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Body size inequality of carabids along an urbanisation gradient
Unterschiede der Körpergröße bei Carabiden entlang eines Urbanisationsgradienten

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Lorenz asymmetry coefficient

Summary

Analysis of size inequality can shed light on coexistence mechanisms and help to interpret patterns in assemblages. We tested several measures for their power to evaluate changes in carabid body size along an urbanisation gradient (city park–suburban area–rural), representing decreasing intensities of human disturbance. Carabids were collected by pitfall traps over two full activity periods in lowland oak forest patches in and near the city of Debrecen, Eastern Hungary.

The average value of skewness was largest in the urban areas compared to the suburban and rural ones, indicating that small individuals were more prominent in the urban areas. The Gini coefficient also decreased from urban towards rural areas, suggesting that inequality in body size of the carabid assemblages decreased along the gradient. However, neither of these trends was significant. The Lorenz asymmetry coefficient was significantly higher in rural areas compared to suburban and urban areas indicating that there was a significant difference in inequality and/or asymmetry of body size across the gradient. This difference was primarily due to more individuals with larger body size in rural area. We suggest that the observed variation in carabid body size along the gradient is related to habitat alteration caused by urbanisation.

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Zusammenfassung

Die Analyse von Größenunterschieden kann die Koexistenzmechanismen beleuchten und helfen, Muster von Ansammlungen zu interpretieren. Wir untersuchten verschiedene Parameter auf ihr Potenzial die Veränderungen der Körpergröße bei Carabiden entlang eines Urbanisationsgradienten (Stadtpark–Vorstadtgebiet–ländlich) zu erklären, der eine abnehmende Intensität der anthropogenen Störung repräsentierte. Die Carabiden wurden in Bodenfallen über zwei vollständige aktive Perioden in Tieflandeichenwäldern und in der Nähe der Stadt Debrecen im östlichen Ungarn gesammelt.

Der durchschnittliche Wert der Schiefe war in den städtischen Gebieten im Vergleich zu den vorstädtischen und ländlichen am größten und wies darauf hin, dass kleine Individuen in den städtischen Gebieten mehr hervortraten. Der Gini-Koeffizient verringerte sich ebenfalls von den städtischen zu den ländlichen Gebieten und läßt vermuten, dass die Unterschiede in der Körpergröße in den Carabiden-Ansammlungen entlang des Gradienten abnahmen. Keiner dieser Trends war jedoch signifikant. Der Lorenz-Asymmetrie-Koeffizient war in den ländlichen Gebieten im Vergleich zu den vorstädtischen und städtischen Gebieten signifikant größer und wies darauf hin, dass es einen signifikanten Unterschied in den Körpergrößeunterschieden und/oder in der Asymmetrie der Körpergröße entlang des Gradienten gab. Dieser Unterschied war vor allem darauf zurückzuführen, dass es in den ländlichen Bereichen mehr Individuen mit einer größeren Körpergröße gab. Wir vermuten, dass die beobachtete Variation in der Körpergröße der Carabiden entlang des Gradienten mit der durch die Urbanisation verursachten Veränderung der Habitate verbunden ist.

Introduction

Relationships between body size and the structure of animal assemblages have been the focus of much attention in ecological studies. Body size is correlated with many aspects of life history (reproduction rate, dispersal, development time, etc.) (Peters, 1983). Body size also has a significant impact on ecological interactions, resource use, and more indirectly, the period of activity, habitat suitability, and numerous other parameters (Peters, 1983). A change in body size, either in individual species, or in the size distribution of the species present in a habitat is also a parameter potentially indicating different types of environmental stress (McGeoch, 1998).

A number of anthropogenic activities, including farming, forestry and urbanisation, have a significant impact on the environment and create patchworks of modified land types that exhibit similar patterns throughout the world (Poschlod, Bakker, & Kahmen, 2005; Ulrich & Buszko, 2004). Global urbanisation has caused the loss of vast amounts of habitat and caused major modifications of the environmental conditions (Tarvainen, Markkola, & Strommer, 2003). However, little is known on whether or not these changes affect biodiversity in similar ways across the globe (Niemelä et al., 2000). In 1998, an international collaborative effort to search for generalisations in urbanisation impacts on biodiversity was initiated. The project, called Globenet (Niemelä et al., 2000), examines urban–suburban–rural gradients, using a common methodology and target invertebrate taxon (ground beetles; Fam. Carabidae) (Niemelä et al., 2000). This taxon was selected, because carabids are especially useful ecological indicators to study environmental impacts, being sensitive to habitat modifications and environmental changes, abundant and sufficiently variable both taxonomically and ecologically (Lövei & Sunderland, 1996). The results published so far focussed mainly on the changes of carabid assemblage composition along the gradient (Niemelä et al., 2002), with some consideration of the effects of urbanisation on body size (Ishitani, Kotze, & Niemelä, 2003; Magura, Tóthmérész, & Molnár, 2004).

