



Diversity of carrion visiting beetles at rural and urban sites

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Abstract: The question whether and to what degree urbanization causes a decrease in diversity of animal and plant species and changes in community structure is still a matter of debate. While many studies used ground beetles, vertebrates, and butterflies as assumed model taxa, little work has been done with other, particularly insect, taxa. Here we report on rural and urban diversities of communities of carcass visiting destruent and predatory beetles (Coleoptera). From 8 rural and 2 city sites, we sampled 15323 destruent beetles representing 58 species and 1871 predators from 43 species. We observed a reduced diversity and changes in community structure of both beetle guilds towards the city. However, these changes were guild specific and our study gives no evidence that there are simple rules that govern rural and urban patterns of diversity. Species abundance distributions did not significantly differ between the study sites. There is also no evidence that the intermediate disturbance hypothesis might apply. Lastly, we found only little support for a homogenizing effect of urban environments on carrion visiting beetles.

Abbreviations: BR – Discrepancy metric of nestedness; NMS – Non-metric Multidimensional Scaling; S – Species number; UAO – The number of unexpected species absences or occurrences per site.

Introduction

Urbanization and the accompanying changes of many ecological patterns and processes is a challenge for ecology and an increasingly important issue in conservation planning (Niemelä 1999a,b, Araujo 2003). Urban environments provide a wide variety of semi-natural to harsh environments. This diversity often causes high species richness and many rare or threatened species occur predominantly or even exclusively in urban environments (Eversham et al. 1996, Niemelä 1999a, Pickett et al. 2004). On the other hand, urbanization is a threat to many natural habitats and therefore to species that depend on them (Ricketts and Imhoff 2003). It is no wonder that urban ecology is at the centre of interest (Gaston et al. 2005, Angold et al. 2006, Chace and Walsh 2006).

Much attention has been paid to the tradeoffs between gains and losses of diversity during urbanization (Olden et al. 2006). With respect to these richness tradeoffs, the

concept of a rural – urban gradient has successfully been applied as a proxy for the ecologically more meaningful undisturbed (rural) – disturbed (urban) gradient (McDonnell and Pickett 1990, Niemelä 1999b, Sadler et al. 2006, Ulrich et al. 2007). For beetles, a series of studies reported a decrease in species richness towards the urban end of this gradient (Niemelä et al. 2002, Ishitani et al. 2003, Magura et al. 2004, Watts and Larivičre 2004, Sadler et al. 2006). Recently, Elek and Lövei (2007) reported a more complicated pattern with different richness gradients in different guilds. Similar richness gradients have been found for birds (Jokimäki and Suhonen 1993, Knapp 2005, Olden et al. 2006, Chace and Walsh 2006) and butterflies (Knapp 2005), but not for isopods (Hornung et al. 2007). In turn, an increasing number of studies report a higher diversity of vascular plants at urban sites (Rebele 1994, Gödde et al. 1995, Ranta et al. 1997, Kühn and Klotz 2006, Wania et al. 2006). From the available, albeit limited, number of studies, we might speculate that there are differences in rural – urban gradients with respect to

trophic level and taxon. It seems that this gradient is more pronounced in higher trophic levels, i.e., in predators (Elek and Lövei 2007).

Closely related to the question about urban biodiversity is the question whether urbanization leads to faunal and floral homogenization (Olden et al. 2004, 2006). Homogenization refers to an increase in the species compositional similarity among sites. It is manifested in a decrease in regional (beta) diversity with respect to local (alpha) diversities and can be measured either from the slopes of species–area curves (Rosenzweig 1995) or from pairwise comparisons of species overlap (Olden et al. 2006). While continental or country wide homogenization is evident for many taxa (cf. Rahel 2002, McKinney 2004), there is still a dispute whether and to what degree urbanization contributes to this. Using models of speciation/extinction tradeoffs, Olden et al. (2006) predicted a significant influence of the process of urbanization on homogenization for all vertebrate classes. In turn, they, Kühn and Klotz (2006), and Smith et al. (2006) found mixed evidence for a similar pattern in plants.

Most of the studies on rural versus urban diversity used standard ecological model taxa like fishes, birds, butterflies, ground beetles, or vascular plants. Much less is known about differences in rural and urban diversities in other, particularly species rich arthropod taxa. Therefore from the present limited knowledge it is difficult to extract common rules about the influence of urban areas on patterns of biodiversity. The objective of the present study is to evaluate the diversity of destruent and predatory beetles associated with dead fish at urban and rural sites. Destrudent arthropods play an important role in most terrestrial ecosystems and often reach high abundances and biomasses (Wolf and Gibbs 2004). It is therefore surprising that rural-urban gradients of destruent arthropods have so far only been studied by Gibbs and Stanton (2001), who reported decreasing Silphidae (Coleoptera) and increasing Muscidae (Diptera) abundances towards the city. We intend to answer the following four questions:

1. Does beetle diversity change along the gradient as had been found for most vertebrates?
2. Do species composition and co-occurrences differ between urban and rural sites?
3. Does urbanization lead to species homogenization manifested in a lowered diversity and a pronounced dominance of widespread species?
4. Are there differences in rural versus urban diversities with respect to trophic level?

