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ORIGINAL ARTICLE

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Body size and biomass distributions of carrion visiting beetles: do cities host smaller species?

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Abstract The question how animal body size changes along urban–rural gradients has received much attention from carabidologists, who noticed that cities harbour smaller species than natural sites. For Carabidae this pattern is frequently connected with increasing disturbance regimes towards cities, which favour smaller winged species of higher dispersal ability. However, whether changes in body size distributions can be generalised and whether common patterns exist are largely unknown. Here we report on body size distributions of carcass-visiting beetles along an urban–rural gradient in northern Poland. Based on samplings of 58 necrophages and 43 predatory beetle species, mainly of the families Catopidae, Silphidae, and Staphylinidae, we found contrary patterns of necrophages and predatory beetles. Body sizes of necrophages decreased towards the city centre and those of predators remained unchanged. Small necrophages and large predators dominated in abundance in the city centre. Necrophage body sizes appeared to be more regularly spaced in the city centre than expected from a random null model and in comparison to the rural pattern, pointing to increased competition.

Keywords Body size · Coleoptera · Rural–urban gradient · Disturbance · Carrion

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Introduction

Animal and plant body size is correlated with many aspects of life history traits and species interactions (dispersal, reproduction, energy intake, competition; Brown et al. 2004; Brose et al. 2006). Therefore, species body size distributions (here understood as the frequency distribution of log body size classes, SSDs) are often used to infer patterns of species assembly and energy use (Peters 1983; Calder 1984; Holling 1992; Gotelli and Graves 1996; Etienne and Olff 2004; Ulrich 2005a, 2006).

Many of the studies on local SSDs focused on the number of modes and the shape. Unimodal distributions appeared to prevail (Loder 1997; Gaston and Blackburn 2000; Ulrich 2006) and can be considered as the null expectation (May 1986) from which any deviation deserves explanation. Vertebrate SSDs were frequently found to be right-skewed with an excess of smaller species (Gaston and Blackburn 2000; Kozłowski and Gawelczyk 2002; Smith et al. 2004). Arthropod communities tend to approach symmetrical distributions at regional and local scales (Chislenko 1981; Espadaler and Gomez 2002; Ulrich 2005a, 2006; but see Gaston et al. 2001), although there is a need for a critical meta-analytical study to infer whether phylum-specific differences exist.

Szyszko (1983) and later Gray (1989) and Blake et al. (1994) hypothesized that human-induced increased levels of disturbance should alter the distribution of body sizes towards a prevalence of small-sized species in highly disturbed habitats. Such a decreasing body size pattern has subsequently been reported for several ground beetle assemblages (Alaruikka et al. 2002; Niemelä et al. 2000, 2002; Braun et al. 2004; Gaublomme et al. 2005; Magura et al. 2004, 2006; but see Lövei and Magura 2004), although in a few cases it was only marginal (Niemelä et al. 2000, 2002).

The causes of this pattern are still not well understood. Lövei and Sunderland (1996) speculated that less mobile larvae are more affected by changing conditions in disturbed habitats, whereas Thorbek and Bilde (2004) argued that lower total abundances under unfavourable conditions result in increased extinction rates of larger and therefore often less abundant species. In ground beetles, smaller species are frequently macropterous whereas larger species are often wingless and therefore potentially less dispersive (Thiele 1977). Thus, smaller species should be more abundant in fragmented or temporary habitats. Lastly, disturbed habitats should particularly attract small-bodied r-strategists, thus shifting the body size distribution towards lower weight classes (Kotze and O'Hara 2003).

Shifts in mean body size along a disturbance gradient might also influence the general shape of the SSD. If the mode of the SSD remains constant, any shift in body size towards smaller species should be visible as a change in the skew towards more negative values (if measured by the third moment). Alternatively, the whole SSD might shift to the left, leaving the shape of the distribution unchanged (Fig. 1). The ecological interpretation of the first case is an accumulation of smaller species at the disturbed sites (assuming similar species richness) due to a reduced proportion of medium-sized species, while larger species still persist in the community. The second case in turn implies the local extinction of larger species at disturbed sites. Both processes, of course, can work together, as has been reported by Sadler et al. (2006) for carabid assemblages.