Variation in body size has traditionally been described and analysed using the skewness of the size distribution, or other statistics derived from the statistical moments of the distribution (Sokal & Rohlf, 1995). Recently, the focus has shifted toward an emphasis on inequality in size. Several measures of inequality, developed for use in economics (Sen, 1973), have been used to analyse variation in size within assemblages. These measures use the Lorenz curve (Lorenz, 1905), where individuals are ranked by size, and the cumulative proportion of study objects is plotted against the cumulative proportion of their total size on the *y*-axis. If all individuals are equal in size, the Lorenz curve is a diagonal line, called the "line of equality" (Fig. 1). Inequality causes the line to run below this line, and the greater the inequality among the study objects, the lower the curve runs below the line of equality. One approach to quantify this is the Gini coefficient (Dixon, Weiner, Mitchell-Olds, & Woodley, 1987; Gini, 1912; Sen, 1973). However, the Gini coefficient is only related to the size (area) and not the shape of the curve. Thus, the Gini coefficient does not contain all the information in the Lorenz curve. Different Lorenz curves can have the same Gini coefficient (Damgaard & Weiner, 2000; Shumway & Koide, 1995; Weiner & Solbrig, 1984). Therefore, Damgaard and Weiner (2000), to characterise the shape of the Lorenz curve, proposed a so-called "Lorenz asymmetry coefficient". This coefficient characterises an important aspect of the shape of a Lorenz curve: it shows which size classes contribute most to the total inequality of the assemblage (Damgaard & Weiner, 2000).

The new index was illustrated by an example from plant ecology, but we seek to extend its use to the analysis of size relationships in animal assemblages. In this study, we used pitfall data, collected across an urban–suburban–rural gradient over 2 years, to analyse the body size inequality of ground beetle (Carabidae) assemblages. Using measures describing asymmetry and/or inequality of body size pattern in carabid assemblages, a hypothesis, suggested by Szyszko (1983), Gray (1989) and Blake, Foster, Eyre, and Luff (1994) was tested.

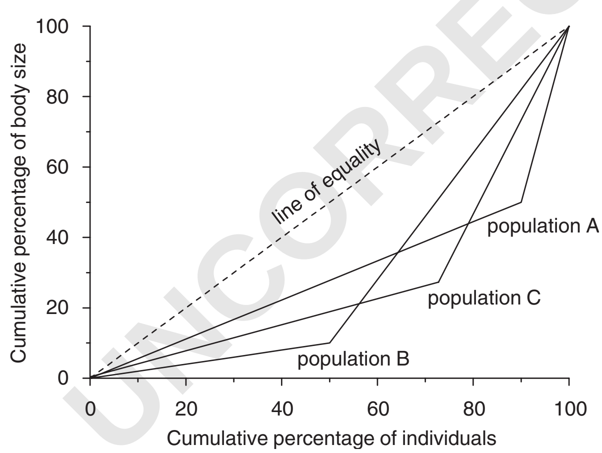

Figure 1. Lorenz curves of three hypothetical populations. All populations have the same Gini coefficient, but different Lorenz asymmetry coefficients. In the case of the population A, the Lorenz asymmetry coefficient (S) is larger than one ($S>1$), in the case of population B, $S<1$, while size distribution in population C is symmetric, leading to $S=1$.

According to this "decreasing body size hypothesis", smaller carabids should be found in habitats with higher disturbance levels than in those with lower disturbance. In our case, the hypothesis predicts that the mean carabid body size should decrease from the rural to the urban area. We found that the Lorenz asymmetry index was the most powerful method to detect trends in size along the gradient.

Material and methods

Characterising the body size distributions

The following measures were used to describe the asymmetry and/or inequality of body size pattern in carabid assemblages.

(1) Skewness. The asymmetry of a univariate continuous distribution is commonly measured by the classical skewness coefficient (Sokal & Rohlf, 1995), which is defined as

$$g = \frac{\Sigma_{i=1}^{n}(x_i - \bar{x})^3}{ns^3},$$

where n is the number of individuals, x_i is the body size of individuals i, $\bar{x}$ is the mean body size and s is the standard deviation of body size. A symmetric distribution has zero skewness, i.e. $g=0$. An asymmetric distribution with a longer left tail has negative skewness (in our case: large individuals are dominant), while a positive g indicates skewness to the right (smaller individuals are dominant).

(2) Medcouple. Since the skewness estimator is based on the first three moments of the data set, it is strongly influenced by the presence of outliers; thus, a robust measure of skewness, the medcouple (Brys, Hubert, & Struyf, 2004) was also used. It has a 25% breakdown value and a bounded influence function. The possible values of medcouple range from -1 to 1.
For notational convenience, the elements of the data set are sorted such that $x_{[1]} \leqslant x_{[2]} \leqslant \cdots \leqslant x_{[n]}$. Let $\mathrm{med}(X_n)$ denote the median of the data set X_n, defined as

$$\mathrm{med}(X_n) = \begin{cases} (x_{[n/2]} + x_{[n/2]+1})/2 & \text{if } n \text{ is even,} \\ x_{[n+1]/2} & \text{if } n \text{ is odd.} \end{cases}$$

The medcouple is defined as

$$\mathrm{MC}_n = \mathrm{med}\{h(x_{[i]}; x_{[j]});\ \ x_{[i]} \leqslant \mathrm{med}(X_n) \leqslant x_{[j]}\},$$

where the kernel function h is defined by

$$h(x_{[i]};x_{[j]}) = \frac{(x_{[i]} - \mathrm{med}(X_n)) - (\mathrm{med}(X_n) - x_{[j]})}{x_{[i]} - x_{[j]}}$$

for all $x_{[i]} \neq x_{[j]}$. Brys et al. (2004) also described a fast algorithm to compute the value of the medcouple.

