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Compositional changes in spider (Araneae) assemblages along an urbanisation gradient near a Danish town

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Abstract

Spider (Araneae) assemblages were studied over two years by pitfall trapping along an urbanisation gradient of forested habitats (rural forest - suburban forest fragment - urban forest fragment) in a Danish town, using the Globenet protocol. During the two years, we collected 4340 individuals of 90 species, with money spiders (Linyphiidae) and wolf spiders (Lycosidae) being most numerous. One species, *Ero aphana*, was new to the Danish fauna. In 2004, 45-47 species were captured in the habitats in various stages of urbanisation, while in 2005 (with a smaller collection effort), 28 (urban) - 37 (rural) species were captured. Twenty-five percent of the collected species occurred in all habitats, but about half of them were only collected in one of the urbanisation stages. The number of shared species was the highest between the suburban and urban habitats. The highest similarities between assemblages (characterized by the Renkonen-index) were the within-habitat, between-year comparisons, indicating assemblage stability. Species turnover between years was lowest in the rural forest and highest in the urban forest patch (56.6% vs. 41.5%). Urbanisation did not reduce diversity in terms of species richness but only a minority of the species present in forests was able to remain attached to the reduced-size forest fragments as urbanisation progressed.

Key words: Globenet, disturbance, biodiversity, arachnids.

Introduction

Humans emerged as one of the major forces shaping the Earth's biota. Now the most numerous mammal on Earth, humans use an enormous amount of natural resources, extant as well as fossil ones. One particular feature of this resource use is profound redistribution of materials and energy, often achieved while eliminating, converting and/or fragmenting original habitats. In the process, space and resources for all other living beings diminish (Haberl *et al*., 2007). This has created an extinction wave, the 6th in the history of the Earth (Wilson, 1999).

Urbanisation, the establishment and growth of settlements with a large number of people is a recurring feature of human societies. Today, more than half of humankind lives in large urban settlements (UNDP, 2000). While cities in different parts of the world are diverse, urbanisation as a process has several characteristics that seem very similar (Gilbert, 1989).

During the development of a city, the original habitat is mostly converted, and by the time a city is "developed", only small and fragmented patches of the original habitats remain (Gilbert, 1989). However, cities are not bereft of plants and animals, because human presence also means resource concentration, and in several respects a more benign environment (Parlow, 2011). Transport of resources, in turn, increases the chances of assisted dispersal (Lundholm and Richardson, 2010). Understanding the overall impact of urbanisation on biodiversity, human inhabitants and the level of benefits provided by nature in urban settings constitutes a challenging research agenda (Magura *et al*., 2010a).

Most urbanisation research has focused on the patterns of biodiversity in urban areas, and more on vertebrates than invertebrates (Clergeau *et al*., 2006; Trollope *et al*., 2009; Garden *et al*., 2010; Stagoll *et al*., 2010). The largest body of evidence on the response of invertebrates to urbanisation emerges from the multi-location Globenet project concerned with forests (Niemelä *et al*., 2002, details see in material and methods section). Most published Globenet studies deal with the beetle family Carabidae (ground beetles). A synthetic evaluation of the studies published up to 2008 (Magura *et al*., 2010a) concluded that 1) overall, the diversity of ground beetles does not necessarily decrease along the urbanisation gradient from the original forest to urban forest fragments, 2) there seems to be no faunal homogenization of ground beetle assemblages as urbanisation progresses, and 3) forest specialists seem to react negatively to the changes that occur as a continuous forest becomes a forest fragment in an urban park.

However, there are differing opinions concerning how can one generalize from ground beetle studies to general ecological trends (Saetersdal *et al*., 2004), and studying other invertebrate groups is useful to assess the generality of the response to urbanisation.

The study of spiders (Araneae) is worthwhile because they form a species-rich group that is ecologically more homogeneous than ground beetles (which have predatory, mixed feeder, and herbivorous species, Lövei and Sunderland, 1996), and are common in many habitats. Spiders are overwhelmingly predators, are important natural enemies (Wise, 1993), and thus provide a valuable ecosystem service of pest control. They are very good dispersers (Pywell *et al*., 2005), adapted to food scarcity (Provencher and Riechert, 1991), and usually prey on several species (Riechert and Lockley, 1984). In spite of the above, there are only a few published articles on the effect of urbanisation on spiders (Finland:

Alaruikka *et al*., 2002; Hungary: Horváth and Szinetár, 2007; Magura *et al*., 2010b). In Hungary, the share of generalist species increases, while those of forest specialist decreases as urbanisation progresses, even if significantly more species are captured in the urban area vs. suburban or the original forest habitat (Magura *et al*., 2010b). In Finland, however, no such differences are present (Alaruikka *et al*., 2002).