Materials and methods

Along two 120 km transects (west – east, north – south, Fig. 1) crossing in the centre of the city of Olsztyn (Mazurian lake district of northern Poland, 53° 47' N; 20° 30' E; 200,000 inhabitants) 80 traps (four at each of 5 sites in four geographical directions) were placed. Additionally, we placed ten identical traps at two park sites of the periphery of the city and in the city centre (Aleksandrowicz and Komosiński 2005). The rural sampling sites covered two important habitat types, a forested (mixed coniferous forests) and an open (grassland) type. Trap position allowed therefore for a pooling of traps to have ten traps (and therefore the same number as in the city) for each habitat type in each geographical direction. Mean trap distance was ca. one km. Both the suburban and urban park sites differed from the forested and open sites in habitat type. The traps operated during August and September 1997. Material was collected at the end of the trapping periods. Traps were made of glass jars (diameter 9 cm) dug into soil and covered with wooden roofs. To avoid the capturing of too many accidental species, the upper edges were 3–4 cm above ground level. Each trap had a layer of 2–3 cm of glycol. 100 gram rotten fish (placed above the glycol layer) served to attract beetle species. Therefore, the species had to enter the traps actively to reach the attractant. Four traps were lost. The voucher specimens are kept at the Department of Zoology of the University of Warmia and Mazury (Aleksandrowicz and Komosiński 2005).

In total, we sampled 29088 individuals of 303 Coleoptera species. Based on standard literature (e.g., Freude et al. 1964–2004), we identified 58 species from the families Anthicidae, (1 species), Catopidae (12), Cryptophagidae



Figure 1. The study area in the vicinity of Olsztyn (northern Poland). The dark points denote the five trapping places along the main roads off the city centre. The two light grey points denote the trapping places in the city centre and its periphery.

Table 1. Total catches of destruent and predatory beetle species.