(3) Gini coefficient. A traditional graphical approach to measure inequality in size distribution is the Lorenz curve (Sen, 1973; Weiner & Solbrig, 1984). Individuals are ranked by size and the cumulative proportion of individuals is plotted against the corresponding cumulative proportion of their total size. When all individuals are of the same size, the Lorenz curve is a straight diagonal line, called the line of equality. If there is any inequality in size, the Lorenz curve runs below the line of equality (Fig. 1). The total amount of size inequality can be quantified by the Gini coefficient (Gini, 1912), which is the ratio between the area enclosed by the line of equality and the Lorenz curve, and the total triangular area under the line of equality. The Gini index of aggregation is based on ordered data by increasing body size as follows (Dixon et al., 1987):

$$G = \frac{\sum_{i=1}^{n}(2i - n - 1)x_{[i]}}{n^2 \bar{x}},$$

where n is the number of individuals, $x_{[i]}$ is the ordered body size of individuals i and $\bar{x}$ is the mean body size. The Gini coefficient calculated by the above equation should be multiplied with $n/(n-1)$ to obtain an unbiased estimate (Glasser, 1962).

The Gini coefficient ranges from a minimum value of zero, if all individuals have the same body size, to a maximum of one in a hypothetical assemblage in which every individual except one has a size of zero. However, it has been demonstrated (Damgaard & Weiner, 2000; Shumway & Koide, 1995; Weiner & Solbrig, 1984) that different Lorenz curves (assemblages with different inequality in size) can have the same Gini coefficient (example on Fig. 1).

(4) Lorenz asymmetry coefficient. To complement the above-mentioned Gini coefficient, Damgaard and Weiner (2000) proposed the Lorenz asymmetry coefficient, to quantify the asymmetry of the Lorenz curve. The coefficient (S) can be calculated from the ordered body size data using the following equations (Damgaard & Weiner, 2000):

$$S = F(\hat{x}) + L(\hat{x}) = \frac{m + \delta}{n} + \frac{L_m + \delta x'_{m+1}}{L_n},$$

where

$$\delta = \frac{\bar{x} - x'_m}{x'_{m+1} - x'_m}$$

and $\bar{x}$ is the mean body size, m is the number of individuals with a body size less than $\bar{x}$, L_m is the cumulative body size of individuals with a body size less than $\bar{x}$, and L_n is the cumulative body size of all individuals.

When $S = 1$, the Lorenz curve of the assemblage is symmetric, while other S values represent asymmetric Lorenz curves. When $S > 1$, most of the inequality within the assemblage is due to the largest individuals, which disproportionately contributes to the cumulative body size (mass) of the assemblage. When $S < 1$, the inequality demonstrated in the assemblage is due primarily to the relatively large number of small individuals (Fig. 1; Damgaard & Weiner, 2000).

Study area and sampling methods

Ground beetles were studied along an urban–suburban–rural gradient in Debrecen (Eastern Hungary), the second largest city of the country (Magura et al., 2004). The urban, suburban and rural sampling areas were all part of a once-continuous forest (Nagyerdő Forest Reserve) bordering the city. All areas were situated in continuous patches of old forest (>100 years) dominated by English oak (*Quercus robur*). The typical, native forest association of the sampling sites was *Convallario-Quercetum*. The criterion for distinguishing sampling areas (urban, suburban, rural) was the ratio of the built-up area to the natural habitats. The area of the built-up environment and the natural habitats was measured by the ArcView GIS program using an aerial photograph. In the urban area the built-up area exceeded 60%, in the suburban area it was approximately 30%, while in the rural area the built-up area was 0%. The forest fragments in the urban area were parks, where several paths with asphalt surfaces had been created and the shrub layer was strongly thinned. In the suburban area fallen trees were removed. There were occasional, low-intensity forestry management operations in the rural site. Distance between the sampling areas (urban, suburban, rural) was at least 1 km, as prescribed by the general methodology of the Globenet project (Niemelä et al., 2000).

Four sites, at least 50 m from each other (in order to achieve independence, see Digweed, Currie, Cárcamo, & Spence, 1995), were selected within each sampling area. Carabids were collected at each of the four sites of the three sampling areas using pitfall traps over two full activity periods in 2001 and 2002. Ten traps were placed randomly at least 10 m apart at each site. This resulted in a total of 120 traps scattered along the urban–rural gradient (3 area × 4 sites × 10 traps). Each pitfall trap was at least 50 m from the nearest forest edge, in order to avoid edge effects (Molnár, Magura, Tóthmérész, & Elek, 2001). Further information on trap design, placement, mode of operation as well as the general description of the collected assemblages are given by Magura et al. (2004). For the present paper, we only used body size, collected from the literature (Hůrka, 1996), and the number of individuals in the catch. For species where minimum and maximum sizes were given, we used the mid-range value (see Table 1).