In this paper, we report on the composition of the forest spider assemblages in different urbanisation stages in a small Danish town, and compare species richness patterns, turnover and assemblage similarity. We hypothesized that as a result of the urbanisation proceeds, conditions for the original, forest-inhabiting spider fauna will become less suitable, and this will be reflected in the assemblage composition: forest specialists were expected to decrease, and in general, evenness to decline as urbanisation advances (Shochat *et al*., 2010). Our results indicate that this predatory group shows more distinct responses to urbanisation than was detected in ground beetles, a higher share of the original, rural fauna is retained under urban conditions, and the share of singletons is higher than in ground beetle assemblages.

Materials and methods

Study area

The study areas lie in and around the city of Sorø (7743 inhabitants, Anonymous, 2010), a regional centre on the island of Zealand (Sjælland) in Denmark (55°26'N 11°34'E). Three differently fragmented areas of the original forest (conforming to an urbanisation gradient with rural, suburban, urban stages) were selected in the city and in the adjacent forests.

The rural (forest) sampling sites were located 3 km west from the town centre, in the extensive forests covering the area around the town. Beech (*Fagus sylvatica*) was the dominant tree species at all sampling sites; with dense canopy and a scarce shrub layer. The forestry management was limited and occasional; during those operations, the understory was not thinned, and the fallen or cut branches were left to rot on the ground. The herb layer was dense in the spring.

The suburban sampling sites were at the northeastern edge of the town, with fewer beeches but with other deciduous trees (*Fraxinus excelsior* and *Quercus robur*) present. There was a thicket of sapling beeches, bushes (*Crategus monogyna*, *Sorbus* spp., *Sambucus nigra*), a rich herb layer and dense stands of nettle (*Urtica dioica*), indicating nitrogen-rich soil (Ellenberg, 1974). The surface of the built-up area was about 20%, and included single houses, gardens, the city cemetery, several unpaved roads and an old, partially dried-out irrigation canal. This habitat was considered more disturbed with respect to the original forest, with more human visitors, partial habitat alteration and fragmentation, an increase in management operations, and nutrient influx.

The urban sampling sites were in the Sorø Akademi park complex, bordered on one side by Sorø Lake, and by the town centre on the other. The built-up area was circa 40%, including several buildings and (mostly unpaved) roads. The forest patches cover an estimated 20%, the rest (40%) being lawn. The forest patches still contained old beech specimens, mixed with other, planted trees such as *Taxus baccata* and *Tilia argentea*, a dense shrub layer with *Crataegus monogyna* and *Buxus sempervirens*. The park management was more intensive than the other two stages of the urbanisation gradient, but it was "soft": paths were graveled (not paved), and the mowed grass, collected fallen leaves and branches cut during park maintenance work were returned to the understory of the forest patches. In spite of this, this was the most disturbed habitat type, with the largest number of human visitors, the most frequent management operations, the highest share of non-native plant species, nutrient influx via fertilizers, predator control (especially of small mammals via poisoning), and the highest share of built-in surface.

Spider collection, handling and identification

Spiders were collected using pitfall traps, set according to the Globenet protocol (Niemelä *et al*., 2002). Four sites were selected in each of the three habitats (rural, suburban, urban). The distance between the edges of sites within a given urbanisation stage was at least 50 m to avoid pseudoreplication. Ten traps were placed at each site with an inter-trap distance of ≥ 10 m. There were 120 traps overall along the rural-suburban-urban gradient (3 areas × 4 sites × 10 traps). Traps consisted of 70 mm diameter plastic cups and contained about 200 ml of killing-preserving solution, 70% ethylene glycol with a drop of odourless detergent. Traps were protected by 20 × 20 cm galvanized iron plates from litter, rain, and bycatch. Spiders were collected fortnightly from early May to mid- October in 2004, and at alternating fortnightly intervals (traps closed during every second fortnight) during the same period in 2005.

In the field, the catch was removed from the trap, sieved and washed into glass vials using 70% ethyl alcohol, and kept at 4 °C until sorting. Spiders were identified to species using keys by Loksa (1969; 1972), Heimer and Nentwig (1991) and Roberts (1995). The nomenclature follows Platnick (2011). Voucher specimens are deposited in the Department of Ecology, University of Debrecen, Hungary. For evaluation, catches were pooled by trap and year.

Evaluation

Assemblage structure was characterized and compared as suggested by Southwood and Henderson (2000). We calculated species turnover and assemblage similarity using the Renkonen index (Renkonen, 1938).

We estimated the species richness in each habitat type with the Chao estimator (Chao, 1987) using the *vegan* package (Oksanen *et al*., 2011) in R version 2.13 (R Development Core Team, 2011). The standard deviations were generated from 10,000 reshufflings of the sample order.

Diversity ordering

The diversity of the spider assemblages was evaluated by a scalable diversity comparison using the Rényi diversity function (Southwood and Henderson, 2000), calculated by the DivOrd program package (Tóthmérész, 1993). The Rényi diversity, $HR(\alpha)$ is defined as:

$$HR(a) = \frac{1}{1-a}(\log \sum_{i=1}^{s} p_i^a)$$

where p_i is the relative frequency of the i-th species, S the total number of species and α is the scale parameter ($\alpha \geq 0, \alpha \neq 1$).