Destruents			Predators		
Species	Family	Total catch	Species	Family	Total catch
<i>Sciodrepoides watsoni</i> (Spence, 1815)	Catopidae	5037	<i>Pterostichus caeruleus</i> (Linnaeus, 1758)	Carabidae	595
<i>Geotrupes stercorosus</i> (Linnaeus, 1758)	Geotrupidae	3031	<i>Philonthus chalcus</i> Stephens, 1832	Staphylinidae	404
<i>Nicrophorus vespilloides</i> Herbst, 1783	Silphidae	1877	<i>Philonthus addendus</i> Sharp, 1867	Staphylinidae	178
<i>Silpha sinuata</i> Fabricius, 1775	Silphidae	1559	<i>Philonthus varians</i> (Paykull, 1798)	Staphylinidae	110
<i>Catops morio</i> (Fabricius, 1792)	Catopidae	756	<i>Saprinus semistriatus</i> (Scriba, 1790)	Histeridae	81
<i>Catops nigrita</i> Erichson, 1837	Catopidae	739	<i>Rugilus rufipes</i> Germar, 1835	Staphylinidae	75
<i>Nicrophorus vespillo</i> (Linnaeus, 1758)	Silphidae	550	<i>Philonthus marginatus</i> (Strom, 1768)	Staphylinidae	60
<i>Nicrophorus investigator</i> (Zetterstedt, 1824)	Silphidae	512	<i>Philonthus fimetarius</i> (Gravenhorst, 1802)	Staphylinidae	59
<i>Silpha tristis</i> Illiger, 1798	Silphidae	217	<i>Hister unicolor</i> Linnaeus, 1758	Histeridae	53
<i>Silpha thoracica</i> Linnaeus, 1758	Silphidae	185	<i>Saprinus aeneus</i> (Fabricius, 1775)	Histeridae	35
<i>Sciodrepoides fumatus</i> (Spence, 1815)	Catopidae	77	<i>Philonthus corruscus</i> (Gravenhorst, 1802)	Staphylinidae	26
<i>Cercyon lateralis</i> (Marshall, 1802)	Hydrophilidae	72	<i>Ontholestes murinus</i> (Linnaeus, 1758)	Staphylinidae	21
<i>Ptomaphagus sericatus</i> (Chaudoir, 1845)	Catopidae	64	<i>Philonthus politus</i> (Linnaeus, 1758)	Staphylinidae	20
<i>Silpha carinata</i> Herbst, 1783	Silphidae	64	<i>Margarinotus carbonarius</i> (Hoffmann, 1803)	Histeridae	18
<i>Omosita colon</i> (Linnaeus, 1758)	Nitidulidae	58	<i>Philonthus fuscipennis</i> (Mannerheim, 1831)	Staphylinidae	16
<i>Nicrophorus vestigator</i> (Herschel, 1807)	Silphidae	52	<i>Margarinotus brunneus</i> (Fabricius, 1775)	Histeridae	14
<i>Catops westi</i> Krogerus, 1931	Catopidae	49	<i>Pterostichus cupreus</i> (Linnaeus, 1758)	Carabidae	13
<i>Silpha rugosa</i> Linnaeus, 1758	Silphidae	49	<i>Philonthus carbonarius</i> (Gyllenhal, 1810)	Staphylinidae	13
<i>Silpha obscura</i> Linnaeus, 1758	Silphidae	44	<i>Ontholestes tessellatus</i> (Fourcroy, 1785)	Staphylinidae	10
<i>Acrotrichis dispar</i> (Matthews, 1865)	Ptilidae	42	<i>Margarinotus striola succicola</i> (Thomson, 1862)	Histeridae	8
<i>Megasternum boletophagum</i> (Marshall, 1802)	Hydrophilidae	41	<i>Margarinotus ventralis</i> (Marseul, 1854)	Histeridae	8
<i>Omosita depressa</i> (Linnaeus, 1758)	Nitidulidae	40	<i>Quedius molochinus</i> (Gravenhorst, 1806)	Staphylinidae	8
<i>Nicrophorus humator</i> Olivier, 1790	Silphidae	40	<i>Saprinus planiusculus</i> Motschulsky, 1849	Histeridae	6
<i>Acrotrichis silvatica</i> Roskothen, 1935	Ptilidae	30	<i>Gyrophypnus punctulatus</i> (Paykull, 1789)	Staphylinidae	6
<i>Nicrophorus sepulchrorum</i> (Charpentier, 1825)	Silphidae	26	<i>Carcinops pumilio</i> (Erichson, 1834)	Histeridae	5
<i>Catops coracinus</i> Kellner, 1846	Catopidae	16	<i>Philonthus sordidus</i> (Gravenhorst, 1802)	Staphylinidae	5
<i>Ptomaphagus medius</i> (Rey, 1889)	Catopidae	9	<i>Ocypus brunnipes</i> (Fabricius, 1781)	Staphylinidae	2
<i>Notoxus monoceros</i> (Linnaeus, 1761)	Anthicidae	8	<i>Ocypus melanarius</i> (Heer, 1839)	Staphylinidae	2
<i>Sciodrepoides alpestris</i> Jeannel, 1934	Catopidae	8	<i>Philonthus cephalotes</i> (Gravenhorst, 1802)	Staphylinidae	2
<i>Catops tristis</i> (Panzer, 1793)	Catopidae	7	<i>Philonthus confinis</i> A. Strand, 1941	Staphylinidae	2
<i>Dermestes laniarius</i> Illiger, 1801	Dermestidae	6	<i>Philonthus puella</i> Nordmann, 1837	Staphylinidae	2
<i>Dermestes murinus</i> Linnaeus, 1758	Dermestidae	6	<i>Stenus bimaculatus</i> Gyllenhal, 1810	Staphylinidae	2
<i>Onthophagus ovatus</i> (Linnaeus, 1767)	Scarabaeidae	6	<i>Stenus lustrator</i> Erichson, 1839	Staphylinidae	2
<i>Cryptophagus pilosus</i> Gyllenhal, 1827	Cryptophagidae	5	<i>Dermestes lardarius</i> Linnaeus, 1758	Dermestidae	1
<i>Necrodes littoralis</i> (Linnaeus, 1758)	Silphidae	5	<i>Gnathonus nannetensis</i> (Marseul, 1862)	Histeridae	1
<i>Catops nigricans</i> (Spence, 1815)	Catopidae	3	<i>Margarinotus merdarius</i> (Hoffmann, 1803)	Histeridae	1
<i>Cryptophagus setulosus</i> Sturm, 1845	Cryptophagidae	3	<i>Gabrieus trossulus</i> (Nordmann, 1837)	Staphylinidae	1
<i>Dermestes undulatus</i> Brahm, 1790	Dermestidae	3	<i>Philonthus laevicollis</i> (Lacordaire, 1835)	Staphylinidae	1
<i>Nanoptilium kunzei</i> (Heer, 1841)	Ptilidae	3	<i>Philonthus rectangulus</i> Sharp, 1874	Staphylinidae	1
<i>Catops subfuscus</i> Kellner, 1846	Catopidae	2	<i>Quedius fuliginosus</i> (Gravenhorst, 1802)	Staphylinidae	1
<i>Cryptophagus pseudodentatus</i> Bruce, 1934	Cryptophagidae	2	<i>Rugilus erichsonii</i> (Fauvel, 1867)	Staphylinidae	1
<i>Acrotrichis fratercula</i> (Matthews, 1878)	Ptilidae	2	<i>Xantholinus clareii</i> Coiffait, 1956	Staphylinidae	1
<i>Acrotrichis rugulosa</i> Roskothen, 1935	Ptilidae	2	<i>Xantholinus linearis</i> (Olivier, 1794)	Staphylinidae	1
<i>Onthophagus nuchicornis</i> (Linnaeus, 1758)	Scarabaeidae	2			
<i>Atomaria basalis</i> Erichson, 1846	Cryptophagidae	1			
<i>Cercyon convexusculus</i> Stephens, 1829	Hydrophilidae	1			
<i>Cercyon impressus</i> (Sturm, 1807)	Hydrophilidae	1			
<i>Cercyon melanocephalus</i> (Linnaeus, 1758)	Hydrophilidae	1			
<i>Cercyon quisquilius</i> (Linnaeus, 1761)	Hydrophilidae	1			
<i>Cercyon tristis</i> (Illiger, 1801)	Hydrophilidae	1			
<i>Cercyon unipunctatus</i> (Linnaeus, 1758)	Hydrophilidae	1			
<i>Nitidula rufipes</i> (Linnaeus, 1767)	Nitidulidae	1			
<i>Omosita discoidea</i> (Fabricius, 1775)	Nitidulidae	1			
<i>Acrotrichis grandicollis</i> (Mannerheim, 1844)	Ptilidae	1			
<i>Acrotrichis intermedia</i> (Gillmeister, 1845)	Ptilidae	1			
<i>Aphodius fimetarius</i> (Linnaeus, 1758)	Scarabaeidae	1			
<i>Nicrophorus interruptus</i> (Stephens, 1830)	Silphidae	1			
<i>Silpha dispar</i> Herbst, 1793	Silphidae	1			