To test for differences in the measures describing asymmetry and/or inequality of body size pattern in carabid assemblages among the three sampling areas, repeated measures analyses of variance (ANOVA) were performed (Sokal & Rohlf, 1995). When the ANOVA revealed a significant difference between the means, LSD (least significant difference) tests were performed for multiple comparisons among means. The analyses were carried out using the R package (R Development Core Team, 2004) and the SPSS-PC program.

Results

In both years, values of skewness were largest in the urban areas and smallest in the suburban ones indicating that more small individuals were present in the urban areas than in either of the other two (Fig. 2A). The differences, however, were not statistically significant (Table 2). Similar results were obtained with the robust measure of skewness, the medcouple. The values were highest in the urban areas and lowest in the suburban ones (Fig. 2B). These differences were considered significant (Table 2). The Gini coefficient was highest in the urban areas, and decreased towards the rural areas, suggesting that body size inequality of carabid assemblages was largest in the urban parks, and decreased along the urbanisation gradient (Fig. 2C). Here the year × treatment interaction was significant, but neither of the component factors was (Table 2). The Lorenz coefficients had values $S > 1$ for all situations, indicating the importance of large individuals for the shape of the Lorenz curve. In urban areas, the value was very close to $S = 1$ in both years. This is a characteristic of a nearly symmetric Lorenz curve. In both years, the rural areas had the highest S values, and the suburban areas had intermediate ones (Fig. 2D). The differences in the Lorenz asymmetry coefficients among the studied areas were significant (Table 2). The value of this coefficient was significantly higher in the rural areas compared to the suburban and urban areas (differences between these two last areas were not statistically significant). Therefore, the significant difference in the shape of the Lorenz curves was caused primarily by a higher number of individuals with larger body size in the rural area vs. the other two areas under higher degree of urbanisation.

Discussion

Analysing inequality has a longer history in plant than animal studies. To describe inequality in plant size, several studies (Creed, Kain, & Norton, 1998; Ditommaso & Watson, 1997; Zammit & Zedler, 1993) used skewness derived from the statistical moments of the size distribution. Several other papers used the Gini coefficient to measure inequality in plant size or biomass (Hanley & Groves, 2002; He, Ma, Brown, & Lynch, 2005; Leiss & Müller-Schärer, 2001; Ramstad & Hestmark, 2001; Shumway & Koide, 1995; Wilson & Gurevitch, 1995). For plants, Damgaard and Weiner (2000) calculated the Lorenz asymmetry coefficient for data from Shumway and Koide (1995) to interpret the effect of mycorrhizae and plant density on the number of capsules produced by *Abutilon theophrasti* (Fam. Malvaceae) individuals. They were able to show that the reported inequality in the number of capsules when the plants contained mycorrhizae was caused by the increased importance of individuals with high capsule production (Damgaard & Weiner, 2000). This, however, remains the only example of using the proposed index.

Skewness is the only method used to evaluate inequality and/or asymmetry in size distribution of animal populations or assemblages (Gomez & Espadaler, 2000; Gregory, 2000; Knouft, 2004; Kozlowski & Gawelczyk, 2002; Novotny & Kindlmann, 1996; Poulin & Morand, 1997). In the present paper, we extended the range of methods applied to analyse the inequality of animal body size distribution using two other parameters (the Gini coefficient and the Lorenz asymmetry coefficient) and showed that the Lorenz asymmetry coefficient, S, is a powerful method for studies describing and interpreting variations in body size.

Published studies in the international Globenet project characterised changes in the carabid body size distribution along the urban–suburban–rural

Table 1. A list of the carabid species, their body size, and the number of individuals collected in the urban, suburban and rural sampling areas during the two study years near Debrecen, Eastern Hungary

Species	Body size (mm)	Urban	Suburban	Rural
Agonum lugens	9.0	2	0	0
Amara anthobia	6.2	10	0	0
Amara communis	6.5	9	0	0
Amara consularis	8.3	0	1	2
Amara convexior	7.7	113	26	47
Amara familiaris	6.3	16	5	4
Amara lucida	5.6	1	0	0
Amara ovata	8.6	10	0	0
Amara saphyrea	8.8	10	16	39
Amara similata	8.6	2	2	2
Anchomenus dorsalis	6.6	1	0	0
Anisodactylus nemorivagus	8.9	52	0	0
Anisodactylus signatus	11.8	1	1	0
Asaphidion flavipes	4.3	2	0	0
Badister bullatus	5.2	11	1	0
Badister lacertosus	6.3	5	15	1
Badister meridionalis	6.7	8	2	0
Bembidion lampros	3.4	38	0	3
Calathus erratus	9.5	2	0	1
Calathus fuscipes	11.1	26	0	3
Calathus melanocephalus	7.1	1	0	0
Calosoma inquisitor	20.0	0	0	10
Carabus convexus	17.0	1	107	124
Carabus granulatus	19.0	6	1	6
Carabus ullrichi	27.0	1	0	0
Carabus violaceus	28.0	75	78	237
Clivina fossor	5.9	3	0	0
Diachromus germanus	8.4	1	0	0
Harpalus distinguendus	9.5	0	1	0
Harpalus latus	9.1	14	1	24
Harpalus luteicornis	7.1	5	20	1
Harpalus tardus	9.4	104	86	69
Harpalus xanthopus winkleri	7.1	21	10	3
Leistus ferrugineus	6.8	0	0	1
Licinus depressus	10.4	7	5	1
Notiophilus biguttatus	4.9	2	0	0
Notiophilus palustris	5.1	5	2	6
Notiophilus rufipes	5.3	38	14	7
Ophonus nitidulus	9.6	1	2	42
Ophonus schaubergerianus	8.8	0	0	1
Oxypselaphus obscurus	5.5	0	1	1
Panagaeus bipustulatus	7.2	7	5	0
Platyderus rufus	6.3	76	41	79
Poecilus cupreus	11.8	3	0	0
Poecilus versicolor	10.5	1	0	0
Pseudoophonus griseus	10.1	2	0	1
Pseudoophonus rufipes	13.1	10	26	19
Pterostichus anthracinus	11.2	5	3	0
Pterostichus macer	12.9	1	0	0
Pterostichus melanarius	15.7	58	3	1
Pterostichus melas	14.9	2	0	3
Pterostichus minor	7.6	0	1	0
Pterostichus niger	18.4	22	15	23
Pterostichus oblongopunctatus	11.5	117	454	1505
Pterostichus ovoideus	7.1	1	0	0
Pterostichus strenuus	6.0	27	52	11

