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Composition of terrestrial isopod assemblages along an urbanisation gradient in Denmark

Ferenc Vilisics[a,*], Zoltán Elek[a,b], Gábor L. Lövei[b], Elizabeth Hornung[a]

[a]*Department of Ecology, Faculty of Veterinary Science, Szent István University, Institute for Zoology, Budapest, Hungary*
[b]*Department of Integrated Pest Management, University of Aarhus, Faculty of Agricultural Sciences, Flakkebjerg Research Centre, Slagelse, Denmark*

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Summary

The effects of urbanisation on isopods were studied in Sorø, Zealand, Denmark in 2004. We sampled woodlice using pitfall traps in a natural beech forest, a suburban beech forest remnant and forest "islands" of the original habitat in a public park. A total of 31 848 individuals comprising six species were collected. Two additional, small-bodied species were excluded from analyses due to their low number in the traps. Three species (*Porcellio scaber, Oniscus asellus*, *Philoscia muscorum*) dominated the assemblages accounting for 95.7% of the total specimens.

Although, we found no difference among the habitats based on species richness or species composition, they did differ according to the Rényi scalable diversity index. This index was highest in the suburban habitat, followed by the urban forest islands and lowest in the natural forest. This was due to the significantly higher total isopod abundance in urban and suburban sites, compared to the forest habitat. The forest woodlice assemblage formed a distinct group in the hierarchical cluster analysis while the assemblages of suburban and urban sites did not separate into distinct groups. We conclude that the effect of urbanisation on woodlice assemblages manifests itself through the abundance and the relative distribution of isopod species, which are both appropriately represented by the scalable diversity index approach.

Introduction

Densely settled human habitats are increasing worldwide. According to predictions (Douglas 1992;

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*Corresponding author. Tel.: +36 20 661 3010.
E-mail address: Vilisics.Ferenc@aotk.size.hu (F. Vilisics).

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Vandruff et al. 1995) the majority of the human population became urban in 2005; that progress of urbanisation, unavoidably, has caused and is continuing to cause radical changes in natural habitats (Shochat et al. 2006). The degree of change varies depending on the level of development of urbanised areas. Human disturbance; however, may also help to form new biotopes and habitats for new/establishing species. Therefore, the value of ecosystems (e.g. flux of matter and energy) cannot be defined only by their species richness (Eversham et al. 1996), but also by the different ecological function of species (Heemsbergen et al. 2004). In most cases, new habitats are colonised by species of broad tolerance, mainly cosmopolitan species. The rate of colonisation might also be biased by geographical and macroclimatic factors (Zapparoli 1997; Niemelä et al. 2000).

Cities, as constructed habitats for humans, show similar features globally, including paved roads, dense residential and commercial city cores, industrial areas, and less developed suburban areas (McKinney 2006). This similarity provides a good opportunity to observe the impact of urbanisation on biodiversity changes under comparable circumstances in different parts of the world and to test whether humans affect biodiversity to the same degree during the process of urbanisation (Niemelä et al. 2000).

The effect of urbanisation has been studied on plants (Guntenspergen and Levenson 1997), reptiles (Germaine and Wakeling 2001), birds (Parsons et al. 2003) and some arthropod groups (e.g. spiders: Shochat et al. 2006; carabid beetles: e.g. Niemelä et al. 2002; Venn et al. 2003; Magura et al. 2004; Sadler et al. 2006; bumble bees: McFrederick and LeBuhn 2006). These studies indicate that urbanisation has significant but often idiosynchratic effects on diversity and species composition (e.g. Zapparoli 1997; Alaruikka et al. 2002; Niemelä et al. 2002; Gibb and Hochuli 2002; Ishitani et al. 2003; Weller and Ganzhorn 2004). However, due to the different protocols used in these studies, results cannot be directly compared.

In the context of the Danglobe research project, we analysed the effects of urbanisation on the diversity of terrestrial isopods (Isopoda, Oniscidea) in Sorø, Denmark. Following the general approach of the Globenet Protocol (Niemelä et al. 2000), we focused on the taxon's species richness, diversity, and abundance along an urbanisation gradient.

