Cylindroiulus luridus</i> (C.L. Koch, 1847), <i>Glomeris hexasticha</i> Brandt, 1833, <i>Glomeris pustulata</i> Latreille, 1804, <i>Glomeris tetrasticha</i> Brandt, 1833, <i>Haploporatia eremita</i> (Verhoeff, 1909), <i>Julus curvicornis</i> Verhoeff, 1899, <i>Julus scandinavicus</i> Latzel, 1884, <i>Julus terrestris</i> Linnaeus, 1758, <i>Kryphioidulus ocellatus</i> (C.L. Koch, 1847), <i>Leptoiulus proximus</i> (Nemec, 1896), <i>Megaphyllum projectum</i> Verhoeff, 1894, <i>Megaphyllum unilineatum</i> (C.L. Koch, 1838), <i>Ommatiulus sabulosus</i> (Linnaeus 1758), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus denticulatus</i> C.L. Koch, 1847, <i>Polyxenus lagurus</i> (Linnaeus, 1758), <i>Polyzonium germanicum</i> Brandt, 1837, <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Strongylosoma stigmatosum</i> (Eichwald, 1830), <i>Trachysphaera costata</i> (Waga, 1857), <i>Unciger foetidus</i> (C.L.Koch, 1838), <i>Unciger transsylvanicus</i> (Verhoeff 1899)	28
Copenhagen	Enghoff 1973	<i>Allajulus nitidus</i> (Verhoeff, 1891), <i>Archiboreoiulus pallidus</i> (Brade-Birks, 1920), <i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Boreoiulus tenuis</i> (Bigler, 1913), <i>Brachydesmus superus</i> Latzel, 1884, <i>Brachyiulus pusillus</i> (Leach, 1814), <i>Craspedosoma rawlinsii</i> Leach, 1814, <i>Cylindroiulus britannicus</i> (Verhoeff, 1891), <i>Cylindroiulus latestriatus</i> (Curtis, 1845), <i>Cylindroiulus londinensis</i> (Leach, 1814), <i>Cylindroiulus punctatus</i> (Leach, 1815), <i>Cylindroiulus truncorum</i> (Silvestri, 1896), <i>Glomeris marginata</i> (Villers 1789), <i>Julus scandinavicus</i> Latzel, 1884, <i>Macrosterodesmus palicola</i> Brolemann, 1908, <i>Melogona voigtii</i> (Verhoeff, 1899), <i>Nemasoma varicornis</i> C.L.Koch, 1847, <i>Nopiulus kochii</i> (Gervais, 1847), <i>Ophiodesmus albonanus</i> (Latzel, 1895), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Polydesmus denticulatus</i> C.L. Koch, 1847, <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Unciger foetidus</i> (C.L.Koch, 1838)	23
Debrecen	Bogyó & Korsós, (2009); Bogyó et al., (2014)	<i>Brachyiulus bagnalli</i> (Brolemann, 1924), <i>Choneiulus palmatus</i> (Nemec, 1895), <i>Cylindroiulus boleti</i> (C.L.Koch, 1847), <i>Cylindroiulus caeruleocinctus</i> (Wood, 1864), <i>Cylindroiulus latestriatus</i> (Curtis, 1845), <i>Enantiulus nanus</i> (Latzel, 1884), <i>Kryphioidulus ocellatus</i> (C.L. Koch, 1847), <i>Leptoiulus proximus</i> (Nemec, 1896), <i>Mastigona bosniensis</i> (Verhoeff, 1897), <i>Megaphyllum projectum</i> Verhoeff, 1894, <i>Megaphyllum unilineatum</i> (C.L. Koch, 1838), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus schaessburgensis</i> Verhoeff, 1898, <i>Proteroiulus fuscus</i> (Am Stein, 1857)	15