Table 1. (*continued*)

Species	Body size (mm)	Urban	Suburban	Rural
Stomis pumicatus	7.5	1	15	27
Synuchus vivalis	7.2	7	6	146
Trechus quadristriatus	3.5	0	1	1

Species sequence is alphabetical.

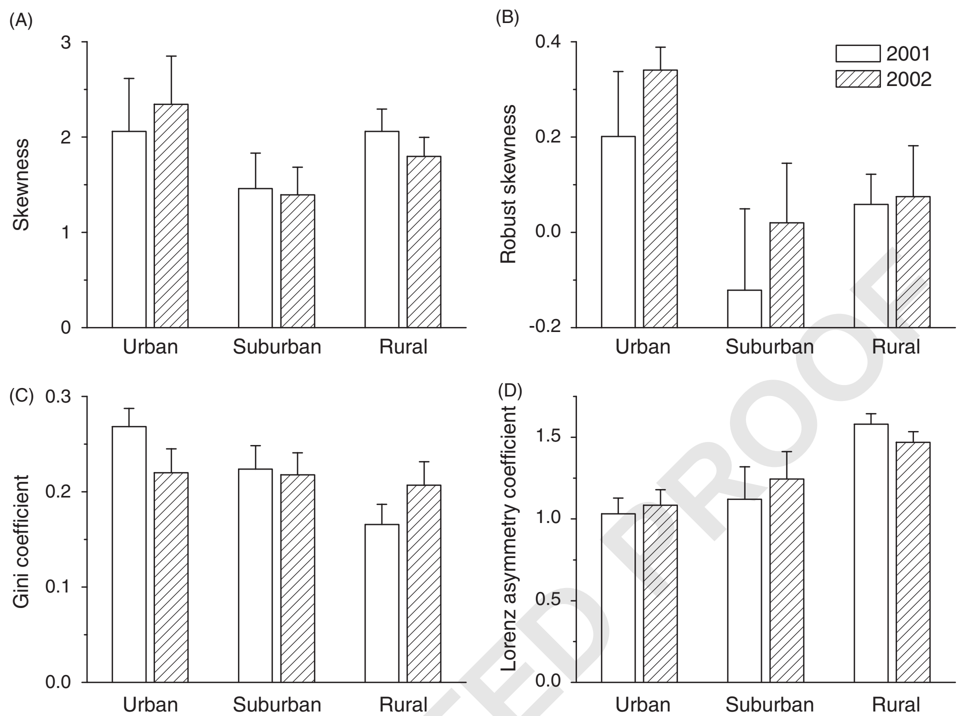

Figure 2. Average values ($\pm$S.E.) of the skewness (A), the robust skewness (B), the Gini coefficient (C) and the Lorenz asymmetry coefficient (D) for the urban, suburban and rural carabid assemblages in the two study years.

gradient using either the distribution among different, arbitrary size classes (Alaruikka, Kotze, Matveinen, & Niemelä, 2002; Ishitani et al., 2003) or the mean body size of the species weighted by their respective abundance (Gaublomme, Dhuyvetter, Verdyck, & Desender, 2005; Magura et al., 2004; Niemelä et al., 2002). In Finland, Alaruikka et al. (2002) investigating the changes of carabid body size across an urbanisation gradient concluded that medium- to large-sized carabid individuals were more likely to be collected in the rural sites than in urban forest fragments. In Japan, there are no large and only few medium-sized specialist species in the urban environment, while many specimens of medium-sized and some large-sized specialist species occur in the suburban and rural sites (Ishitani et al., 2003). Mean carabid body size changed significantly from small values in the urban area to larger ones in both suburban and rural areas in Bulgaria (Niemelä et al., 2002), Hungary (Magura et al., 2004) and Belgium (Gaublomme et al., 2005). There was a marginally significant change in the same direction along the same gradient in Finland, but none in Canada (Niemelä et al., 2002). However, not only body size of the carabid assemblages may change across an urbanisation gradient; there could be changes among different populations of the same species. The body size of *Carabus nemoralis* decreased significantly from the rural surroundings of Hamburg, Germany, towards the city centre (Weller & Ganzhorn, 2004).