At four values of the scale parameter α, the Rényi diversity index value corresponds to commonly used diversity indices (Lövei, 2005): (i) at $\alpha = 0$, the value of the Rényi diversity is equal to the logarithm of the number of species of the community; (ii) at $\alpha \rightarrow 1$ (it cannot take that value due to producing a division with zero, but as a continuous function, α can take values indefinitely close to 1), the Rényi diversity is identical to the Shannon diversity; (iii) at $\alpha = 2$, the value of the Rényi diversity is related to the Simpson diversity, and (iv) at $\alpha \rightarrow +\infty$, the value of the Rényi diversity is the inverse of the Berger-Parker dominance index (Berger and Parker, 1970).

At small values of the scale parameter, the Rényi diversity value is influenced by rare species; as the scale parameter increases, the diversity value is increasingly influenced by the common species (see above). Near infinity, only the abundance of the most common species will determine the diversity (Tóthmérész, 1998). This approach produces a diversity profile, allowing a synthetic assessment of diversity relations among different assemblages than the often-used single-value diversity indices (Patil and Taillie, 1982; Lövei, 2005).

If two diversity profiles do not intersect each other, the assemblage whose diversity profile runs above the other one is unequivocally more diverse. If the profiles cross, the assemblages cannot be unequivocally ordered, as one assemblage is more diverse for the rare species, while the other one is more diverse for the common species.

Results

Taxonomic composition

Spiders belonging to 16 families were captured in the two years. At the species level, the families with most species present were Linyphiidae and Lycosidae. The families with most individuals collected were Linyphiidae, Lycosidae and Amaurobiidae.

The total capture was 4340 individuals belonging to 90 species. One of them, *Ero aphana* was new to the Danish fauna, 11 species were new to the South Zealand region (*Labulla thoracica*, *Micrargus apertus*, *Philodromus albidus*, *Philodromus collinus*, *Porrhomma errans*, *Porrhomma microphthalmum*, *Porrhomma microps*, *Porrhomma oblitum*, *Porrhomma pallidum*, *Walckenaeria incisa* and *Xysticus lanio*) and a further nine were rare nationwide (*Coelotes atropos*, *Coelotes terrestris*, *Haplodrassus silvestris*, *Philodromus albidus*, *Philodromus praedatus*, *Porhomma errans*, *Porhomma microps*, *Walckenaeria corniculans* and *Walckenaeria incisa*).

Assemblage diversity

In 2004, we caught 3075 individuals, belonging to 80 species while 1265 individuals of 55 species were collected in 2005 (table 1). In 2004, there were nearly equal numbers of species in the three habitats (table 1). Of these, 12, 14 and 17 species were singletons in the rural, suburban and urban stages, respectively 26, 31 and 36%.

In 2005, the rural habitat was the most species rich, followed by the suburban and urban habitats (table 1). The number of singletons was 13 (35%) in the rural, 15 (45%) in the suburban habitat and 8 (28.5%) at the urban sites.

In 2004, the spider assemblage in the rural was the most diverse (showing the shallowest slope of the rank abundance curves, figure 1), while the other two differed little from each other. In 2005, the urban assemblage showed the highest diversity, and the other two were less diverse (figure 2).

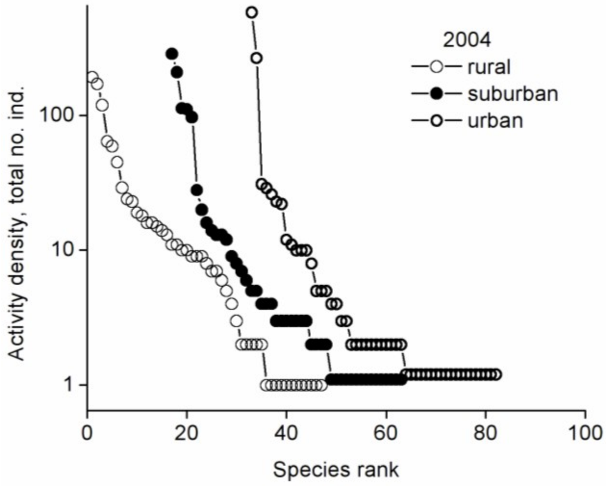

Figure 1. Rank-abundance curves of spider assemblages collected by pitfall traps at three different urbanisation stages near the city of Sorø, Denmark, in 2004. Note that for better visibility, the curves are staggered.