Table 1. continued

City	Reference	Species list	Species no.
Kiel	Tischler 1980	<i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Brachydesmus superus</i> Latzel, 1884, <i>Choneiulus palmatus</i> (Nemec, 1895), <i>Cylindroiulus latestriatus</i> (Curtis, 1845), <i>Cylindroiulus londinensis</i> (Leach, 1814), <i>Cylindroiulus luridus</i> (C.L. Koch, 1847), <i>Enantiulus nanus</i> (Latzel, 1884), <i>Julus scandinavicus</i> Latzel, 1884, <i>Kryphioiulus occultus</i> (C.L. Koch, 1847), <i>Leptoiulus proximus</i> (Nemec, 1896), <i>Melogona voigtii</i> (Verhoeff, 1899), <i>Nemasoma varicornis</i> C.L.Koch, 1847, <i>Ophiulus pilosus</i> (Newport, 1842), <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Unciger foetidus</i> (C.L.Koch, 1838)	15
London	Davis 1979, Smith et al. 2006	<i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Brachydesmus superus</i> Latzel, 1884, <i>Brachyiulus pusillus</i> (Leach, 1814), <i>Choneiulus palmatus</i> (Nemec, 1895), <i>Cylindroiulus britannicus</i> (Verhoeff, 1891), <i>Cylindroiulus caeruleocinctus</i> (Wood, 1864), <i>Cylindroiulus vulnerarius</i> (Berlese, 1888), <i>Macrosternodesmus palicola</i> Brolemann, 1908, <i>Ophiodesmus albonanus</i> (Latzel, 1895), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Polydesmus angustus</i> Latzel, 1884, <i>Polydesmus coriaceus</i> Porat, 1871, <i>Tachypodoiulus niger</i> (Leach, 1814)	13
Lublin	Bielak 1964, Kania 2011	<i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Boreoiulus tenuis</i> (Bigler, 1913), <i>Brachydesmus superus</i> Latzel, 1884, <i>Brachyiulus pusillus</i> (Leach, 1814), <i>Choneiulus palmatus</i> (Nemec, 1895), <i>Craspedosoma rawlinsii</i> Leach, 1814, <i>Cylindroiulus arborum</i> Verhoeff, 1928, <i>Cylindroiulus britannicus</i> (Verhoeff, 1891), <i>Cylindroiulus caeruleocinctus</i> (Wood, 1864), <i>Cylindroiulus latestriatus</i> (Curtis, 1845), <i>Cylindroiulus parisiorum</i> (Brolemann & Verhoeff, 1896), <i>Cylindroiulus truncorum</i> (Silvestri, 1896), <i>Glomeris hexasticha</i> Brandt, 1833, <i>Kryphioiulus occultus</i> (C.L. Koch, 1847), <i>Leptoiulus proximus</i> (Nemec, 1896), <i>Mastigona bosniensis</i> (Verhoeff, 1897), <i>Nemasoma varicornis</i> C.L.Koch, 1847, <i>Nopiulus kochii</i> (Gervais, 1847), <i>Ommatiulus sabulosus</i> (Linnaeus 1758), <i>Oxidus gracilis</i> (C.L. Koch 1847), <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus denticulatus</i> C.L. Koch, 1847, <i>Polydesmus inconstans</i> Latzel, 1884, <i>Polyxenus lagurus</i> (Linnaeus, 1758), <i>Polyzonium germanicum</i> Brandt, 1837, <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Strongylosoma stigmatosum</i> (Eichwald, 1830), <i>Unciger foetidus</i> (C.L.Koch, 1838)	28
Lucerne	Vilics et al. 2012	<i>Ophiulus pilosus</i> (Newport, 1842), <i>Oxidus gracilis</i> (C.L. Koch 1847), <i>Polydesmus angustus</i> Latzel, 1884	3
Lugano	Vilics et al. 2012	<i>Brachydesmus superus</i> Latzel, 1884, <i>Cylindroiulus verhoeffi</i> (Brolemann, 1896), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Oxidus gracilis</i> (C.L. Koch 1847)	4
Moscow	Lokshina 1960	<i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Brachydesmus superus</i> Latzel, 1884, <i>Brachyiulus jawlowski</i> Lohmander, 1928, <i>Cylindroiulus boleti</i> (C.L.Koch, 1847), <i>Cylindroiulus britannicus</i> (Verhoeff, 1891), <i>Kryphioiulus occultus</i> (C.L. Koch, 1847), <i>Leptoiulus proximus</i> (Nemec, 1896), <i>Megaphyllum sjællandicum</i> (Meinert 1868), <i>Nopiulus kochii</i> (Gervais, 1847), <i>Ommatiulus sabulosus</i> (Linnaeus 1758), <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus denticulatus</i> C.L. Koch, 1847, <i>Polyzonium germanicum</i> Brandt, 1837, <i>Schizoturanius dmitriewi</i> (Timotheew, 1897), <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Rossiulus kessleri</i> (Lohmander, 1927), <i>Strongylosoma stigmatosum</i> (Eichwald, 1830), <i>Xestoiulus laeticollis</i> (Porat, 1889)	18
Olomouc	Reidel et al. 2009	<i>Allajulus nitidus</i> (Verhoeff, 1891), <i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Brachyiulus bagnalli</i> (Brolemann, 1924), <i>Choneiulus palmatus</i> (Nemec, 1895), <i>Cylindroiulus boleti</i> (C.L.Koch, 1847), <i>Cylindroiulus caeruleocinctus</i> (Wood, 1864), <i>Cylindroiulus latestriatus</i> (Curtis, 1845), <i>Geoglomeris subterranea</i> Verhoeff, 1908, <i>Kryphioiulus occultus</i> (C.L. Koch, 1847), <i>Melogona broelemanni</i> (Verhoeff, 1897), <i>Melogona voigtii</i> (Verhoeff, 1899), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Oxidus gracilis</i> (C.L. Koch 1847), <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus inconstans</i> Latzel, 1884, <i>Polyxenus lagurus</i> (Linnaeus, 1758), <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Unciger foetidus</i> (C.L.Koch, 1838)	18