Changes in body size distributions might also cause changes in the respective competitive regimes. Under the assumption that species of similar size also have similar resource requirements, interspecific competition should cause a more regular spacing of body sizes along the size axis than expected from a random draw (Strong et al. 1979; Gotelli and Graves 1996). Most studies on arthropods rejected a regular spacing (Gotelli and Graves 1996; Ulrich 2006) or found only weak evidence for nonrandom distributions (Weller and Ganzhorn 2004; Ulrich 2005a). However, a detailed meta-analytical study is still missing.

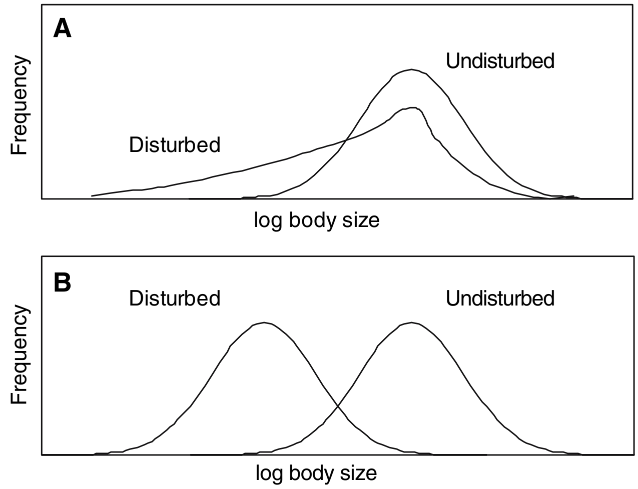


Fig. 1A–B Two ways in which a shift towards smaller species could change a SSD. **A** The skew of the distribution changes and the proportion of medium-sized species is reduced. **B** The whole distribution shifts to the left and the large species become extinct. Both mechanisms can occur in combination

While the diversity patterns of arthropods, particularly ground beetles, along disturbance gradients are now well known (Niemelä et al. 2002, Weller and Ganzhorn 2004; Angold et al. 2006; Magura et al. 2006), there are astonishingly few detailed studies on the respective arthropod size distributions (Braun et al. 2004; Weller and Ganzhorn 2004; Magura et al. 2004, 2006; Sadler et al. 2006; Lövei and Magura 2004; Ulrich 2006). The present study uses size distributions of beetle species (necrophages and their predators) that were trapped from decaying dead fish exposed along an urban–rural gradient in Northern Poland. Carrion-visiting species seem to be well suited to study size distributions because they form well-defined communities that depend on the same type of resource.

The present paper intends to answer the following questions:

1. Can the decreasing body size pattern be generalized?
2. Are size distributions habitat-type-specific?
3. Do beetle body size distributions differ between trophic groups?
4. Do SSD shapes differ with respect to disturbance?
5. Are body sizes in disturbed habitats more regularly spaced than in undisturbed sites?

We will show that there are marked differences in the size distributions of necrophagous beetles along the gradient, while these differences are less pronounced in the predators.

Materials and methods

Eighty traps (four at each of 20 sites) were placed along two 120 km transects (west–east, north–south, Fig. 2) crossing in the centre of the city of Olsztyn (Mazurian lake district of northern Poland, 53°47′N; 20°30′E). Additionally we placed ten identical traps at two sites on the periphery of the city and in the city centre (Aleksandrowicz and Komosiński 2005). The sampling sites covered two major habitat types, a forested (mixed coniferous forests) and an open (grassland) type. Mean trap distance was ca. 1 km. The traps operated during August and September 1997. Material was collected at the end of the trapping period. Traps were made of glass jars (diameter 9 cm) dug into soil and covered with wooden roofs. To avoid the capture 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. One hundred grams of rotten fish (placed above the glycol layer) served to attract beetle species. 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).