The present study, using a more sophisticated method (the Lorenz asymmetry coefficient), not only proved the existence of a significant change in inequality of carabid body size across the urban–suburban–rural gradient, but indicated that this difference was primarily due to an increase in the contribution of individuals with larger body size in the rural area. The mean body size of ground beetles also increased (Magura et al., 2004), but

Table 2. The results of repeated-measures ANOVA for the values describing asymmetry and/or inequality of body size pattern in carabid assemblages

Source	SS	df	MS	F	p	LSD test
Skewness						
Tests of within-subjects contrasts						
Year	0.001	1	0.001	0.008	0.931	
Year × Area	0.306	2	0.153	0.890	0.444	
Error	1.547	9	0.172			
Tests of between-subjects effects						
Area	2.473	2	1.237	1.235	0.336	
Error	9.011	9	1.001			
Robust skewness						
Tests of within-subjects contrasts						
Year	0.058	1	0.058	1.099	0.322	
Year × Area	0.020	2	0.010	0.192	0.828	
Error	0.479	9	0.053			
Tests of between-subjects effects						
Area	0.424	2	0.212	3.868	0.061	$U>S$
Error	0.493	9	0.055			
Gini coefficient						
Tests of within-subjects contrasts						
Year	0.0001	1	0.0001	0.142	0.715	
Year × Area	0.008	2	0.004	5.073	0.033	
Error	0.007	9	0.0007			
Tests of between-subjects effects						
Area	0.014	2	0.007	1.974	0.195	
Error	0.031	9	0.003			
Lorenz asymmetry coefficient						
Tests of within-subjects contrasts						
Year	0.003	1	0.003	0.044	0.839	
Year × Area	0.058	2	0.029	0.469	0.640	
Error	0.558	9	0.062			
Tests of between-subjects effects						
Area	0.932	2	0.466	7.315	0.013	$U=S<R$
Error	0.573	9	0.064			

Year = the effect of study year (2001 and 2002), Area = the urban, suburban and rural sampling areas. Results of the LSD test indicate which area(s) differ(s) significantly ($p<0.05$) from the others; for example $U=S<R$ indicates that the measured value was significantly higher in the rural area than in the urban and suburban area (these two areas, however, were not different).

this change can result from a decrease in the importance of small species, from the increase in medium-sized or large species, or a combination of these. By evaluating the mean body size, we cannot distinguish among these possibilities. The Lorenz asymmetry coefficient allowed us to demonstrate which of these theoretical possibilities was responsible for the observed effect. The larger carabid body size in the less disturbed area (rural area) and the smaller body size in the moderately or highly disturbed areas (suburban and urban areas) could be explained by the hypothesis postulated by Szyszko (1983), Gray (1989) and Blake et al. (1994).

Szyszko (1983), studying the regeneration of pine plantations after clear-cutting in Poland, suggested and used the mean individual biomass (MIB) index. This index is simply calculated as the ratio of the total fresh body mass of the catch in a trap, divided by the number of carabid individuals caught. Szyszko (1983) showed that as regeneration in the plantation proceeds, the average value of the MIB index also increases. Mean body size is positively related to body mass, and thus the conclusion is that the mean body size in carabid assemblages will also increase. Gray (1989) hypothesised that the mean body size of species should decrease from undisturbed towards disturbed habitats. Carabid assemblages of differently managed grasslands gave support to this hypothesis (Blake et al., 1994). Highly disturbed areas support carabid assemblages with species of smaller average body size than do less disturbed sites (Blake et al., 1994; Grandchamp, Niemelä, & Kotze, 2000; Holliday, 1991; Magura, Elek, & Tóthmérész, 2002; Ribera, Dolédec, Downie, & Foster, 2001; Šustek, 1987). The causes of this can be manifold. Carabids have ground-living larvae that are weakly chitinised, limited in mobility, and thus more sensitive to changing conditions than adults (Lövei & Sunderland, 1996). Disturbance will frequently create unfavourable conditions for ground beetle adults as well as larvae, when their densities decrease (Thorbek & Bilde, 2004) and species may become locally extinct. Small-sized carabid species may suffer less mortality during such disturbance events. Their densities are also usually higher than that of large-sized species (Luff, 2002), so they have a lower probability of local extinction. Small species are more often winged than are large-sized species (Ribera et al., 2001). Consequently, small species are more vagile than large species and can colonise disturbed and unstable areas more easily (Thiele, 1977). Smaller species may also need fewer resources and/or may develop faster than large species (Peters, 1983). In carabids, large species have longer larval periods, making them more vulnerable to disturbance events (Kotze & O'Hara, 2003). Small species can use the small ''windows of suitability'' to survive in the disturbed habitat. Lövei and Sunderland (1996) also call attention to the importance of larvae to explain trends in adults.

Along the studied urbanisation gradient, the degree of disturbance is higher in the urban (paved paths, thinned shrub layer, intensive landscape management) and in the suburban area (management of moderate intensity, e.g. fallen trees are removed) than in the rural area (rare occasions of intervention, low intensity management). Disturbance caused by urbanisation appears to eliminate favourable microsites for forest species with larger body size and create altered, relatively homogeneous micro-habitats invaded by small-sized species capable of flying. All these habitat alterations accompanied by urbanisation contributed to the observed variation in carabid body size across the urban–suburban–rural gradient.