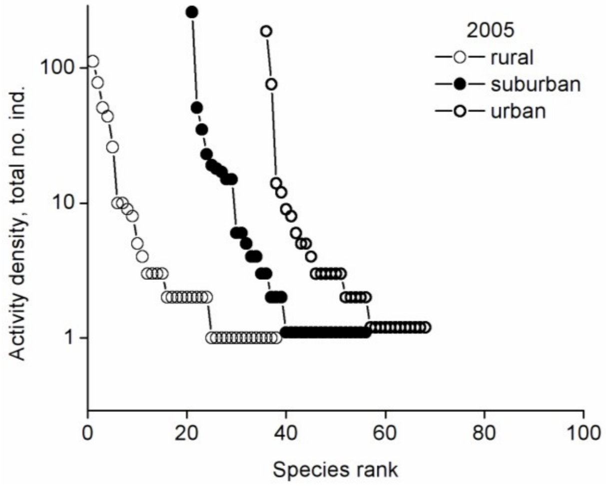

Figure 2. Rank-abundance curves of spider assemblages collected by pitfall traps at three different urbanisation stages near the city of Sorø, Denmark, in 2005. Note that for better visibility, the curves are staggered.

Table 1. The list of the spider species in different stages of a forest urbanisation gradient near Sorø, S Zealand, Denmark, 2004-2005. The species are ranked according to the number of sites where they were present, then by total numbers collected. Zero (0) indicates no capture at that site/year.

Species	2004				2005			
	Rural	Suburban	Urban	Total	Rural	Suburban	Urban	Total
Diplostyla concolor (Wider 1834)	192	209	581	982	44	35	188	267
Microneta viaria (Blackwall 1841)	171	111	267	549	51	17	76	144
Pardosa saltans Topfer-Hofmann 2000	119	286	31	436	112	51	10	173
Coelotes atropos (Walckenaer 1830)	64	113	1	178	78	260	1	339
Diplocephalus picinus (Blackwall 1841)	11	97	22	130	0	1	6	7
Clubiona terrestris Westring 1851	45	28	23	96	10	15	8	33
Trochosa terricola Thorell 1856	59	7	8	74	26	4	3	33
Walckenaeria corniculans (O. P.-Cambridge 1875)	29	14	1	44	8	23	0	31
Tenuiphantes flavipes (Blackwall 1854)	24	5	12	41	2	6	6	14
Palliduphantes pallidus (O. P.-Cambridge 1871)	15	13	10	38	1	2	2	5
Diplocephalus latifrons (O. P.-Cambridge 1863)	2	8	26	36	3	1	14	18
Walckenaeria acuminata Blackwall 1833	10	17	5	32	3	19	2	24
Walckenaeria cucullata (C. L. Koch 1836)	18	12	1	31	9	4	0	13
Gongylidium rufipes (L. 1758)	0	2	29	31	0	0	12	12
Tenuiphantes tenebricola (Wider 1834)	19	1	10	30	2	1	3	6
Saaristoa abnormis (Blackwall 1841)	23	2	2	27	1	6	0	7
Ozyptila praticola (C. L. Koch 1837)	0	20	4	24	0	0	0	0
Pachygnatha listeri Sundevall 1830	8	13	2	23	4	3	3	10
Ceratinella brevis (Wider 1834)	7	6	5	18	3	19	3	25
Tapinocyba insecta (L. Koch 1869)	16	0	2	18	2	1	0	3
Zora spinimana (Sundevall 1833)	7	5	2	14	2	2	0	4
Pirata hygrophilus Thorell 1872	0	4	10	14	0	1	0	1
Saloca diceros (O. P.-Cambridge 1871)	14	0	0	14	1	0	0	1
Robertus lividus (Blackwall 1836)	13	0	0	13	6	2	0	8
Gonatium rubellum (Blackwall 1841)	9	4	0	13	2	5	0	7
Amaurobius fenestralis (Strom 1768)	10	0	2	12	10	0	1	11
Ozyptila trux (Blackwall 1846)	9	3	0	12	1	0	0	1
Pardosa amentata (Clerck 1757)	0	9	2	11	0	15	1	16
Walckenaeria obtusa Blackwall 1836	11	0	0	11	3	0	0	3
Walckenaeria dysderoides (Wider 1834)	9	0	0	9	0	0	0	0
Pardosa prativaga (L. Koch 1870)	0	3	5	8	0	0	5	5
Maso sundevalli (Westring 1851)	1	3	3	7	0	0	0	0
Porrhomma oblitum (O. P.-Cambridge 1871)	2	3	2	7	0	0	0	0
Tenuiphantes zimmermanni (Bertkau 1890)	6	0	0	6	0	1	2	3
Haplodrassus silvestris (Blackwall 1833)	5	0	0	5	2	0	0	2
Centromerus sylvaticus (Blackwall 1841)	3	1	0	4	1	0	1	2
Linyphia hortensis Sundevall 1830	0	3	1	4	0	0	2	2
Tegenaria domestica (Clerck 1757)	0	4	0	4	0	0	1	1
Tegenaria atrica C. L. Koch 1843	0	3	1	4	0	0	0	0
Agyneta ramosa Jackson 1912	4	0	0	4	0	0	0	0
Ceratinella brevipes (Westring 1851)	0	0	4	4	0	0	0	0
Ero furcata (Villers 1789)	2	0	1	3	0	0	0	0
Tetragnatha montana Simon 1874	0	0	3	3	0	0	0	0
Diplocephalus cristatus (Blackwall 1833)	0	0	3	3	2	0	1	3
Bathyphantes gracilis (Blackwall 1841)	1	0	2	3	0	1	3	4
Anyphaena accentuata (Walckenaer 1802)	2	0	0	2	1	1	0	2
Clubiona pallidula (Clerck 1757)	1	0	1	2	2	0	0	2
Neriene montana (Clerck 1757)	0	0	2	2	1	0	0	1
Enoplognatha ovata (Clerck 1757)	1	1	0	2	0	0	0	0
Erigone dentipalpis (Wider 1834)	0	1	1	2	0	0	0	0
Neriene peltata (Wider 1834)	0	1	1	2	0	0	0	0
Zelotes subterraneus (C. L. Koch 1833)	2	0	0	2	0	0	0	0
Dicymbuim nigrum (Blackwall 1834)	0	2	0	2	0	0	0	0
Micrargus apertus (O. P.-Cambridge 1871)	0	2	0	2	0	0	0	0
Micrargus subaequalis (Westring 1851)	0	0	2	2	0	0	0	0