The literature on Danish woodlice is scarce with the last published data more than 40 years old (Meinertz 1964); urban isopod assemblages specifically, have been even less studied (Magura et al. 2006). Given the importance of woodlice among soil-dwelling macrodecomposers (Hassall et al. 1987), the current study is justified. Results could also help to understand the impact of urbanisation in areas with lower human densities, which is the case in northern Europe. The size and the population density of Sorø municipality differ from the areas that have been investigated earlier under the Globenet research project. Sorø is a small town, where the key parameters of urban ecosystems (e.g. considerable heat island effect, high traffic) are lower compared to other, previously studied settlements such as Hamburg (Weller and Ganzhorn 2004) and Helsinki (Niemelä et al. 2002).

Several hypotheses have been invoked to explain the effects of urbanisation on various taxa (e.g. carabids, Magura et al. 2004, 2006; Elek and Lövei 2005) within the Globenet project: (a) diversity is highest in areas under intermediate disturbance ["Intermediate Disturbance Hypothesis (IDH)" (Connell 1978)], (b) diversity gradually decreases with increasing disturbance ["Increasing Disturbance Hypothesis" (Gray 1989)] and (c) the richness of species living in natural habitats decreases with increasing disturbance ["Habitat Specialist Hypothesis" (Magura et al. 2004)]. We extended Connell's IDH with an interpretation of diversity (Rényi) that considers relative frequency in addition to species richness. A further hypothesis referred to as the "Invader Species Hypothesis (ISH)" has emerged from other urban studies (Korsós et al. 2002; Vilisics 2005; Magura et al. 2006). This hypothesis states that species' richness in disturbed habitats (e.g. suburban, urban) should be low in stenotopic specialists, but should show a higher value in eurytopic and introduced species. The latter is logically connected to the "Opportunistic Species Hypothesis" described by Magura et al. (2004), but since introduced isopod species cannot automatically be deemed opportunistic, we considered the ISH a separate hypothesis.

In this paper, we present data that show few differences in woodlice species richness and composition, but indicate that their responses to urbanisation can be tracked by changes in their abundance and an appropriately chosen diversity index.

Materials and methods

Study area and sampling method

The town of Sorø (6996 inhabitants in 2003) is located in West-Zealand, Denmark (55°26′00″N; 11°34′00″E; UTM: PG64). Three habitat types were

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selected to represent different levels of human disturbance (i.e. rural, suburban, and urban).

The vicinity of Sorø originally had an extensive coverage of forests (beech woods, *Fagus sylvatica* L.) that, due to the expansion of the settlement, became fragmented. The appropriate "rural" habitat is therefore a beech forest, with its typical dense canopy, a scarce continuous herb layer and lack of shrubs. The forested sampling area (55°26′13.98″N; 11°31′27.32″E) was located ca. 1.5 km from the town centre.

The suburban sampling area (55°25′48.33″N; 11°33′58.85″E) was located in a beech forest remnant on the outskirts of Sorø, where the original forest was thinned out. This habitat type differed greatly from the natural forest, being characterised by low-density beech, with ash (*Fraxinus excelsior* L.) trees and various bushes, and a rich herb layer, often composed of a carpet of beech saplings. Detached houses, gardens, a cemetery, paved and unpaved roads and a ditch were found in the area.

The urban site was in one of the extensive park areas belonging to the Sorø Akademi (55°25′N; 11°33′E), a foundation that maintains town parks, its school as well as various monuments and protected buildings. The site contained patches of the original beech forest, but many of these have been enriched by exotic trees and bushes, separated by lawns. The park complex is partly bordered by a lake.

Sampling was performed according to the Globenet protocol (see Niemelä et al. 2000 for details on the trapping methodology). A total number of 120 (3×40) pitfall traps were set out in the three habitat types. There were four replicates (sites) per habitat, each consisting of 10 traps. A minimum distance between replicates of 50 m was used to achieve sample independence. The between-trap distance was 10 m. Traps were emptied fortnightly. In the present study we analysed data from four samplings, which represented peak activity periods for above-ground isopods: 6–21 May; 2–19 July; 16–30 August and 23 September–11 October 2004.

Data analyses

Diversity was analysed by rank-abundance curves and the Rényi diversity profiles. Rank-abundance plots provide a useful initial approach for comparison of assemblages (Southwood and Henderson 2000) by listing species in decreasing order of abundance.