Table 1. continued

City	Reference	Species list	Species no.
Prague	Kocourek 2014	<p><i>Allajulus nitidus</i> (Verhoeff, 1891), <i>Amphitomeus attensis</i> (Schubart, 1934), <i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Brachydesmus superus</i> Latzel, 1884, <i>Brachyiulus bagnalli</i> (Brolemann, 1924), <i>Brachyiulus lusitanus</i> Verhoeff, 1898, <i>Choneiulus palmatus</i> (Nemec, 1895), <i>Craspedosoma rawlinsii</i> Leach, 1814, <i>Cylindroiulus arborum</i> Verhoeff, 1928, <i>Cylindroiulus britannicus</i> (Verhoeff, 1891), <i>Cylindroiulus caeruleocinctus</i> (Wood, 1864), <i>Cylindroiulus latestriatus</i> (Curtis, 1845), <i>Cylindroiulus luridus</i> (C.L. Koch, 1847), <i>Cylindroiulus parisiorum</i> (Brolemann & Verhoeff, 1896), <i>Cylindroiulus punctatus</i> (Leach, 1815), <i>Cylindroiulus truncorum</i> (Silvestri, 1896), <i>Cylindroiulus vulnerarius</i> (Berlese, 1888), <i>Enantiulus nanus</i> (Latzel, 1884), <i>Glomeris connexa</i> C.L.Koch, 1847, <i>Glomeris hexasticha</i> Brandt, 1833, <i>Glomeris pustulata</i> Latreille, 1804, <i>Haasea flavescens</i> (Latzel, 1884), <i>Haploporatia eremita</i> (Verhoeff, 1909), <i>Julus scandinavicus</i> Latzel, 1884, <i>Kryphioiulus occultus</i> (C.L. Koch, 1847), <i>Leptoiulus proximus</i> (Nemec, 1896), <i>Mastigophorophyllon saxonicum</i> Verhoeff, 1916, <i>Mastigona bosniensis</i> (Verhoeff, 1897), <i>Megaphyllum projectum</i> Verhoeff, 1894, <i>Megaphyllum unilineatum</i> (C.L. Koch, 1838), <i>Melogona broelemanni</i> (Verhoeff, 1897), <i>Melogona voigtii</i> (Verhoeff, 1899), <i>Nemasoma varicorne</i> C.L.Koch, 1847, <i>Nopiulus kochii</i> (Gervais, 1847), <i>Ochogona caroli</i> (Rothenbuhler, 1900), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Oxidus gracilis</i> (C.L. Koch 1847), <i>Polydesmus angustus</i> Latzel, 1884, <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus denticulatus</i> C.L. Koch, 1847, <i>Polydesmus inconstans</i> Latzel, 1884, <i>Polyxenus lagurus</i> (Linnaeus, 1758), <i>Polyzonium germanicum</i> Brandt, 1837, <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Rossiulus vilnensis</i> (Jawlowski, 1925), <i>Strongylosoma stigmatosum</i> (Eichwald, 1830), <i>Trachysphaera costata</i> (Waga, 1857), <i>Unciger foetidus</i> (C.L.Koch, 1838), <i>Unciger transsylvanicus</i> (Verhoeff 1899)</p>	50
Sofia	Strasser 1966, Stoev 2004	<p><i>Cylindroiulus arborum</i> Verhoeff, 1928, <i>Cylindroiulus boleti</i> (C.L.Koch, 1847), <i>Cylindroiulus horvathi</i> (Verhoeff, 1897), <i>Glomeris hexasticha</i> Brandt, 1833, <i>Leptoiulus borisi</i> Verhoeff, 1926, <i>Leptoiulus trilineatus</i> (C.L.Koch, 1847), <i>Megaphyllum bosniensis</i> (Verhoeff, 1897), <i>Megaphyllum unilineatum</i> (C.L. Koch, 1838), <i>Melogona broelemanni</i> (Verhoeff, 1897), <i>Nopiulus kochii</i> (Gervais, 1847), <i>Oxidus gracilis</i> (C.L. Koch 1847), <i>Pachyiulus hungaricus</i> (Karsch, 1881), <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus renschi</i> Schubart, 1934</p>	14
Vienna	Bogyó et al. unpublished.	<p><i>Blaniulus guttulatus</i> (Fabricius, 1798), <i>Brachydesmus superus</i> Latzel, 1884, <i>Brachyiulus bagnalli</i> (Brolemann, 1924), <i>Craspedosoma rawlinsii</i> Leach, 1814, <i>Cylindroiulus boleti</i> (C.L.Koch, 1847), <i>Cylindroiulus caeruleocinctus</i> (Wood, 1864), <i>Cylindroiulus luridus</i> (C.L. Koch, 1847), <i>Cylindroiulus parisiorum</i> (Brolemann & Verhoeff, 1896), <i>Cylindroiulus punctatus</i> (Leach, 1815), <i>Glomeris hexasticha</i> Brandt, 1833, <i>Haploglomeris multistriata</i> (C.L.Koch, 1844), <i>Julus scandinavicus</i> Latzel, 1884, <i>Kryphioiulus occultus</i> (C.L. Koch, 1847), <i>Mastigona bosniensis</i> (Verhoeff, 1897), <i>Megaphyllum unilineatum</i> (C.L. Koch, 1838), <i>Melogona gallica</i> (Latzel, 1884), <i>Nopiulus kochii</i> (Gervais, 1847), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Ommaiulus sabulosus</i> (Linnaeus 1758), <i>Polydesmus angustus</i> Latzel, 1884, <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus denticulatus</i> C.L. Koch, 1847, <i>Stosatea italica</i> (Latzel, 1886), <i>Unciger foetidus</i> (C.L.Koch, 1838), <i>Unciger transsylvanicus</i> (Verhoeff 1899)</p>	25