(Continued)

(Table 1 continued)

Species	2004				2005			
	Rural	Suburban	Urban	Total	Rural	Suburban	Urban	Total
Metellina mengei (Blackwall 1870)	0	1	0	1	1	1	0	2
Helophora insignis (Blackwall 1841)	1	0	0	1	1	1	0	2
Erigone atra Blackwall 1833	0	0	1	1	0	0	2	2
Clubiona comta C. L. Koch 1839	0	0	1	1	1	0	0	1
Coelotes terrestris (Wider 1834)	0	1	0	1	0	1	0	1
Xysticus lanio C. L. Koch 1835	1	0	0	1	1	0	0	1
Gnathonarium dentatum (Wider 1834)	1	0	0	1	0	0	0	0
Macrargus rufus (Wider 1834)	1	0	0	1	0	0	0	0
Oedothorax apicatus (Blackwall 1850)	1	0	0	1	0	0	0	0
Porrhomma microps (Roewer 1931)	1	0	0	1	0	0	0	0
Porrhomma pallidum Jackson 1913	1	0	0	1	0	0	0	0
Tiso vagans (Blackwall 1834)	1	0	0	1	0	0	0	0
Scotophaeus blackwalli (Thorell 1871)	0	1	0	1	0	0	0	0
Xysticus sp.	0	1	0	1	0	0	0	0
Neriene clathrata(Sundevall 1830)	0	1	0	1	0	0	0	0
Alopecosa pulverulenta (Clerck 1757)	0	1	0	1	0	0	0	0
Bathyphantes parvulus (Westring 1851)	0	1	0	1	0	0	0	0
Ero aphana (Walckenaer 1802)	0	1	0	1	0	0	0	0
Euophrys frontalis (Walckenaer 1802)	0	1	0	1	0	0	0	0
Walckenaeria cuspidata Blackwall 1833	0	0	1	1	0	0	0	0
Walckenaeria unicornis O. P.-Cambridge 1861	0	0	1	1	0	0	0	0
Araneus diadematus Clerck 1757	0	0	1	1	0	0	0	0
Clubiona lutescens Westring 1851	0	0	1	1	0	0	0	0
Philodromus albidus Kulczynski 1811	0	0	1	1	0	0	0	0
Porrhomma errans (Blackwall 1841)	0	0	1	1	0	0	0	0
Segestria senoculata (L. 1758)	0	0	0	0	0	0	3	3
Neriene emphana (Walckenaer 1841)	0	0	0	0	2	0	0	2
Philodromus collinus C. L. Koch 1835	0	0	0	0	1	0	0	1
Micaria sp.	0	0	0	0	1	0	0	1
Porrhomma microphthalmum (O. P.-Cambridge 1871)	0	0	0	0	0	1	0	1
Trochosa ruricola (De Geer 1778)	0	0	0	0	0	1	0	1
Walckenaeria incisa (O. P.-Cambridge 1871)	0	0	0	0	0	1	0	1
Labulla thoracica (Wider 1834)	0	0	0	0	0	1	0	1
Philodromus praedatus O. P.-Cambridge 1871	0	0	0	0	0	0	1	1
Savignia frontana Blackwall 1833	0	0	0	0	0	0	1	1
Total number of individuals	952	1025	1098	3075	401	503	361	1265
Species number	46	45	47	80	37	33	28	55
Number of unique species	17	12	13		11	6	8	

The species richness estimation indicated assemblage of different species richness in 2004 vs. 2005 (figure 3). According to the Chao estimators for 40 samples per habitat types, there were 46 species in the rural (forest) habitat, 45 species in the suburban and 47 species in urban forest fragments in 2004. However, these estimates were not yet at their asymptote (figure 3).