The diversity of the samples (pooled by habitat type) was compared using the Rényi one-parametric diversity index family. This method characterises the diversity of an assemblage by a family of diversity values (Tóthmérész, 1995), which can be presented graphically to visualise the diversity relationships of assemblages (Lövei, 2005). Such a curve is frequently referred to as the diversity profile of assemblages/communities. Members of a one-parametric diversity index family have varying sensitivities to the rare and abundant species as the scale parameter, α, changes (Tóthmérész, 1998). The Rényi diversity is a typical member of the generalised entropy functions (Ricotta, 2005). In some cases it can include the number of species, Shannon diversity, Simpson or quadratic diversity and the dominance index (Tóthmérész, 1998). When the value of the scale parameter is zero the Rényi diversity becomes extremely sensitive to the contribution of rare species to the diversity of an assemblage. As the value of the scale parameter approaches 1, the Rényi diversity equals the Shannon diversity, and while still sensitive to rare species it is less so than when $\alpha = 0$. When the value of the scale parameter is 2, the Rényi diversity is related to the quadratic (Simpson) diversity. In this case the index becomes more sensitive to frequent rather than rare species. On the other hand, when the value of the scale parameter is large the Rényi diversity is related to the Berger–Parker dominance index that is determined only by the relative abundance of the most common species.

The Rényi diversity profiles allow for partial ranking of ecological communities by diversity. An assemblage of higher diversity will, for example, also have a diversity profile that is above profiles of other assemblages (Tóthmérész, 1995). Diversity profiles offer a more effective and comprehensive way to investigate differences in diversity than the one-dimensional diversity indices, since the latter do not provide sufficient information to order communities according to their diversity (Southwood and Henderson 2000). We calculated the Rényi diversity profiles with the DivOrd program package (Tóthmérész 1993).

We classified isopods according to their occurrence and abundance as follows:

1. Dominant ($>30\%$ of total number of individuals) species with high density in suburban and urban areas.
2. Frequent species ($>20\%$ of total) that appeared in each habitat and at most sites and showed similar densities in the sites along the gradient.
3. Species with low-density values ($<5\%$ of total).

Comparison of species abundances among the three localities was carried out by Kruskal–Wallis non-parametric ANOVA.

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Average population densities were analysed with one-way ANOVAs and Tukey post-hoc tests. In order to achieve normality, the data were log(x+1) transformed.

Hierarchical clustering was performed with SYN-TAX program package (Podani 1997) using a fusion algorithm, and the Czekanowski–Bray–Curtis dissimilarity.

Data from the 12 trap-groups (sites) were analysed with a hierarchical ANOVA and subjected to Fisher's-LSD post-hoc test to explore the differences among three species' groups (i.e. dominant species, frequent species, species with low population densities). Analyses were carried out with the Statistica 7.0 program package (Statsoft 2004).

Results

Species composition

Eight species were collected along the rural–suburban–urban gradient in Sorø. Data for two species (*Trichoniscus pusillus* (Brandt, 1833) and *Haplophthalmus mengii* (Zaddach, 1844)) were excluded from further analyses because, due to their pigmy size and their soil dwelling (endogeic) habit, they rarely fall into pitfall traps and thus, their presence could be highly underestimated. The remaining six species were found in all three habitat types (Table 1).

The three most common species made up 95.7% of all the woodlice specimens analysed: *Porcellio scaber* Latreille, 1804 (38.6% of the total captures), *Oniscus asellus* Linnaeus, 1758 (33.6%) and *Philoscia muscorum* (Scopoli, 1763) (23.5%) (Table 1).

Abundance patterns

A total of 31 848 individuals were included in the analyses. The overall population density of isopods (Table 1) was lowest in the natural beech forest (3145 individuals in total), which was much lower than the density observed in the suburban (12 301) and urban (16 402) areas. The average number of individuals per trap showed similar and significant ($p<0.001$; $F_{2,\ 117}=42.89$) differences among the habitat types. Post-hoc comparisons (Tukey HSD) indicated that the average number of isopods were significantly lower in the forest ($p<0.001$; $H=1.08$) compared to both suburban ($H=1.63$) and urban ($H=1.69$) areas. No such significant differences were found between the latter two habitat types.

With the exception of *Philoscia muscorum*, significant differences were found in species abundance along the urbanisation gradient. The species *Armadillidium vulgare* and *Ligidium hypnorum* were most common in the suburban site, while *Porcellio scaber, O. asellus* and *Trachelipus rathkii* were more abundant in the urban park.