(4), Dermestidae (3), Geotrupidae (1), Hydrophilidae (8), Nitidulidae (4), Ptilidae (7), Scarabaeidae (3), and Silphidae (15) as being necrophagous/saprophagous and/or mycetophagous and frequently associated with carcasses (termed destruent below). 43 species were classified as carrion visiting predators (termed predators below), and included species from the families Carabidae (2), Dermestidae (1), Histeridae (11), and Staphylinidae (29) (Table 1). The other beetle species were considered occasional visitors (species not known to be associated with carcass) and were mainly trapped accidentally. They are

not considered in the present analysis. A complete species list with numbers of individuals per species as well as the classification into trophic groups is contained in Aleksandrowicz and Komosiński (2005).

We used C-scores, checkerboard scores, and species combination scores (cf. Gotelli 2000) to study species co-occurrence patterns of presence-absence matrices. The C-score and the checkerboard score measure mean matrix-wide under-dispersion (segregation) between sites (checkerboard patterns); the species combination score by

contrast screens for unique species combinations (Gotelli and McCabe 2002). Standardized scores are Z-transformed and thus have a mean of zero and a standard deviation of one. Significant species under-dispersion or over-dispersion, on the other hand, should result in Z-transformed scores above 1.96 or below -1.96 (at the 5% error level). Random matrices for generating standardized scores and significance levels were computed with EcoSim 7.72 (Gotelli and Entsminger 2005). We used fixed sum row and column constraints and the sequential swap algorithm for randomization as advocated by Gotelli (2000) and Ulrich and Gotelli (2007).

We assessed differences in species composition and idiosyncratic sites from a nestedness analysis (using the *Nestedness* software; Ulrich 2006) that measures whether the faunal composition of different study sites form perfect subsamples from a larger common species pool (a nested pattern) or whether local peculiarities occur. The degree of nestedness was estimated using the Brualdi and Sanderson (1999) measure BR which counts how many absences or presences have to be erased to get a perfectly nested species \times sites matrix. Idiosyncratic sites were assessed from the nestedness temperatures (Atmar and Patterson 1993) and the site specific BR value (the quotient of unexpected absences or occurrences per site UAO divided through the total number of species S). Random expectations and respective standard errors were obtained from 100 randomizations of the data matrix using the sequential swap algorithms (fixed row-fixed columns constraint; 5000 swaps).

Because of the different individual and species numbers per site we could not compare species composition directly. Therefore, we compared the observed species overlap between the city and the rural sites from a random sample null model. We sampled for both guilds and both city sites the number of individuals observed from the total samples of destruent (15323 individuals) and predators (1871 individuals) of the rural sites according to the respective abundance distribution (Table 1). We then compared the observed species overlap (measured by the Soerensen index) with the expected one. The respective confidence limits of the null model were obtained from 50 random draws each. We further used Spearman's rank order correlation ρ to infer whether species abundances differed between the sites. We computed all pairwise combinations of ρ between the city sites and the rural sites and of all combinations of the random draws. If the city sites deviated from the rural sites with respect to species abundances, their ρ values should be significantly lower than the respective ρ values within rural sites and within the random draw. To infer whether the city sites

contained higher frequencies of widespread species, we compared the observed numbers of species that occurred at the rural sites 1, 2, 3...7 times and at all rural sites with the expected numbers of the null model.

Lastly, we performed non-metric multidimensional scaling (NMS) for grouping sites according to species abundances using the NMS module of PC-Ord (McCune & Mefford 1999; Bray Curtis distance, 100 randomizations for comparing observed and expected stress per dimensionality). NMS appears to be the best alternative to metric ordination methods if we are unsure about the data structure (Clarke 1993).

We used rarefaction (Heck et al. 1975) and the first order Jackknife (Burnham and Overton 1978) to estimate total and study site species richness. Because all species - abundance distributions were well fitted by log-series (see below), we applied the associated α -measure of evenness (Fisher et al. 1943). Model fitting was done with the non-linear estimation modules of Statistica 7 (Statsoft 2005). Logarithmic transformations always refer to natural (ln) logarithms, errors to standard deviations.

Results

The city centre and periphery had lower species numbers and abundances of destruent beetles in comparison to the open and forested rural sites. We found at both city sites 17 species. Only the destruent *Omosita discoidea* (Nitidulidae) was present in the city (in the centre) while absent at all rural sites. The Jackknife I and the rarefaction estimates of species richness also pointed to a reduced species diversity at the city sites (17 to 21 species) compared to the rural sites (21 to 38 species). In total, the jackknife I estimator pointed to 72 species of destruent and 53 predator species within the study area. Open and forested rural sites did not significantly differ in species richness (all pairwise comparisons $p > 0.1$).

The open rural sites contained on average 308 ± 44 individuals of destruent per trap, the forested sites 133 ± 39 individuals (Table 2). In turn, the mean abundances in the city were only 17 ± 16 (centre) and 29 ± 18 (periphery) beetles per trap. The species abundance distributions of rural and city sites were similar and followed log-series distributions (Fig. 2.A). However, the abundance distributions of the city communities were less steep than the respective rural ones (Fig. 2.A). Nevertheless, the evenness values of city and rural sites did not significantly differ (Table 2).