Using the Lorenz asymmetry coefficient (Damgaard & Weiner, 2000), we were able to more completely analyse the size distributions of the ground beetle assemblages along the urbanisation gradient. This index has proven to be more powerful than more traditional methods such as skewness, robust skewness (medcouple), or the Gini coefficient. The biological interpretation of the index is not problematic, and we suggest that it is a useful tool for future studies of size/biomass distribution in animal assemblages.

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References

Alaruikka, D. M., Kotze, D. J., Matveinen, K., & Niemelä, J. (2002). Carabid and spider assemblages along an urban to rural gradient in Southern Finland. *Journal of Insect Conservation*, *6*, 195–206.

Blake, S., Foster, G. N., Eyre, M. D., & Luff, M. L. (1994). Effects of habitat type and grassland management practices on the body size distribution of carabid beetles. *Pedobiologia*, *38*, 502–512.

Brys, G., Hubert, A., & Struyf, A. (2004). A robust measure of skewness. *Journal of Computational & Graphical Statistics*, *13*, 996–1017.

Creed, J. C., Kain, J. M., & Norton, T. A. (1998). An experimental evaluation of density and plant size in two large brown seaweeds. *Journal of Phycology*, *34*, 39–52.

Damgaard, C., & Weiner, J. (2000). Describing inequality in plant size or fecundity. *Ecology*, *81*, 1139–1142.

Digweed, S. C., Currie, C. R., Cárcamo, H. A., & Spence, J. R. (1995). Digging out the digging-in effect of pitfall traps: influences of depletion and disturbance on catches of ground beetles (Coleoptera: Carabidae). *Pedobiologia*, *39*, 561–576.

Ditommaso, A., & Watson, A. K. (1997). Effect of the fungal pathogen, *Colletotrichum coccodes*, on *Abutilon theophrasti* height hierarchy development. *Journal of Applied Ecology*, *34*, 518–529.

Dixon, P. M., Weiner, J., Mitchell-Olds, T., & Woodley, R. (1987). Bootstrapping the Gini coefficient of inequality. *Ecology*, *6*, 1548–1551.

Gaublomme, E., Dhuyvetter, H., Verdyck, P., & Desender, K. (2005). Effects of urbanisation on carabid beetles in old beech forests. In: Lövei, G. L., & Toft, S. (Eds.), European carabidology 2003. Proceedings of the 11th European carabidologists' meeting, DIAS Report, Vol. 114, pp. 111–123.

Gini, C. (1912). Variabilita e mutabilita. In E. Pizzetti, & T. Salvemini (Eds.), *Memorie di metodologica statistica* (pp. 211–382). Rome, Italy: Eredi Virgilio Veschi.

Glasser, G. J. (1962). Variance formulas for the mean difference and coefficient of concentration. *Journal of the American Statistical Association*, *57*, 648–654.

Gomez, C., & Espadaler, X. (2000). Species body-size distribution and spatial scale in Iberian ants. *Vie et milieu*, *50*, 289–295.

Grandchamp, A. C., Niemelä, J., & Kotze, J. (2000). The effects of trampling on assemblages of ground beetles (Coleoptera, Carabidae) in urban forests in Helsinki, Finland. *Urban Ecosystems*, *4*, 321–332.

Gray, J. S. (1989). Effects of environmental stress on species rich assemblages. *Biological Journal of the Linnean Society*, *37*, 19–32.

Gregory, R. D. (2000). Abundance patterns of European breeding birds. *Ecography*, *23*, 201–208.

Hanley, M. E., & Groves, R. H. (2002). Effect of the rust fungus *Puccinia chondrillina* TU 788 on plant size and plant size variability in *Chondrilla juncea*. *Weed Research*, *42*, 370–376.

He, Z. X., Ma, Z., Brown, K. M., & Lynch, J. P. (2005). Assessment of inequality of root hair density in *Arabidopsis thaliana* using the Gini coefficient: A close look at the effect of phosphorus and its interaction with ethylene. *Annals of Botany*, *95*, 287–293.

Holliday, N. J. (1991). Species responses of carabid beetles (Coleoptera, Carabidae) during postfire regeneration of boreal forest. *The Canadian Entomologist*, *123*, 1369–1389.

Hůrka, K. (1996). *Carabidae of the Czech and Slovak Republics*. Zlin, Czech Republic: Kabourek.

Ishitani, M., Kotze, D. J., & Niemelä, J. (2003). Changes in carabid beetle assemblages across an urban–rural gradient in Japan. *Ecography*, *26*, 481–489.

Knouft, J. H. (2004). Latitudinal variation in the shape of the species body size distribution: An analysis using freshwater fishes. *Oecologia*, *139*, 408–417.

Kotze, D. J., & O'Hara, R. B. (2003). Species decline – But why? Explanations of carabid beetle (Coleoptera, Carabidae) declines in Europe. *Oecologia*, *13*, 138–148.