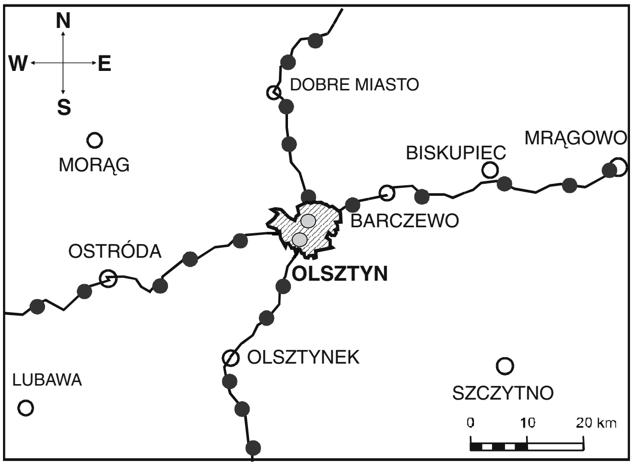


Fig. 2 The study area in the vicinity of Olsztyn (northern Poland). The *grey points* denote the five trapping places along the main roads off the city centre. The two *light grey points* denote the trapping places in the city centre and its periphery

In total we sampled 29,088 individuals of 303 Coleoptera species. Based on the standard literature (e.g. Freude et al. 1964 onwards; Koch 1989), we identified 58 species from the families Anthicidae, (1 species), Catopidae (12), Cryptophagidae (4), Dermestidae (3), Geotrupidae (1), Hydrophilidae (8), Nitidulidae (4), Ptilidae (7), Scarabaeidae (3), and Silphidae (15) as being necrophagous and/or mycetophagous and frequently associated with carcasses (termed necrophages below). Forty-three 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). The other beetle species were considered occasional visitors 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 the classification into trophic groups is contained in Aleksandrowicz and Komosiñski (2005).

We used the third moment, the skewness γ, to assess the shape of the ln-transformed body length–frequency distribution. Body length data were taken from the literature. To infer whether the study sites differ with respect to the distribution of body sizes, we used the ratio test of Strong et al. (1979). We first tested whether the mean ratio $\alpha = L_x/L_{x-1}$ (L_x being species x in the sequence of species ordered according to body size) differs from what is expected if body lengths were simple random draws from the common species pool. We then tested whether the species were regularly spaced or have an aggregated distribution within the observed range of body sizes. To do this we compared the observed standard deviation σ_α of all $\alpha = L_x/L_{x\text{-}1}$ with the respective standard deviation of the random draw null model. The 58 necrophagous and 43 predatory species obtained from all study sites served as the respective species pools. Null model confidence limits were obtained in all cases from 1,000 random draws. Computations were made with the software *Structure* (Ulrich 2005b).

An often used graphical representation that links body size distributions to abundance data is the Lorenz curve (Lorenz 1905), where the cumulative percentage of individuals is plotted against cumulative percentage of body size (Damgaard and Weiner 2000; Magura et al. 2006). If all individuals are of the same body size, the curve follows the isocline of equality. Increasing differences in body size force the curve below this line. While the Lorenz curve allows for the identification of size inequalities, the fact that it is always a concave function often makes it difficult to compare different communities (Dixon et al. 1987; Damgaard and Weiner 2000; Magura et al. 2006). Therefore, in the present study we use a slightly different approach and plot cumulative percentage of ranked species body size against the cumulative percentage of individuals per species. Such plots can be concave or convex and can easily be compared by the significances of the quadratic terms after fitting a second-order algebraic function. Fitting was done with the nonlinear estimation modules of Statistica 7 (Statsoft 2005). Logarithmic transformations always refer to natural (ln) logarithms. Errors are given as standard errors.

Lastly, we performed non-metrical multidimensional scaling (NMS) of a grouping of sites according to species biomasses using the NMS module of PC-Ord (McCune and Mefford 1999; Euclidean distance, 100 randomizations for assessing dimensionality). NMS appears to be the best alternative to metrical ordination methods if we are unsure about the data structure (Clarke 1993). Biomass B per site was estimated from the product of site abundance and mean species body weight. Species body weight was estimated from the equation of Ganihar (1997):

$$W(\mathrm{mg}) = 0.038 \times L(\mathrm{mm})^{2.46} \tag{1}$$

Results

SSDs of the necrophagous beetles differed significantly between the rural and the urban sites. All rural necrophages SSDs were significantly left-skewed, irrespective of whether they stemmed from open or forested sites (Table 1). In turn, the two urban SSDs were not significantly skewed. Necrophagous beetles at the open rural sites had significantly higher mean body length than those at forested sites ($P(t)$ < 0.01). Mean body sizes at both urban sites were similar to those at the open rural sites, and consequently were also significantly higher than those at the forested sites ($P(t)$ < 0.01). The body size distributions of the predators did not significantly differ between the study sites.