Diversity ordering

In 2004, the urban assemblage was, according to the Rényi-curves, unequivocally more diverse than either of the other two (figure 4). The rural assemblage was more diverse when rare species were given a higher weight, but was also dominated by a few species, while the suburban assemblage had a higher evenness.

In 2005, the urban assemblage had fewer rare species (low $H(R)$ at low α values) but quickly emerged as the most diverse assemblage (figure 5). The relationship between the suburban and forest areas were nearly the same as in 2004: the forest habitats supported more rare species, but otherwise was less diverse. In both years, the rural (forest) habitats had an assemblage that was less even (dominated more by some common species) than the suburban habitat.

Shared vs. unique species by habitat

In 2004, 25% (20 species) of the collected species occurred in all three, 22% (18 species) in two, and 53% (42 species) in only one habitat type (figure 6). Largely similar trends were found in 2005: 24% (13 species) present in all habitat types, 31% (17 species) occurred in two habitat types, and 45% (25 species) unique for one habitat (figure 6). The only larger difference was that more species were shared by the rural and suburban habitats in 2005 than in 2004, with a corresponding decrease in the suburban-only species in 2005.

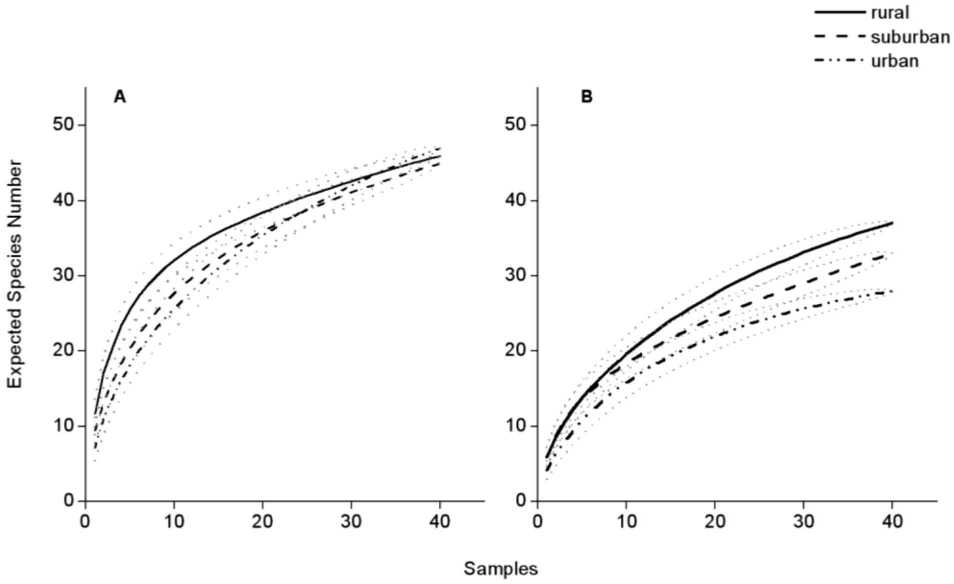

Figure 3. The species richness estimation according to Chao estimators (with 95 % confidence intervals) at three habitat types near the city of Sorø, Denmark, in 2004 (A) and in 2005 (B).

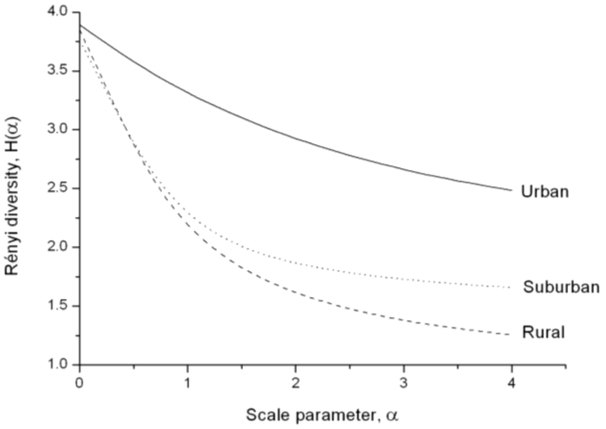

Figure 4. Diversity profiles based on the Rényi one-parametric diversity index family for spider assemblages collected by pitfall traps at three different urbanisation stages near the city of Sorø, Denmark, in 2004.

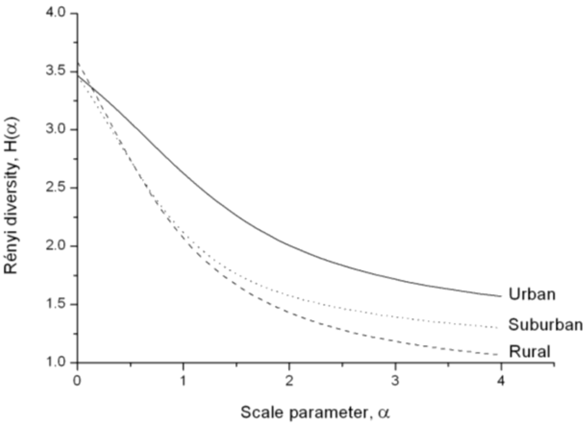

Figure 5. Diversity profiles based on the Rényi one-parametric diversity index family for spider assemblages collected by pitfall traps at three different urbanisation stages near the city of Sorø, Denmark, in 2005.