Kozlowski, J., & Gawelczyk, A. T. (2002). Why are species' body size distributions usually skewed to the right? *Functional Ecology*, *16*, 419–432.

Leiss, K. A., & Müller-Schärer, H. (2001). Population dynamics of the annual plant *Senecio vulgaris* in ruderal and agricultural habitats. *Basic and Applied Ecology*, *2*, 53–64.

Lorenz, M. O. (1905). Methods for measuring the concentration of wealth. *American Statistics Association*, *9*, 209–219.

Lövei, G. L., & Sunderland, K. D. (1996). Ecology and behavior of ground beetles (Coleoptera: Carabidae). *Annual Review of Entomology*, *41*, 231–256.

Luff, M. L. (2002). Carabid assemblage organisation and species composition. In J. M. Holland (Ed.), *The agroecology of carabid beetles* (pp. 41–79). Andover, UK: Intercept.

Magura, T., Elek, Z., & Tóthmérész, B. (2002). Impacts of non-native spruce reforestation on ground beetles. *European Journal of Soil Biology*, *38*, 291–295.

Magura, T., Tóthmérész, B., & Molnár, T. (2004). Changes in carabid beetle assemblages along an urbanisation gradient in the city of Debrecen, Hungary. *Landscape Ecology*, *19*, 747–759.

McGeoch, M. A. (1998). The selection, testing, and application of terrestrial insects as bioindicators. *Biological Reviews*, *73*, 181–201.

Molnár, T., Magura, T., Tóthmérész, B., & Elek, Z. (2001). Ground beetles (Carabidae) and edge effect in oak-hornbeam forest and grassland transects. *European Journal of Soil Biology*, *37*, 297–300.

Niemelä, J., Kotze, J., Ashworth, A., Brandmayr, P., Desender, K., New, T., et al. (2000). The search for common anthropogenic impacts on biodiversity: A global network. *Journal of Insect Conservation*, *4*, 3–9.

Niemelä, J., Kotze, J. D., Venn, S., Penev, L., Stoyanov, I., Spence, J., et al. (2002). Carabid beetle assemblages (Coleoptera, Carabidae) across urban–rural gradients: An international comparison. *Landscape Ecology*, *17*, 387–401.

Novotny, V., & Kindlmann, P. (1996). Distribution of body sizes in arthropod taxa and communities. *Oikos*, *75*, 75–82.

Peters, R. H. (1983). *The ecological implications of body size*. Cambridge: Cambridge University Press.

Poschlod, P., Bakker, J. P., & Kahmen, S. (2005). Changing land use and its impact on biodiversity. *Basic and Applied Ecology*, *6*, 93–98.

Poulin, R., & Morand, S. (1997). Parasite body size distributions: Interpreting patterns of skewness. *International Journal for Parasitology*, *27*, 959–964.

Ramstad, S., & Hestmark, G. (2001). Population structure and size-dependent reproductive effort in *Umbilicaria spodochroa*. *Mycologia*, *93*, 453–458.

R Development Core Team. (2004). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing (http://www.R-project.org).

Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on species traits of ground beetles assemblages. *Ecology*, *82*, 1112–1129.

Sen, A. (1973). *On economic inequality*. Oxford, UK.: Clarendon.

Shumway, D. L., & Koide, R. T. (1995). Size and reproductive inequality in mycorrhizal and nonmycorrhizal populations of *Abutilon theophrasti*. *Journal of Ecology*, *83*, 613–620.

Sokal, R. R., & Rohlf, F. J. (1995). *Biometry*. New York, USA: Freeman.

Šustek, Z. (1987). Changes in body size structure of carabid communities (Coleoptera, Carabidae) along an urbanisation gradient. *Biológia (Bratislava)*, *42*, 145–156.

Szyszko, J. (1983). *State of Carabidae (Col.) fauna in fresh pine forest and tentative valorisation of this environment*. Warsaw, Poland: Warsaw Agricultural University Press.

Tarvainen, O., Markkola, A. M., & Strommer, R. (2003). Diversity of macrofungi and plants in Scots pine forests along an urban pollution gradient. *Basic and Applied Ecology*, *4*, 547–556.

Thiele, H. U. (1977). *Carabid beetles in their environments*. New York, USA: Springer.

Thorbek, P., & Bilde, T. (2004). Reduced numbers of generalist arthropod predators after crop management. *Journal of Applied Ecology*, *41*, 526–538.

Ulrich, W., & Buszko, J. (2004). Habitat reduction and patterns of species loss. *Basic and Applied Ecology*, *5*, 231–240.

Weiner, J., & Solbrig, O. T. (1984). The meaning and measurement of size hierarchies in plant populations. *Oecologia*, *61*, 334–336.

Weller, B., & Ganzhorn, J. U. (2004). Carabid beetle community composition, body size, and fluctuating asymmetry along an urban–rural gradient. *Basic and Applied Ecology*, *5*, 193–201.

Wilson, C., & Gurevitch, J. (1995). Plant size and spatial pattern in a natural population of *Myosotis micrantha*. *Journal of Vegetation Science*, *6*, 847–852.

Zammit, C. A., & Zedler, P. H. (1993). Size structure and seed production in even-aged populations of *Ceanothus greggii* in mixed chaparral. *Journal of Ecology*, *81*, 499–511.