All necrophagous SSDs were unimodal. The SSDs of the predatory beetles, on the other hand, did not significantly differ between the rural and the urban sites

Table 1 Species numbers, mean body length (mm), mean biomass (g), coefficients of variation (CV), skewness, and test values for the ratio test and the variance test of the body length distribution at each study site

Site	Type	Species	Mean body length	Mean biomass	Mode	CV	Skewness	Ratio test	Variance test
Necrophages									
East	Forest	21	1.10	41.1	1.15	0.54	−1.21*	1.14	0.22
East	Open	26	1.37	35.1	1.66	0.32	−1.33**	1.09	0.18
North	Forest	21	1.07	29.5	1.15	0.59	−1.19*	1.14	0.25
North	Open	21	1.22	4.5	1.55	0.49	−1.52*	1.14	0.24
South	Forest	23	1.20	38.6	1.40	0.57	−1.64**	1.15	0.40
South	Open	22	1.31	15.4	1.63	0.46	−1.73*	1.13	0.21
West	Forest	26	1.05	46.6	1.16	0.68	−1.00*	1.11	0.17
West	Open	27	1.32	18.0	1.55	0.37	−1.93***	1.13	0.38
Periphery		17	1.39	4.0	1.61	0.24	−0.23	1.06*	0.08*
Centre		17	1.31	1.8	1.57	0.24	0.14	1.07*	0.05*
Predators									
East	Forest	15	2.50	19.8	2.76	0.12	−0.05	1.08	0.08
East	Open	23	2.47	14.0	2.76	0.14	−0.04	1.06	0.08
North	Forest	12	2.51	21.4	2.63	0.11	0.26	1.09	0.06
North	Open	16	2.54	23.4	2.79	0.11	−0.60	1.06	0.05
South	Forest	14	2.52	17.1	2.75	0.13	−0.57	1.06	0.09
South	Open	17	2.41	100.1	2.76	0.13	−0.18	1.06	0.08
West	Forest	18	2.41	27.5	2.10	0.14	0.20	1.07	0.06
West	Open	20	2.46	94.3	2.77	0.13	−0.49	1.05	0.07
Periphery		14	2.48	29.4	2.12	0.14	0.43	1.09	0.08
Centre		12	2.49	39.6	2.78	0.12	−0.43	1.09	0.10

* $P(t) < 0.05$, ** $P(t) < 0.01$, *** $P(t) < 0.001$. Significance values of the ratio test and the variance test refer to the one-sided probability that the observed values are lower than the null model expectation