Table 1. continued

City	Literature	Species list	Species no.
Warsaw	Jedryczkowski 1982, 1996	<p><i>Blianiulus guttulatus</i> (Fabricius, 1798), <i>Boreoiulus tenuis</i> (Bigler, 1913), <i>Brachydesmus superus</i> Latzel, 1884, <i>Brachyiulus pusillus</i> (Leach, 1814), <i>Choneiulus palmatus</i> (Nemec, 1895), <i>Craspedosoma rawlinsii</i> Leach, 1814, <i>Cylindroiulus arborum</i> Verhoeff, 1928, <i>Cylindroiulus britannicus</i> (Verhoeff, 1891), <i>Cylindroiulus caeruleocinctus</i> (Wood, 1864), <i>Cylindroiulus latestriatus</i> (Curtis, 1845), <i>Cylindroiulus truncorum</i> (Silvestri, 1896), <i>Glomeris connexa</i> C.L.Koch, 1847, <i>Glomeris hexasticha</i> Brandt, 1833, <i>Julus terrestris</i> Linnaeus, 1758, <i>Kryphioidulus occultus</i> (C.L. Koch, 1847), <i>Leptoiulus proximus</i> (Nemec, 1896), <i>Mastigophorophyllon saxonicum</i> Verhoeff, 1916, <i>Mastigona bosniensis</i> (Verhoeff, 1897), <i>Megaphyllum bosniensis</i> (Verhoeff, 1897), <i>Megaphyllum projectum</i> Verhoeff, 1894, <i>Nemasoma varicorne</i> C.L.Koch, 1847, <i>Nopiulus kochii</i> (Gervais, 1847), <i>Ommatiulus sabulosus</i> (Linnaeus 1758), <i>Ophiodesmus albanus</i> (Latzel, 1895), <i>Ophiulus pilosus</i> (Newport, 1842), <i>Oxidus gracilis</i> (C.L. Koch 1847), <i>Polydesmus complanatus</i> (Linnaeus, 1761), <i>Polydesmus inconstans</i> Latzel, 1884, <i>Polyxenus lagurus</i> (Linnaeus, 1758), <i>Polyzonium germanicum</i> Brandt, 1837, <i>Proteroiulus fuscus</i> (Am Stein, 1857), <i>Strongylosoma stigmatosum</i> (Eichwald, 1830), <i>Trachysphaera costata</i> (Waga, 1857), <i>Unciger foetidus</i> (C.L.Koch, 1838)</p>	34
Zürich	Vilisics et al. 2012	<p><i>Brachydesmus superus</i> Latzel, 1884, <i>Cylindroiulus caeruleocinctus</i> (Wood, 1864), <i>Nemasoma varicorne</i> C.L.Koch, 1847, <i>Ophiulus pilosus</i> (Newport, 1842), <i>Propolydesmus testaceus</i> (C.L. Koch, 1847),</p>	5

Table 2.