Contrary to the destruent pattern we did not find significant differences in species richness and abundances of the predatory beetles between rural and city sites (Fig. 2,

Table 2. Observed species richness, total catches, mean catches per trap, rarefied species numbers and the respective standard deviations, Jackknife I estimates of species richness, and the a measure of evenness.

Destruents	S observed	N	Mean N	Rarefied S	StDev	Jackknife I	Alpha
East forested	21	2746	275	38	2.4	25	3.09
East open	26	2212	221	36	2.4	33	4.13
North forested	21	1788	199	35	2.3	24	3.34
North open	21	297	30	21	2.3	30	5.15
South forested	23	2645	265	38	2.4	25	3.46
South open	22	1311	146	32	2.3	28	3.75
West forested	26	2645	294	38	2.4	31	4.00
West open	27	1222	136	32	2.3	36	4.88
Periphery	17	287	29	21	2.3	21	3.95
Centre	17	170	17	17	2.2	21	4.70

Predators	S observed	N	Mean N	Rarefied S	StDev	Jackknife I	Alpha
East forested	15	98	10	18	2.1	21	4.93
East open	23	523	52	31	2.1	29	4.91
North forested	12	94	10	18	2.1	15	3.65
North open	16	81	8	17	2.1	20	5.97
South forested	14	62	6	15	2.0	21	5.63
South open	17	335	37	28	2.2	24	3.78
West forested	18	124	14	20	2.2	24	5.78
West open	20	338	38	28	2.2	25	4.65
Periphery	14	92	9	18	2.1	21	4.59
Centre	12	124	12	20	2.2	16	3.27

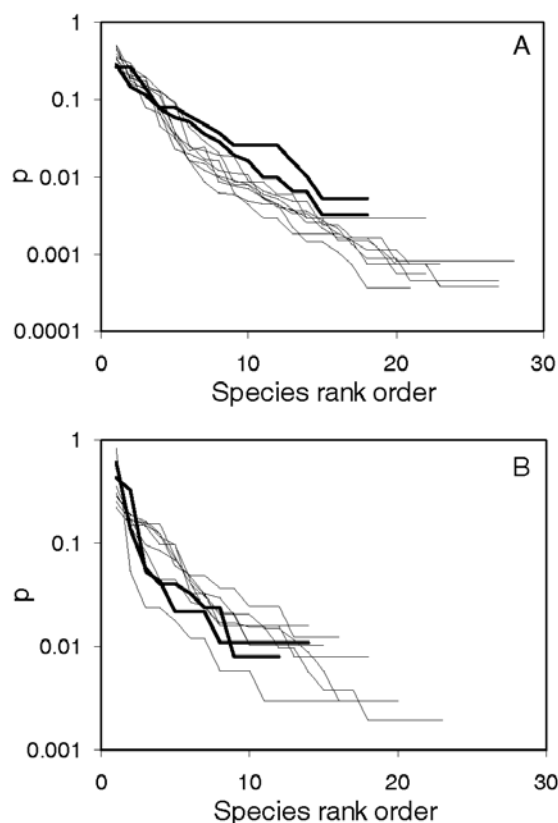
**Figure 2.** Relative abundance – rank order plots of destruents (A) and predators (B). The thin lines stem from the rural sites, the bold lines from the city sites.

Table 2). We estimate 16 to 21 species at the city sites and 15 to 31 species at the rural sites with a mean of 22 ± 2 species. However, the city species numbers are at the lower end of the observed spectrum and estimated species richness of the city sites were within the 95% confidence limits of the respective rural estimates. The abundance distributions and therefore the evenness in the city did not differ from the rural sites (Fig. 2.B).

The sites were not significantly nested. The Brualdi and Sanderson measure of nestedness gave for the destruent beetles $BR = 59$ flops to get a maximally nested matrix, while the random null model expected $BR = 58 \pm 2$. For predators, we got $BR = 54$ and a null model expectation of $BR = 53 \pm 1$. In the case of the destruents, both city sites did not differ from the rural sites with respect to idiosyncrasy (Patterson and Atmar 2000), that means numbers of unexpected species absences or presences (Table 3). The predator communities of the city centre, in turn, appeared to be less idiosyncratic and had also fewer unexpected species absences or presences than the rural sites. Our data also imply the trend of open sites to be more idiosyncratic and therefore less predictable than forested sites (Table 3). The open sites had higher temperatures and UAO/S ratios in six out of eight pairwise comparisons (predators and destruents combined).

Our next question was whether the community composition differed between the rural and the urban sites. A comparison of the observed numbers of species in the city that occurred once to always at the rural sites with the numbers expected from a random draw (Fig. 3) did not

Table 3. Idiosyncratic site temperatures (T), numbers of unexpected species absences and occurrences (UAO), and the quotient of UAO/S observed as a measure of site distinctness.