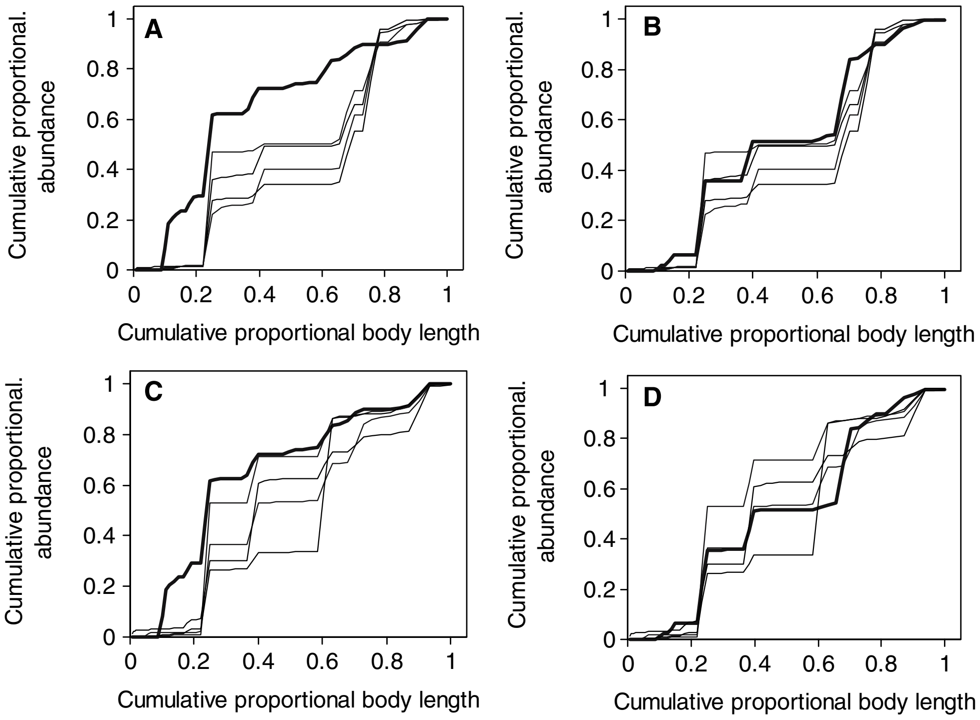


Fig. 3A–D Modified Lorenz curves of size distributions of necrophagous beetles. City centre (**A**, **C**) and city periphery (**B**, **D**) are shown with *bold lines*. The cumulative trappings of the forested sites (**A**, **B**) and the rural sites (**C**, **D**) along the four rural gradients are shown with *thin lines*

and within the rural sites (Table 1). Mean body sizes, modes, and SSD skews were similar (all pairwise $P(t) > 0.05$).

The modified Lorenz curves of the necrophagous beetles were significantly concave in the city centre (Fig. 3A,C; Table 2). Hence small-bodied species accounted for most of the total beetle abundance. The forested sites in turn tended to be convex and the larger species were most abundant. The open rural sites and the city periphery were intermediate (Fig. 3B,D).

The opposite trend was observed for the predators (Fig. 4). Five out of six modified Lorenz curves of the

Table 2 Values of the quadratic terms of fits of second-order algebraic functions to the plots of Figs. 1 (necrophages) and 2 (predators)

Guild	Sites	Direction				City	
		East	North	South	West	Periphery	Centre
Necrophages	Forested	0.08	0.58**	−0.18	0.70***	−0.11	−1.38****
	Open	0.36*	−0.40**	−1.10****	−0.25		
Predators	Forested	−0.98****	−0.52***	0.21	−0.41**	1.07****	0.96***
	Open	0.35	0.64**	0.74*	0.60***		