The rank abundance curves showed major changes in rank positions and abundances along gradient (Fig. 1). The forest was dominated by *Philoscia muscorum* while the cosmopolitan species (*Porcellio scaber, A. vulgare*) were infrequent in that habitat. Classification of isopods resulted in three groups of species: *Porcellio scaber* and *O. asellus* formed the "dominant species", *Philoscia muscorum* represented the "frequent species" while *Ligidium hypnorum* (Cuvier, 1792), *Trachelipus rathkii* (Brandt, 1833), *Armadillidium vulgare* (Latreille, 1804) were the "species with low population density".

Dominant and frequent species showed a preference for disturbed areas, while species with low densities preferred the suburban area (Table 2).

Table 1. The number of species, individuals, and the activity densities of woodlouse species (Isopoda, Oniscidea) along the urbanisation gradient in Sorø, Denmark in 2004

Species	Abundance values in the three habitat types		
	Natural forest	Suburban forest remnant	Urban park
Porcellio scaber	55	4392	7867
Oniscus asellus	827	4496	5376
Philoscia muscorum	2240	2337	2896
Armadillidium vulgare	21	669	126
Ligidium hypnorum	1	399	81
Trachelipus rathkii	1	8	56
Total species number	6	6	6
Total abundance	3145	12 301	16 402

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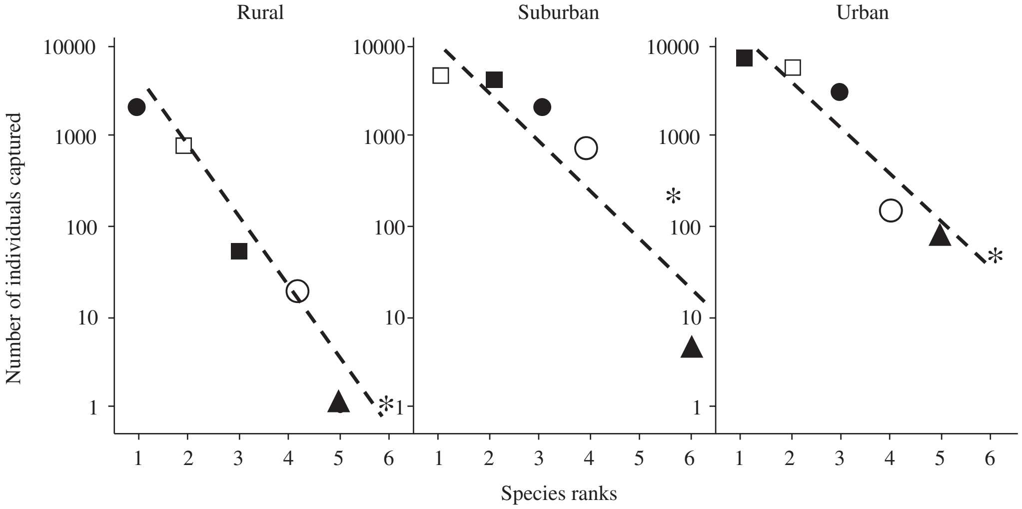

Figure 1. Rank-abundance curves of isopod assemblages at the three disturbance levels in Sorø, Zealand, Denmark, in 2004. Note the logarithmic scale on the *y*-axis: (A) rural; (B) suburban; (C) urban □: *Oniscus asellus*; ■: *Porcellio scaber*; ●: *Philoscia muscorum*; ○: *Armadillidium vulgare*; ▲: *Trachelipus rathkii*; ∗: *Ligidium hypnorum*.

Table 2. Comparison of the three isopod species groups – collected at the three levels of urbanisation near Sorø, Denmark, in 2004, according to their abundance and occurrence patterns in the three habitat types (hierarchical ANOVA)

	d.f.	MS	*F*-value	*Significance*	Fisher–LSD-test
Dominant species					
Gradient	2	882 392.60	7.62	<0.01	Forest < suburban = urban
Trap sites	9	115 797.80	4.38	0.000069	
Error	108	26 439.50			
Frequent species					
Gradient	2	31 345.81	10.44	<0.001	Forest < suburban = urban
Trap sites	9	3001.89	4.02	0.000184	
Error	108	746.36			
Species of low-activity density					
Gradient	2	8352.11	16.25	<0.001	Suburban > forest = urban
Trap sites	9	513.75	3.54	0.000708	
Error	108	145.26			

Hierarchical clustering (Fig. 2) indicated no major difference in species' composition between urban and suburban areas. The rural sites formed a distinct group, clearly separated from the two disturbed areas with more than 90% dissimilarity.