Destruents				
Site	S observed	T	UAO	UAO/S
East forested	21	12	4	0.19
East open	26	8	14	0.54
North forested	21	13	6	0.29
North open	21	42	6	0.29
South forested	23	1	3	0.13
South open	22	20	6	0.27
West forested	26	17	16	0.62
West open	27	71	23	0.85
Periphery	17	8	3	0.18
Centre	17	16	5	0.29

Predators				
Site	S observed	T	UAO	UAO/S
East forested	15	13	4	0.27
East open	23	52	14	0.61
North forested	12	11	4	0.33
North open	16	30	8	0.50
South forested	14	28	6	0.43
South open	17	2	4	0.24
West forested	18	13	10	0.56
West open	20	28	13	0.65
Periphery	14	32	5	0.36
Centre	12	11	2	0.17

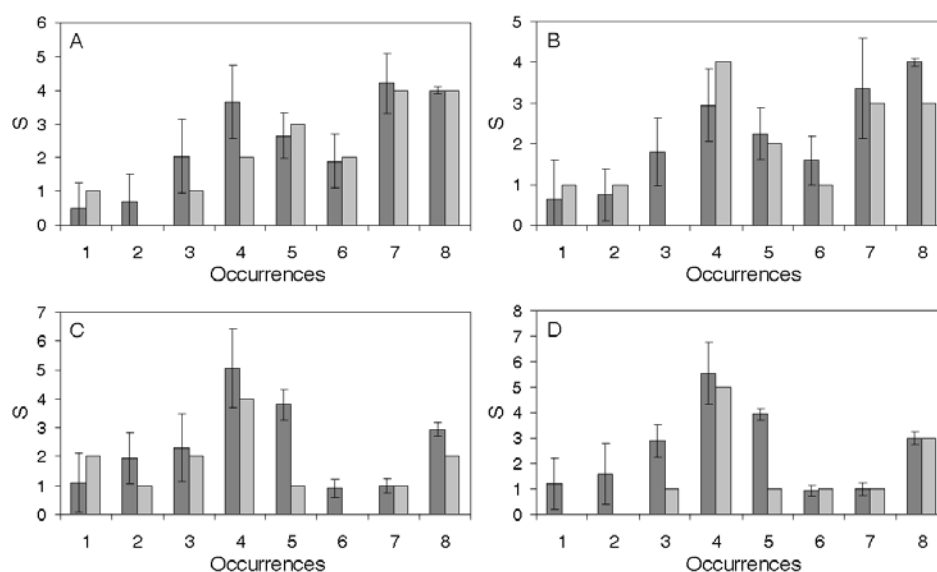


Figure 3. Observed (light bars) and expected (dark bars) numbers of species of destruents (A, B) and predators (C, D) of the city periphery (A, C) and the city centre (B, D) that occurred exactly at 1, 2, 3...8 of the rural sites.

point for the destruents to significant trends towards higher numbers of widespread and lower numbers of infrequent species in the city. Expected and observed species numbers were for 15 of the 16 pairwise comparisons within the 95% confidence level of the null model expectations (Fig. 3.A, B). The same results hold for the predators in the case of the city periphery (Fig. 3.C). However, the centre was depauperate of those species that occurred

at the rural sites only infrequently (Fig. 3.D) while frequent species occurred again according to the null model expectation.

A comparison of Spearman's rank order correlations ρ of species abundances across the sites and between observed city abundances and the respective null model expectations revealed that the abundance rank orders of the destruents in the city differed from those at the other

sites (Fig. 4.A). Correlation coefficients of the centre – forested sites and centre – open sites comparisons were significantly lower ($p(t) < 0.01$) than the null model expectation pointing to marked changes in the respective abundance rank orders. The abundance distributions of the city periphery, in turn, did not significantly differ either from those of the rural sites nor from the null expectation as judged from the high and very similar coefficients of correlations. Destrudent abundance distributions appeared to be most similar within the forested sites (mean $\rho = 0.75$).

In the case of the predators this picture was reversed. The abundance distribution of the periphery appeared to differ from those of the rural sites and from the null expectation (Fig. 4.B, all pairwise $p(t) < 0.01$). The respec-

tive distributions in the centre appeared to be more similar to those of the rural sites and those of the null model.

The NMS ordination revealed habitat-specific abundance patterns for both guilds (Fig. 5). The forested sites appeared to be most similar and we did not find a true gradient in species composition. The city sites of both guilds rather ranged between the rural sites.

Lastly, we looked at whether possible differences in species composition were manifested in patterns of co-occurrence. In the case of the destruent species, co-occurrences appeared to be random (Table 4). In turn, the checkerboard scores of the predators that measure mutual species exclusions was consistently shifted towards positive values, that means towards pairwise exclusions and a non-random pattern of co-occurrence (Table 4). The spe-