* $P(t) < 0.05$, ** $P(t) < 0.01$, *** $P(t) < 0.001$, **** $P(t) < 0.0001$

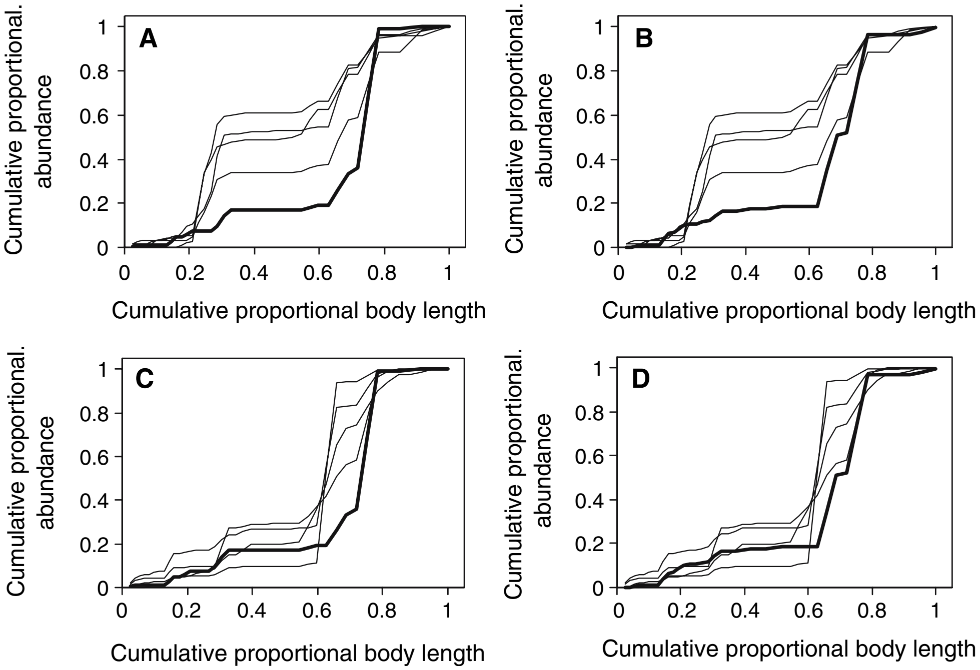


Fig. 4A–D Modified Lorenz curves of size distributions of predatory beetles of forested sites. City centre (**A**, **C**) and city periphery (**B**, **D**) are shown with *bold lines*. The cumulative trappings of the forested sites (**A**, **B**) and the rural sites (**C**, **D**) along the four rural gradients are shown with *thin lines*

open rural and city sites were significantly convex (Table 2). There, larger predators dominated in abundance. In turn, three of the four forested rural sites had concave curves and smaller species dominated (Table 2).

These differences were mirrored by the differences in total biomass per site. The rural site produced 4.5–46.6 g of necrophage biomass per 100 g fish, and we found higher biomasses at open rural sites (Table 1). Both city sites, in turn, produced less biomass of 1.0 g (centre) to 4.0 g (periphery) per 100 g fish. Additionally, biomass and species richness per site were positively correlated ($R^2 = 0.50$; $P(t) = 0.02$). For the predators, city and rural sites did not differ with respect to mean biomass. At the rural site we found 17.1–100.1 g biomass, and at the city sites 29.4 (periphery) and 39.6 (centre) g per 100 g fish. Species richness and biomass were not correlated.

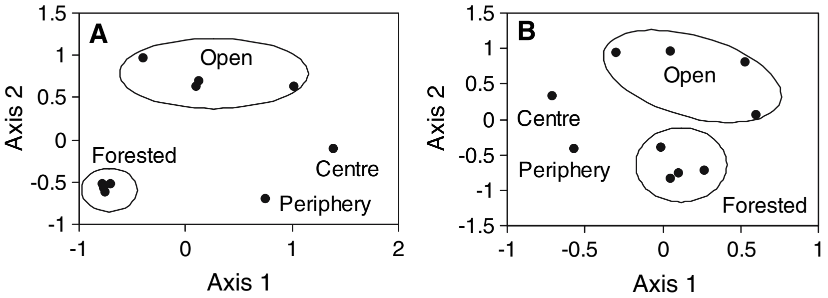
Differences between necrophages and predators and between the rural and city sites also appeared with respect to the spacing of body length within the observed range. The spacing of predator body lengths of the two city sites did not differ from what was expected from a random scattering and also did not differ from the spacing of the rural sites. On the other hand, the necrophagous beetles had a lower mean difference in body length (mean $\alpha = L_x/L_{x-1}$) than expected from a random spacing ($P < 0.05$, Table 1) and from the mean α-values of the open and forested rural sites ($P(t) < 0.01$). Body length was also more regularly spaced than expected from a random draw ($P < 0.05$, Table 1) and from the standard deviation of the open and forested rural sites ($P(t) < 0.01$).

Lastly, we investigated whether the rural urban gradient can be detected using the distribution of species biomasses. As expected from the previous results, the NMS ordination grouped the forested sites closely together (Fig. 5A), The open sites appeared to be more heterogeneous but were also clustered together. The NMS separated the city centre and periphery from both types of rural sites. A similar result emerged for the predators (Fig. 5B). The NMS separated forested, open and city sites. Again the forest sites appeared to be most similar.

Discussion

There is a growing body of literature on carabid body sizes along urban–rural gradients (compiled at the Globenet homepage http://www.helsinki.fi/science/

Fig. 5A–B First two axes of the NMS scaling of species biomass of necrophages (**A**) and predators (**B**). Final stress in **A**: 0.34 (two-dimensional solution); in **B**: 1.22 (four-dimensional solution)



globenet/). However, similar studies on other arthropods are scarce. Only Gibbs and Stanton (2001) studied a rural–urban diversity gradient of necrophagous Silphidae and Muscidae and reported decreasing silphid and increasing muscid abundances. This would coincide with the smaller species hypothesis reported here.