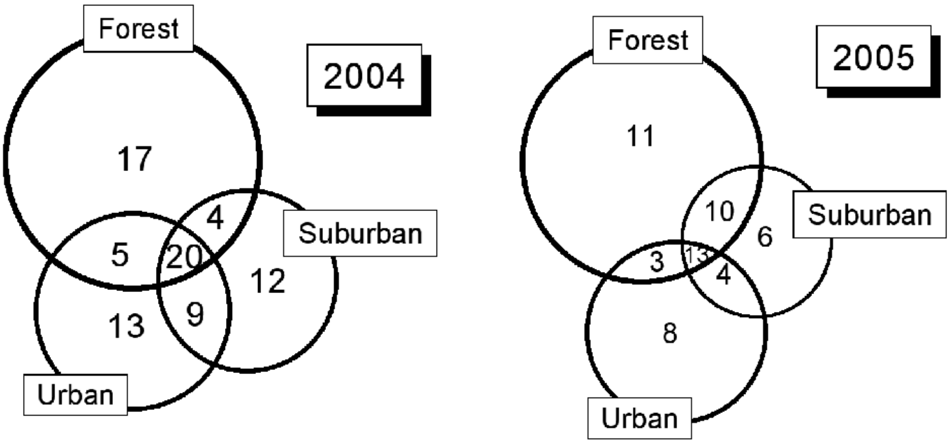

Figure 6. Number of shared/unique species at three different urbanisation stages near the city of Sorø, Denmark, in 2004 and in 2005.

Table 2. The similarities of spider assemblages according to the Renkonen-index between different sampling sites and two sampling years in Sorø, Denmark. Numbers in bold indicate same-year comparisons, numbers in Roman are the between-year similarities of the same urbanisation stage; in Italics are the unrelated (different site-different year) comparisons.

	Suburban 2004	Urban 2004	Rural 2005	Suburban 2005	Urban 2005
Rural 2004	**0.637**	**0.507**	0.665	*0.431*	*0.518*
Suburban 2004	--	**0.451**	*0.719*	0.436	*0.436*
Urban 2004	--	--	*0.341*	*0.205*	0.904
Rural 2005	--	--	--	**0.516**	**0.345**
Suburban 2005	--	--	--	--	**0.21**

Assemblage similarities

The spider assemblage similarities were highest, on average, for same habitat, between-years comparisons (mean of Renkonen index = 0.668). The highest between-habitat similarity was recorded between the rural and suburban sampling sites in both years (Renkonen index: 0.637 and 0.516, respectively), and the largest difference was detected between the suburban and urban habitat types, also in both years (Renkonen index: 0.451 and 0.21, respectively). The between-year similarities were highest at the urban sites and lowest at the suburban sites (table 2).

Species turnover trends

The number of species collected decreased from 80 species in 2004 to 55 species in 2005. This decrease was the highest at the urban sites (19 species), followed by the suburban habitats (12 species) and smallest change was at the rural sites (9 species). Overall, 35 species present in 2004 were not collected in 2005.

Ten species were caught only in 2005. Forty-six species were common between the two years. Species density (characterized as no. of species collected/trapping effort) was lower (0.03 species/trap-week) in 2004, than in 2005 (0.038 species/trap-week).

At the rural sites, 16 species were caught only in 2004, while seven species only in 2005. There were 30 species common for both years. In the suburban habitat, 22 of the 45 species present in 2004 were not caught in 2005, while there were 10 “new” species. Twenty-three species were common between the two years. At the urban area, 25 species occurred only in the first, and six only in the second year. The number of shared species was 22.

Activity density relations

Overall, the activity density was higher in 2004 (1.17 individuals/ trap-week) than in 2005 (0.88 individuals/ trap-week). In 2004, spider activity-density was the highest in the urban (1.25 individuals/ trap-week) and in the suburban habitats (1.17 individuals/ trap-week) and it was the lowest in the rural habitat (1.08 individuals/ trap-week). In 2005 this trend changed, because spider activity density was the highest in the suburban (1.05 individuals/ trap-week) and rural areas (0.84 individuals/ trap-week) and lowest in the urban areas (0.75 individuals/ trap-week).

There were four dominant species (relative abundance > 5%) at the three habitat types (*Diplostyla concolor*, *Microneta viaria*, *Pardosa saltans*, *Coelosia atropos*). The dominant species in the rural habitats made up 38% of all individuals, 48% in the suburban habitats, while 77% in the urban habitats. Two species dominated in at least two urbanisation stages in 2004. *D. concolor* was dominant in all three habitats (192 individuals in the rural, 209 individuals in the suburban habitat and 581 in the urban habitats). *M. viaria* was dominant in the rural (171 individuals) and the urban habitats (267 individuals). In the suburban habitats, *P. saltans* (286 individuals) was also dominant.