Average values (\pm SD) of the environmental variables in the study areas along a rural-suburban-urban gradient in Debrecen, Hungary.

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

Table 3.

Habitat preference and quantitative character values of the millipede species. The IndVal column shows the species character value for the corresponding cluster level. Notations: ns – not significant; * – $p < 0.05$. A: the number of specimens present, B: the number of traps where the species is present in the sample group.

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

Table 4.

Incidence of millipede species in sampling sites in the cities of Zürich, Lucerne and Lugano (Switzerland).

Species	Species occurrences in traps		
	Zürich (n=36)	Lucerne (n=34)	Lugano (n=36)
<i>Brachydesmus superus</i>	+	0	+
<i>Cylindroiulus caeruleocinctus</i>	+	0	0
<i>Cylindroiulus verhoeffi</i>	0	0	+
<i>Nemasoma varicorne</i>	+	0	0
<i>Ophiulus pilosus</i>	+	+	+!
<i>Oxidus gracilis</i>	0	+	+
<i>Polydesmus angustus</i>	0	+	0
<i>Propolydesmus testaceus</i>	+	0	0
<i>Chordeumatidae fam. sp.</i>	0	+	0
<i>Craspedosomatidae fam. sp.</i>	0	0	+
<i>indet +</i>	+	0	0
Millipede species ()	5	3	4
Millipede specimens	32	27	46

Table 5. Occurrence of *Cylindroiulus caeruleocinctus* (Wood, 1864) in European cities.

	Natural habitats	Synanthropic habitats	Both	Reference
Austria		+		Thaler, 1988
Belgium			+	Kime, 1992
Czech Republic		+		Kocourek, 2004; Mock, 2006
Denmark			+	Enghoff, 1974
Estonia		+		Blower, 1985; Enghoff, 2007
Finland		+		Palmén, 1949
France			+	Geoffroy, 1996; David, 1995; David, 2008 in litt.
Germany			+	Blower, 1985; Kime, 1990; Schubart, 1934
Great Britain			+	Blower, 1985
Hungary		+		Bogyó & Korsós, 2010
Ireland			+	Blower, 1985
Italy		?		Foddai et al., 1995
Latvia		+		Blower, 1985; Enghoff, 2007
Lithuania		+		Blower, 1985; Enghoff, 2007
Luxemburg			+	Kime, 1996, 1999
Netherlands			+	Blower, 1986; Berg, M. P., 1995; Jeekel, 2000
Norway			+	Andersson et al., 2005; Djursvoll et al., 2006
Poland		+		Jedryczkowski, 1992
Portugal		?		Kime, 1990
Slovakia		+		Mock, 2006
Spain		?		Vicente, 1985
Sweden			?	Blower, 1985; Kime, 1990
Switzerland			+	Pedroli-Christen, 1993
(former) USSR		+		Chorneyi & Golovatch, 1993; Golovatch, 1992; Lokshina, 1962

Figure 1.

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

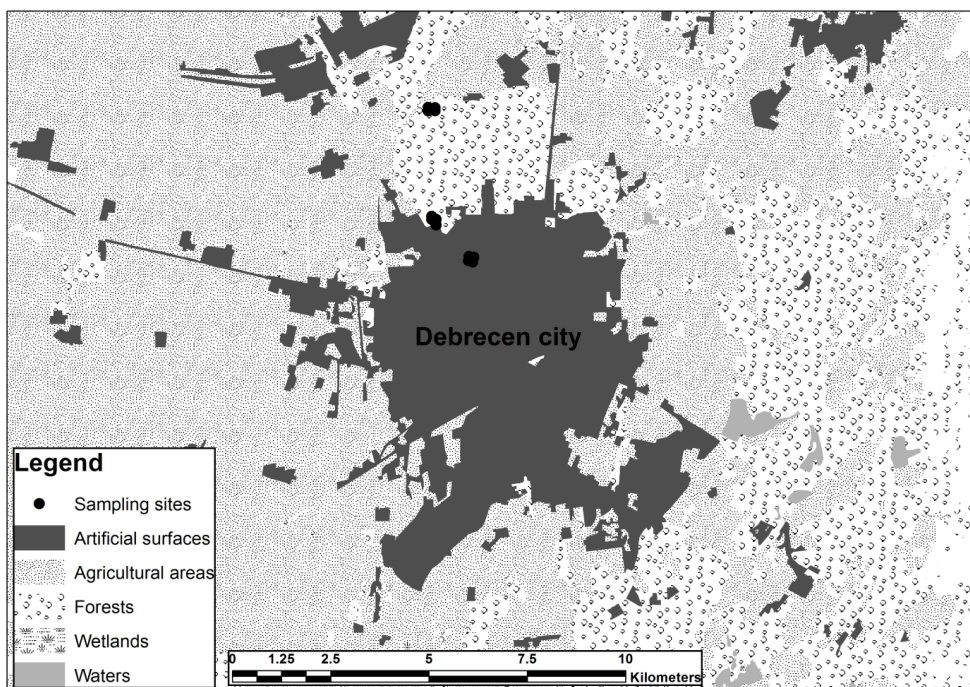


Figure 2.