The present study points to guild-specific changes in SSDs along the urban–rural gradient. While the necrophagous beetles conform to the smaller species hypothesis (Szyszko 1983; Gray 1989; Fig. 3), their predators showed the opposite pattern (Fig. 4). The predators of the present study came largely from the Staphylinidae (29 species) and Histeridae (11 species) families. Larger rove beetles of the genus *Philonthus* (*P. addendus*, *P. politus*, *P. chalceus*) dominated at both city sites and accounted for 78% (centre) and 79% (periphery) of the total predator abundance. At the rural sites these three species on average accounted for only 32 ± 5% of total abundance. Hence, the shift in the body size—abundance distribution shown in Fig. 4 is mainly caused by the dominance of three large rove beetle species in the city.

In turn, we observed a clear increase in relative abundance of smaller necrophagous species along the rural–urban gradient in accordance with the decreasing body size hypothesis (Fig. 3). This trend resulted in the comparably low total biomass of the necrophagous beetles at both city sites (Table 1). Contrary to the predator pattern, this shift was not caused by an increase in abundance of smaller species. Only the small Catopid *Ptomaphagus sericatus* increased significantly ($P(t) < 0.01$) in abundance towards the city centre, whereas none of the other species differed significantly (at the 5% error level) between the rural and the city sites. Rather larger necrophagous species like *Geotrupes stercorosus* (Geotrupidae) and five species of the genus *Nicrophorus* (Silphidae) decreased. At the rural sites, these species accounted for 25 ± 4% of the total abundance. In the city periphery they decreased to 15% and in the centre to 10% of the total abundance. Only two of the five *Nicrophorus* occurred in the city.

Neither the SSD shape nor the mean body length of the predators changed along the urban rural gradient (Table 1). Unexpectedly, and despite the increasing abundance of smaller species and the absence of three larger *Nicrophorus* species, mean body length of the necrophages increased towards the city centre. The SSD skew vanished and the new mode of the distribution was at a lower body length (Table 1). An initially left-skewed SSD became symmetrical towards the city due to an increase in mean body size, while the mode remained unchanged.

Lorenz curves give us an impression of how body weight and abundances are distributed across sites. NMS is better suited to grouping sites according to body size and abundances. We were surprised to see how well NMS was able to group the study sites according to the distribution of biomass. Forested and open rural sites and (to a lesser extent) the city sites form distinct units for necrophages and predatory beetles with respect to abundance and body size (Fig. 5). This was not obvious from the SSDs and the analysis of the spacing of body sizes. Because biomass is closely related to total energy use, our finding adds to the view that community structure is at least in part under the control of energy availability or diversity (Ernest 2005; Vedeller et al. 2006).

Body size distributions of the open rural sites appeared to be more similar to the city than to the forested sites (Table 1). Similar patterns have been previously reported with respect to species composition (cf. McIntyre 2000 for a review; Sadler et al. 2006). While species composition directly affects size distributions, this should also influence the distribution of body sizes. Hence our findings appear to be in line with the notion that cities accumulate species that favour open and often warmer sites. However, we are not aware of any study that explicitly studies body size distributions of open and forested sites as sources for urban arthropod communities.

The present results allow us to answer our five initial questions. The decreasing body size hypothesis cannot be generalized. In contrast to the mostly predatory ground beetles for which this hypothesis was formulated (Szyszko 1983; Gray 1989; but see Lövei and Magura 2004), the mean body size of our carrion-visiting predator assemblages (mostly rove beetles) did not decrease towards the city centre. SSDs of carrion-visiting beetles differed between trophic groups, while those of necrophagous species were mostly left-skewed. These findings also contrast with the common view that SSDs should be right-skewed (Kozłowski and Gawelczyk

2002). Disturbance could not be unequivocally related to body size distribution. While the body size distributions of necrophagous species changed along the disturbance gradient, that of predators remained unaffected. Lastly, the hypothesis that disturbance increases interspecific competition, which should then result in more regular body-size spacing, was only partially corroborated by our data, since it was only found to hold for the necrophages.

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