Species with low abundance (*A. vulgare*, *L. hypnorum* and *T. rathkii*) preferred certain urbanisation levels and formed single-species clusters in the analysis. *L. hypnorum* tended to prefer the suburban site while *T. rathkii* was common in the urban area.

Diversity

The Rényi diversity profiles showed clear differences between isopod assemblages along the urbanisation gradient (Fig. 3). The three assemblages can be unequivocally ordered (because the profiles, while starting from the same point, do not intersect as the scale parameter increases). The most diverse was the suburban assemblage, followed by the urban one – an observation that supports Connell's "Intermediate Disturbance Hypothesis". The least diverse was the isopod assemblage of the forested area (Fig. 3).

Discussion

In contrast to results of studies on species such as ground beetles (e.g. Niemelä et al. 2002; Elek and Lövei 2005), spiders (Gibb and Hochuli 2002),

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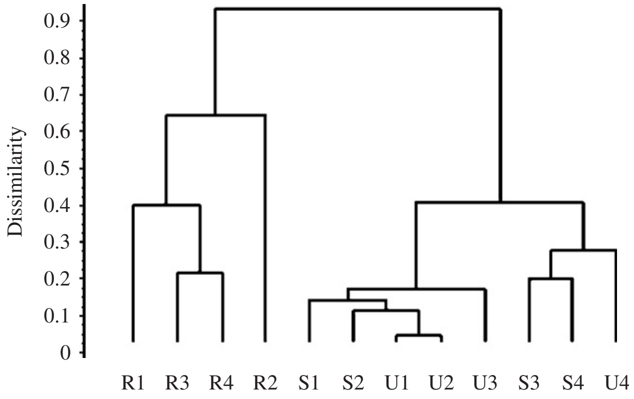

Figure 2. Dissimilarities of the isopod assemblages within and among habitat types in Sorø, Zealand, Denmark, in 2004: R1–4: rural sites (forest); S5–8: suburban sites; U9–12: urban sites.

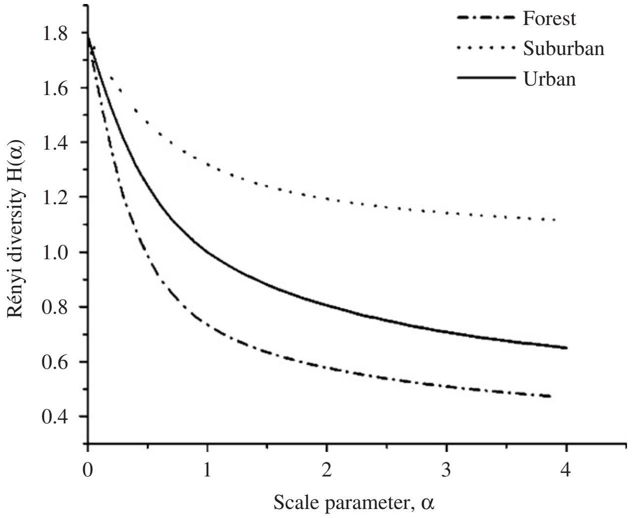

Figure 3. Diversity comparison of isopod assemblages by Rényi diversity profiles along the urbanisation gradient in Sorø, Zealand, Denmark, in 2004.

reptiles (Germaine and Wakeling 2001) and birds (Parsons et al. 2003), we did not find differences in the species richness of isopod assemblages along the urbanisation gradient in Sorø. Nevertheless, the seemingly low number of species we recovered, still represents 27.5% of the isopods known in Denmark (Meinertz 1964).

The diversity profiles indicated a clear difference along the gradient. The results on diversity ordering supports the "Intermediate Disturbance Hypothesis" rather than the "Increasing Disturbance Hypothesis". The "Habitat Specialist Hypothesis" can hardly be interpreted on the observed scale given the low observed species richness and our sampling method, which gives reliable data only on surface-active species.