Abundances of isopods and millipedes in Zürich, Lucerne and Lugano in logarithmic scale. Dashed line separates isopods (on the left) from millipedes. Black bars represent abundances, white circles show the species' incidences per all sites per city.

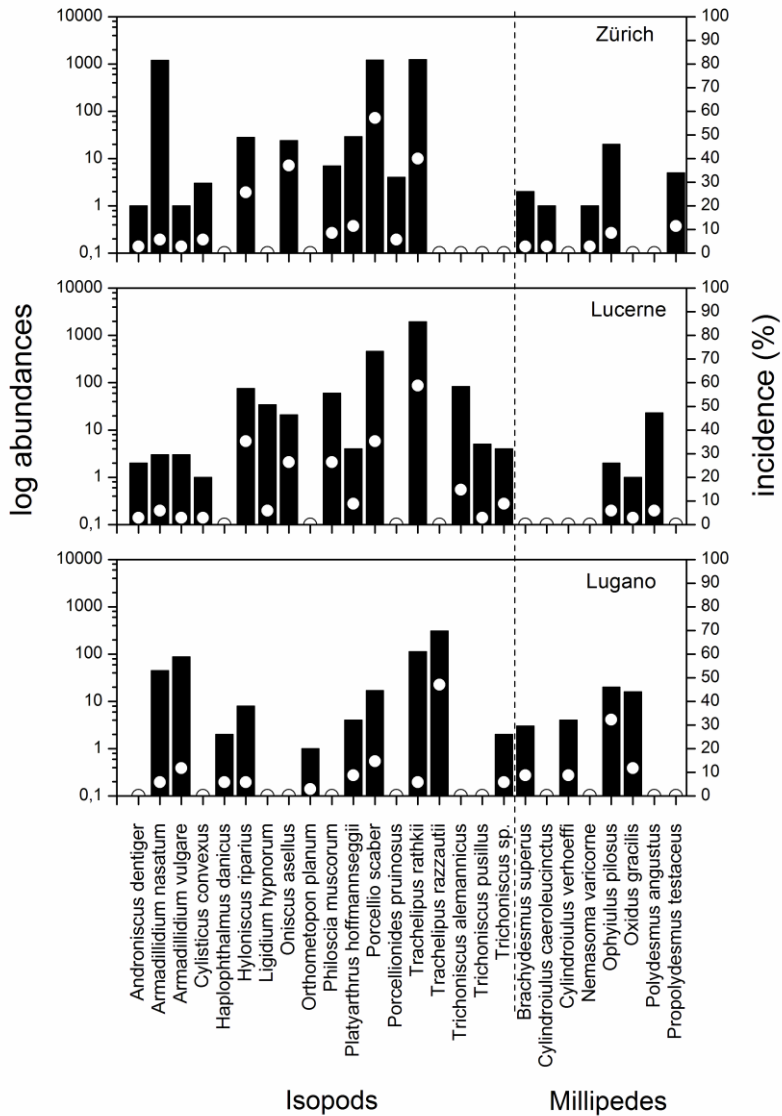


Figure 3.