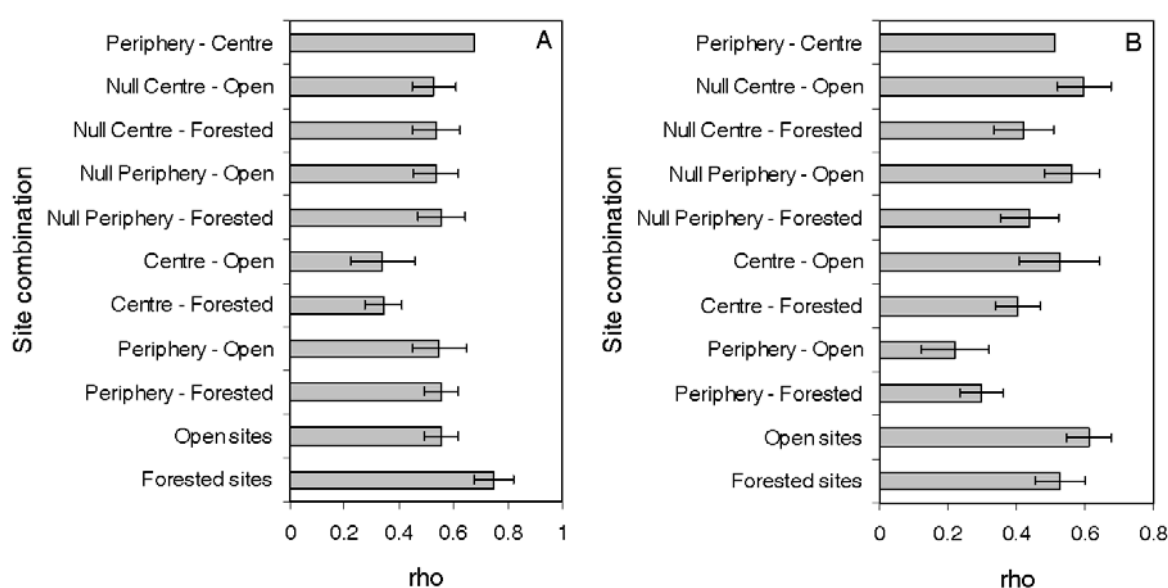


Figure 4. Spearman's rank correlation coefficients ρ between all pairwise combinations of forested and open sites, between the city periphery and centre and the rural sites (forested and open), between null model predictions and rural sites, and between city periphery and centre. **A:** destruent, **B:** predators. Error bars denote standard deviations.

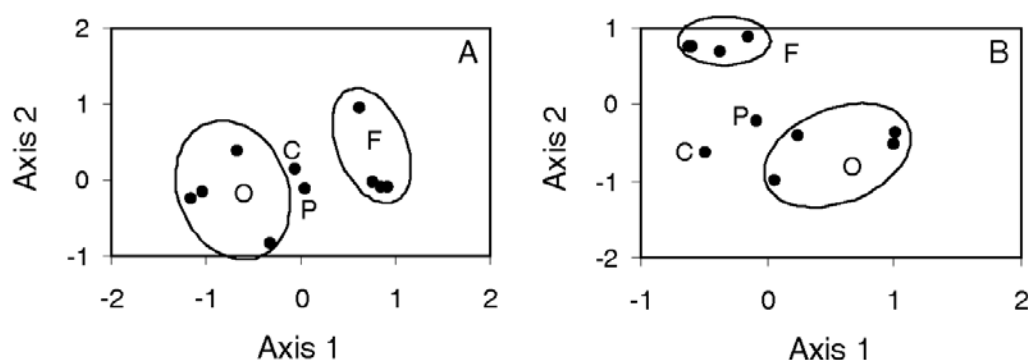


Figure 5. NMS ordination (Bray Curtis distance) using ranked abundances of destruent (A) and predators (B). O: open sites; F: forested sites; C: city centre; P: city periphery. Both ordinations favoured a three dimensional solution of which the first two axes are shown. The ellipses show the O and F sites.

Table 4. Z-transformed species co-occurrence scores estimated from the replicates at each study site.

Destruents	Checkerboard Combination		
	C-score	score	score
East forested	-0.55	1.37	0.10
East open	-1.59	-1.08	0.00
North forested	3.14	-0.17	0.00
North open	0.91	-0.89	0.22
South forested	-0.06	-0.63	0.06
South open	0.51	0.16	0.10
West forested	1.36	1.44	0.00
West open	0.37	1.23	0.00
Periphery	0.10	2.56	0.28
Centre	-1.50	1.60	0.05

Predators	Checkerboard Combination		
	C-score	score	score
East forested	-0.90	0.07	0.00
East open	1.43	5.05	0.00
North forested	-1.53	0.23	0.75
North open	-0.93	0.83	0.05
South forested	0.18	0.47	0.95
South open	-0.47	3.37	0.37
West forested	-1.31	1.46	0.35
West open	0.15	2.09	0.26
Periphery	0.78	-0.08	-1.21
Centre	-0.13	1.41	-1.36

cies combinations score that measures unique species co-occurrences was at both city sites shifted towards negative values indicating the existence of unique species combinations, although these were statistically not significant ($p > 0.05$).

Discussion

The present paper is the first to directly compare guilds of different trophic levels with respect to rural – urban gradients. It allows for answering the questions raised in the introduction. First, we found guild specific differences. Destruent beetles decreased markedly in species richness and abundance towards the city centre while predator richness was only slightly lower than the mean of the rural sites. In both guilds, we did not observe occurrences of species absent from the rural sites. Such idiosyncratic occurrences have been reported for plants (Cousins and Eriksson 2001, Zhao et al. 2006) and ground beetles (Eversham et al. 1996).

We were surprised by the low destruent abundances at both city sites. These decreased nearly tenfold. Predator abundances also decreased by a factor of two, although this was due to high variability at the rural sites and statistically not significant. Destruent species are in the majority obligatory carrion visitors and therefore microhabitat specialists. Predators, in turn, might use alternative microhabitats with different prey species. Hence, we interpret the different decrease in abundance and species

richness as being caused by different levels of specialization. This interpretation fits into the observation of decreasing species numbers of specialist species along rural – urban gradients (Niemelä et al. 2002, Ishitani et al. 2003, Chace and Walsh 2006, Sadler et al. 2006).