The "Invader Species Hypothesis" that predicts the appearance of introduced and cosmopolitan species in disturbed habitats, is partially supported by the present results: most of individuals of the cosmopolitan woodlice *A. vulgare* and *Porcellio scaber* (99% and 95%) were trapped in disturbed habitats, but no exotic species were found. The lack of introduced species may be explained by the broad climatic difference and the great geographic distance between Denmark and the important centres of isopod biodiversity, the Middle East and the Mediterranean Basin (e.g. Schmalfuss 1998; Sfenthourakis and Giokas 1998). The number of isopod species shows a clear decrease from the Mediterranean to the north.

In contrast to the majority of studies on invertebrates, isopods had a certain preference towards the urban and/or suburban habitats in the present study. "Dominant species" showed clear preferences to disturbed sites while the level of

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disturbance had no significant impact on the distribution of *Philoscia muscorum* (''frequent species'') along the gradient. Spatial distribution of species with low population density values in Sorø might correlate with the microclimate and the patchiness of the habitat.

Our research indicates that the influence of human disturbance at the scale of urbanisation categories is apparent in the abundance patterns of dominant species. Species classified as dominant are native to Denmark and common across Northern Europe (Gruner 1966).

Meinertz (1964) claims that *Porcellio scaber* is widespread in Denmark and specifically prefers disturbed and dry habitats, while *O. asellus* occurs both in synanthropic areas and deciduous woodlands. At Sorø, this species was the second most abundant isopod in urban habitats.

The high abundance of *Porcellio scaber* and *O. asellus* possibly reflects the higher diversity of microhabitats and the higher quality food sources (Rushton and Hassall 1983) in disturbed habitats. As a consequence of the general structure of beech forests (well-developed canopy level formed exclusively by beech, and scarce scrub and herb layer) the litter layer in the rural sites consisted mostly of beech. In comparison with other coniferous and deciduous litter, beech offers one of the lowest quality food sources in the soil food web (Bjørnlund and Christensen 2005; Sariyildiz et al. 2005). Population parameters of *Porcellio scaber* depend on pH and microbial activity of leaf litter, therefore the food preference of isopods is "not governed by the leaf litter itself, but merely reflects the colonisation preference of microorganisms for the litter of different trees…" (Zimmer and Topp 1997). Consequently, abiotic and microbial factors are likely better in mixed stands than pure beech stands (Sariyildiz et al. 2005). Moreover, leaf litter-colonising microorganisms might serve as food supply for isopods (Zimmer et al. 2003). Still, there is no clear explanation for the high isopod abundance found in the urban park of Sorø, but it is probably related to the differences in habitat structure and plant species composition in the sampled sites.

Philoscia muscorum, a frequent species, was considered a native species in natural habitats in Denmark (Meinertz 1950), and has been colonising new areas in Denmark in the mid-20th century (Meinertz 1964). This species was present in all three habitat types along the gradient with approximately equal abundance in each area. This indicates no preference for any of the habitat types on the studied scale.

The third species group (''species with low population density''), consisting of *L. hypnorum*, *T. rathkii* and *A. vulgare*, occurred mainly in the disturbed habitat types, particularly in the suburban zone. Given the low abundance of these three species, we cannot make any conclusions about their responses to urbanisation.

The present results provide additional evidence that suburban and urban areas are equally suitable for isopods (Hassall et al. 1987). Our observations can probably be explained by the management system used in the urban (park) area. There was no removal of plant material, and cut grass, litter and trimmed branches were returned to the understory of forest patches. Nevertheless, the presence of species with low abundance draws our attention to the importance of both microhabitats and habitat patchiness. In our study, *L. hypnorum* showed preference for the suburban area. Both literature data and our field experience prove the dependence of the species' distribution to permanently wet habitats, even in the humid Denmark (Meinertz 1950; Gruner 1966). A ditch with varying water level ran alongside the suburban sampling sites while the park areas were bordered by a lake. The presence of *L. hypnorum* is probably connected to these wet habitats. This pinpoints the importance of studies to be done at the appropriate, in our case a finer, scale (Savard et al. 2000; Weller and Ganzhorn 2004).

The different level of anthropogenic activity had an effect on the abundance of isopod species present in the different habitats studied. Changes in abundance, caused initially by habitat modifications during the urbanisation process would influence the decomposition process, which, in turn, may modify nutrient cycling in the soil as a secondary effect of urbanisation.

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