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

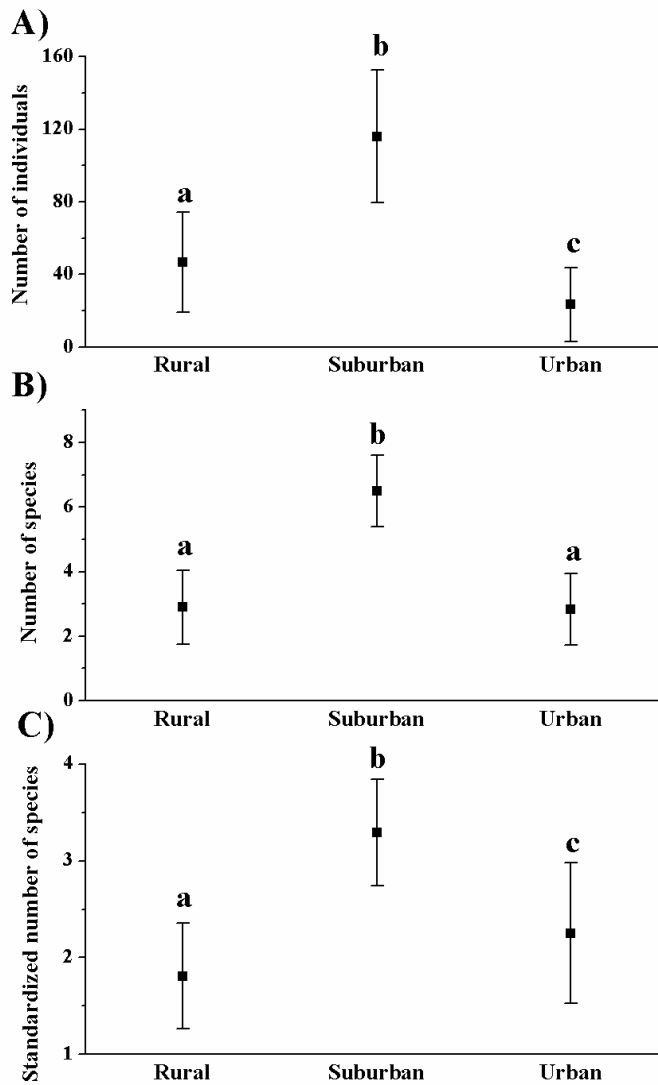


Figure 4.

Mean value of the ratio (\pm 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.

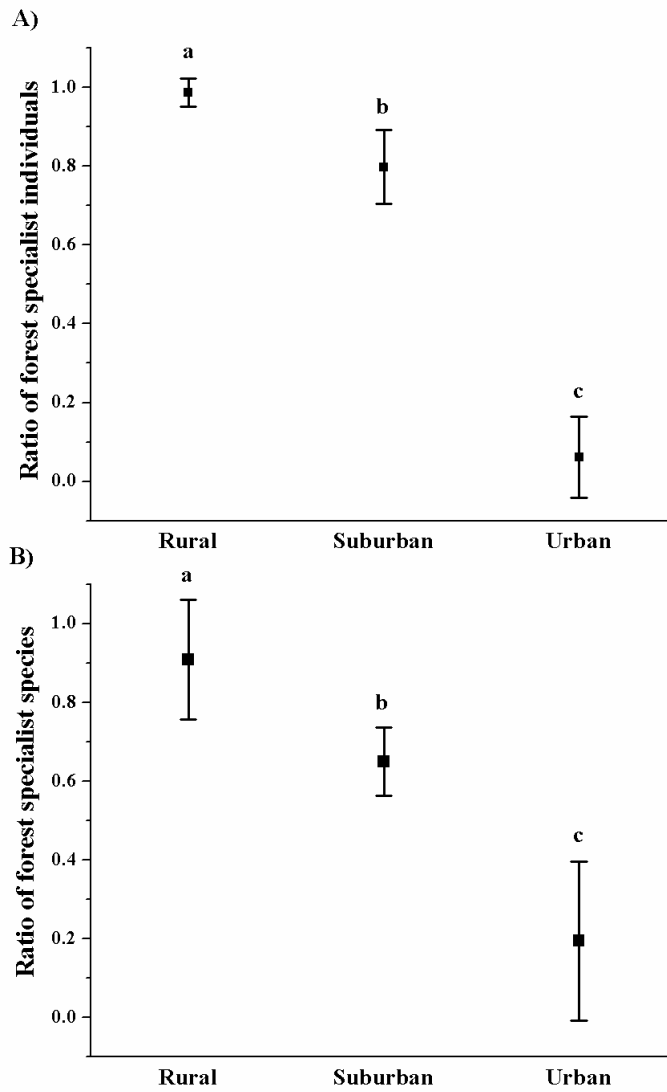


Figure 5.

Mean value of the ratio (\pm 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.