We can only speculate about the causes of the low destruent abundances in the city. One reason might be the common street- and park-cleaning practice of immediate removing visible larger carcasses. Habitat fragmentation in the city might also cause lower abundances per habitat patch although other studies on the influence of urban habitat fragmentation of arthropod diversities gave mixed results (Fahrig 2003, Angold et al. 2006). The only city specific destruent species was *Omosita discoidea*, a common North American and European species that was also in Germany frequently reported from cities (cited from Löbbecke Museum Düsseldorf; URL: <http://www.biologie.uni-ulm.de/cgi-bin/>).

Our results also point to an increase in predator prey (P/R) ratios (numbers of predator species/numbers of prey species P/R) towards the city centre (based on rarefaction estimates, Tab. 2). The rural sites had a mean $P/R = 0.67 \pm 0.20$, the city periphery $P/R = 0.86$, and the city centre $P/R = 1.18$. Hence, the proportion of predator species increased towards the city centre. These changes might also have a functional aspect. Reduced abundances of destruent beetles might alter the process of decomposition.

However, we are not aware of any study that addresses this question in detail.

The changes in species richness and abundances caused differences in species composition. First, the city sites were less idiosyncratic (had fewer unexpected species occurrences or absences) than the rural sites (Table 3). This fits into the notion of the lack of city specific species and points to a homogenizing influence of the city. However, dominance rank orders (Fig. 2) and evenness (Table 1) of both guilds did not markedly differ between the sites as had been reported from carabid (Sadler et al. 2006) and butterfly and bird studies (Blair 1999). On the other hand, Magura et al. (2004) found an increase in beta diversity among urban sites and speculated that a higher patchiness of urban sites might facilitate the co-occurrence of urban and forest as well as specialist and generalist species and thus leading to an increased species richness. Further studies on urban and rural degrees of patchiness have to clarify these contrasting views.

The intermediate disturbance hypothesis predicts highest species numbers at intermediate positions along disturbance gradients (Connell 1978, Sheil and Burslem 2003). This has been interpreted in such a way that suburbs and city peripheries should be most species rich within the rural – urban gradients under the premise that city centres represent the most disturbed habitats in this sequence (Niemelä et al. 2002, Sadler et al. 2006). Our results do not corroborate this hypothesis. Neither predator nor destruent beetles were most diverse at the periphery site as had been reported for butterflies by Blair and Launer (1997) and for birds by Jokimäki and Suhonen (1993) and Blair (1999). A similar result was reported by Hornung et al. (2007) in their study of isopods along an urban-rural gradient. However, it remains of course an open question whether our sites indeed reflect disturbance directions and whether city peripheries are intermediate with respect to disturbance (Gödde et al. 1995). There is clearly a lack of studies that relate rural–urban gradients to respective gradients of environmental disturbance.

We did not find increased frequencies of widespread species towards the city sites (Fig. 3). Such an increase is predicted by current theory (Gray 1989, Niemelä 1999a) and has been reported for Carabidae (Niemelä et al. 2002, Sadler et al. 2006) and birds (Clergeau et al. 1998). However, we should note that we defined widespread as being present at most of the rural sites (forested and open). The cited studies used distribution maps and literature data. Nevertheless, the fact that species occurring frequently in the surroundings of cities did not occur in higher frequencies at city sites cannot be judged as a corroboration of current theory. Being widespread is often used as a proxy

of being a generalist species (Kotze et al. 2003). Unfortunately, for most of our species appropriate data about habitat requirements and life history traits are not available. Therefore we could not separate our species into generalists and specialists and relate our rural – urban differences to niche width.

The city centre lacked infrequent predator species of the rural sites (Fig. 3.C, D), a pattern that is in line with other work that reported a similar reduction in infrequent and habitat specialist species (Niemelä et al. 2002, Blair 2004). However, we did not find this pattern in the destruent species (Fig. 3.A, B). This difference points again to guild specificities and demands caution regarding any generalisations of gradient patterns.

An integrated approach to the study of gradients is ordination. Our NMS ordination based on total catches per site pointed for both beetle guilds to very similar community structures at the forested sites (Fig. 5). This result reflects the high between-site correlation coefficients of Fig. 4. However, the analysis did not return a clear and unambiguous signal for a gradient in community composition. The city sites rather ranged between the open and forested rural sites. Gradients came up in other studies that used ordination to infer rural – urban gradients in beetles and birds (McIntyre et al. 2001, Natuhara and Imai 2006, Sadler et al. 2006, Elek and Lövei 2007) and to a lesser degree in isopods (Vilisics et al. 2007). Niemelä et al. (2002) used ordinary cluster analysis on species occurrences and found only mixed support for any gradient in composition. In turn, Elek and Lövei (2007) in their study on ground beetles reported a clear separation of faunal composition along the urban – rural gradient. We were surprised how well (and stably) NMS separated our four habitat types. We interpret this as evidence for site specific community structures that are not simple effects of reduced species richness. This interpretation is in accordance with our finding that the sites were not significantly nested. In turn, judged by the idiosyncrasy analysis (Table 3) they were not so distinct that we can speak of city specific communities.

In summary, we found evidence for a reduced diversity and changes in community structure of destruent and predatory beetles towards the city centre. However, both guilds differed in this respect and our study gives no evidence that there are simple rules that govern rural – urban gradients. There is no evidence that the intermediate disturbance hypothesis might apply along such gradients. Lastly, we found only little support for a homogenizing effect of urban environments on carrion visiting beetles.

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