In 2005, similar trends were found among the three urbanisation stages based on the rank-abundance plots (figure 2): the same four species were dominant. In the rural, *P. saltans* (112 individuals) and *C. atropos* (78 individuals) were dominant (47% to the total catch). In the suburban habitat, one species, *C. atropos* (260 individuals, 52% of total) and in the urban habitat, two species, *D. concolor* (188 individuals) and *M. viaria* (76 individuals), were dominant, contributing 74% of the total catch.

Discussion

Our sampling indicated a species-rich spider fauna in all urbanisation stages. The total number of species found (90 species) is 32% of the regional fauna of 288 species (Scharff and Gudik-Sörensen, 2009). This is higher than for ground beetles: using the same trapping effort and arrangement, Elek and Lövei (2005) collected 18% of the carabid species known from South Zealand (234 species, Bangsholt, 1983). The reasons for this could be that spiders are more efficient dispersers, but also that they are easier to catch and do not escape so easily from pitfall traps than ground beetles (Lange *et al.*, 2011). Sampling Danish hedgerows in Jytland, also by pitfall trapping, found a comparable spider species richness, 72 species (Toft and Lövei, 2002).

Of the other urbanisation gradients studied, species richness in Finland was about the same as in Denmark: 85 species, of which 34 were common (13% of the Finnish fauna, Koponen, 2008). The reason for this similarity could be that both are Northern European countries and lie at comparable latitudes. The species number in Hungary - under the same trapping arrangement and effort - was much lower with 20 species (only about 3% of the Hungarian fauna, Samu and Szinetár, 1999), of which five were abundant. This goes against a general species richness gradient that should increase towards the south (Hawkins *et al*., 2007). The causes can include a drier climate as well as management differences. The forests in the eastern lowlands of Hungary have historically been subjected to isolation, destruction and disturbance (Meglécz *et al*., 1999), which did not favour a species-rich assemblage of forest-associated ground dwellers.

We found a high share of rare species (singletons and doubletons), which is a common phenomenon in spider assemblages (figure 6). On the basis of three studies, no generalization is possible about rarity patterns. The highest number of singleton species was in the suburban forest (26 species) in Denmark (this study), in the urban habitat (eight species) in Hungary (Magura *et al*., 2010b) and the rural habitat (coniferous forest) in Finland (17 species, Alaruikka *et al*., 2002). The second most singleton- rich were the urban forest fragments in both Denmark (24 species) and Finland (16 species). The number of singleton species was high in urban forest fragments in all countries. This could be an effect of the matrix - the forest becomes a fragment in the urban setting, with extensive surrounding matrix areas, which influences the faunal composition of the fragments as well (Lövei *et al*., 2006). The diversity ordering indicated that urbanisation did not decrease overall spider diversity occurring in forest habitats, but this may be only part of the answer when the effects of urbanisation on diversity are examined (Horváth *et al*., 2012).

The activity density was higher in Denmark (0.88-1.17 specimens/trap-week) and Finland (1.21 specimen/trap-week) than in Hungary (0.13 specimen/trap-week). This ratio remains the same when we only consider activity densities in the original forest habitat. We believe the reason for this is the lack of sufficient humidity in Hungary, where the climate during the growing season is often warm and dry (Fábián and Matyasovszky, 2010), which is unfavourable to spiders, especially young ones, so there may be low development success. A similar activity density relationship between the northern countries and Hungary was observed in ground beetles (Magura *et al*., 2010a).

Our method, pitfall trapping, has recognized limitations. Ground-active species are easily trapped, but web-builders are less so. Also, sampling effort was different in the two years (even though the same spatial setup was used), and while the specific sampling regime results in comparable patterns in ground beetles (Sapia *et al*., 2006), comparisons between the two years should be made cautiously.

In conclusion, a purely predatory group of ground-active arthropods also demonstrated that urbanisation, while taking away existence opportunities from some species, also provides suitable conditions for others. It should be examined, once suitable material is available, whether urbanisation creates homogenization in spider assemblages like found in some other groups (Olden and Poff, 2004) or whether the lack of homogenization found for ground beetles (Magura *et al*., 2010a) is also valid for spiders? From the limited data available, it seems that many rare (forest) species disappear as urbanisation progresses, but some of these species may remain in the fragments depending on urban park conditions. Our result showed that the suburban and urban habitat type can play a role in the preservation of ground-dwelling spider assemblages, because several rare species occurred only in those sites.

Another unexplored question is whether assemblages in more urbanised habitats are subject to larger year-to-year compositional changes than less disturbed forest habitats? We found some evidence that this may be the case, at least under Danish conditions but current evidence is far from sufficient.

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