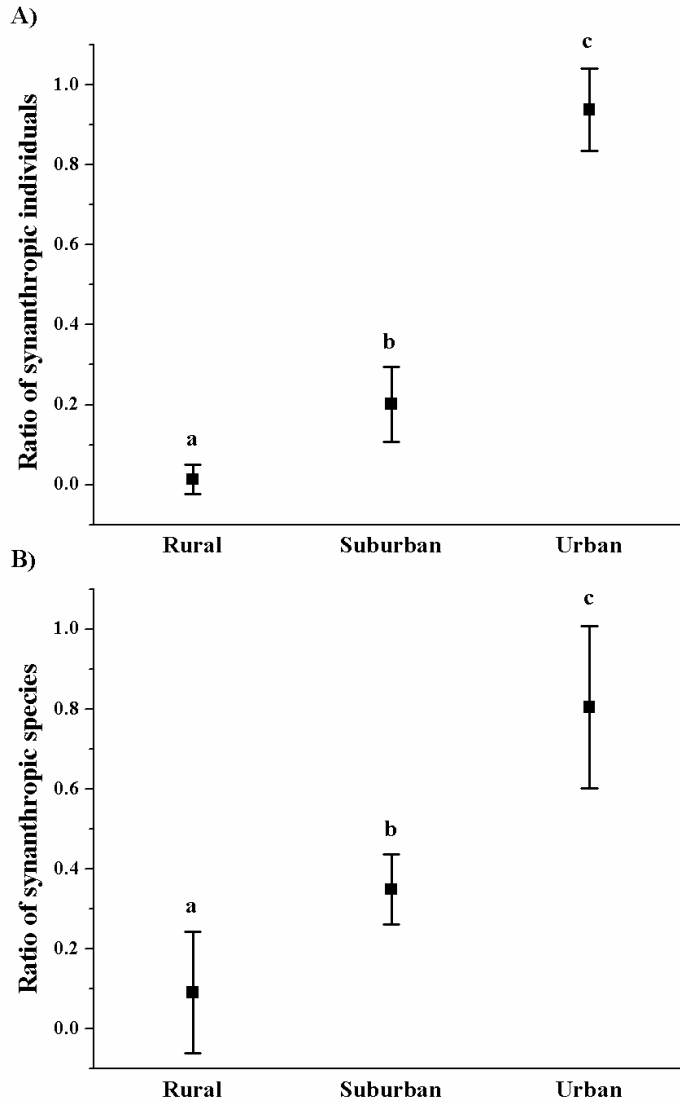


Figure 6.

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

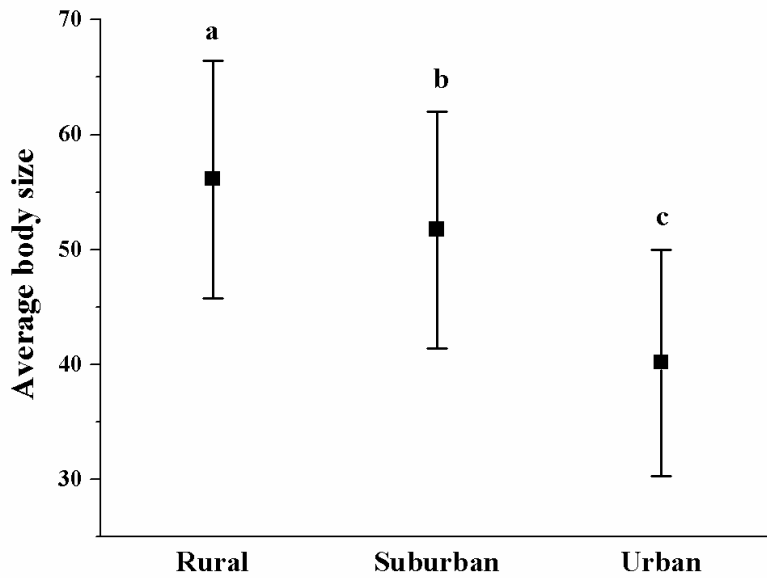


Figure 7.

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 2cm 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, pH: pH of the soil, Pb: lead, 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*; OPHPYL: *Ophiulus pilosus*; POLCOM: *Polydesmus complanatus*; POLSCH: *Polydesmus schaessburgensis*).

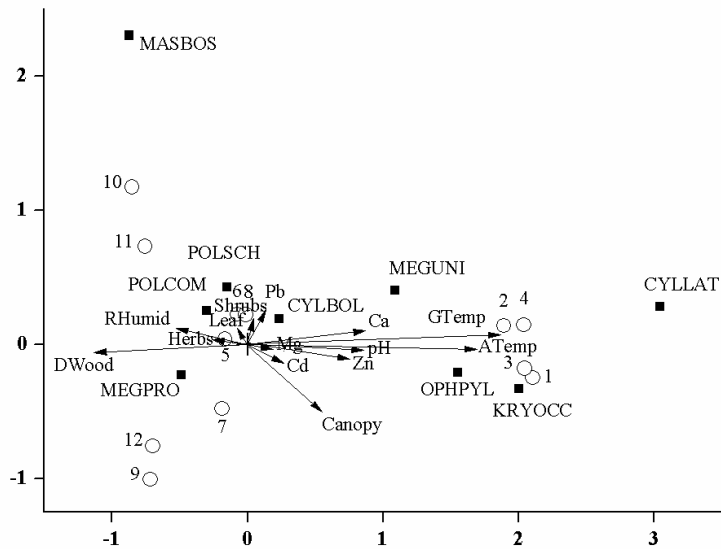


Figure 8.

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

