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Changes in carabid beetle assemblages across an urban-rural gradient in Japan

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As part of the international Globenet project, carabid beetles (Coleoptera, Carabidae) were collected using pitfall traps from four urban, four suburban and four rural sites in Hiroshima City, Japan, during the 2001 summer season. In agreement with expectation, carabid abundance and species richness decreased significantly from rural to urban sites. Furthermore, no large, and only few individuals of medium-sized specialist species were collected from the urban environment, while many specimens of medium-sized and some large-sized specialist species were collected from the suburban and rural sites. Hiroshima city was characterised by medium-sized generalist carabids, while the suburbs and the rural environments were characterised by small-sized generalist beetles. These results did not apply at the species level. To summarise, we found a significant effect of urbanisation on the composition of carabid beetle assemblages in Hiroshima City. These changes were similar to those found in previous studies performed in Sofia (Bulgaria), Edmonton (Canada) and Helsinki (Finland). Thus, it appears that urbanisation has some similar and predictable effects on carabid assemblages in various parts of the world.

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Today, most people live in and around cities (Douglas 1992, Vandruff et al. 1995), yet ecological research is focussed on rural areas or wilderness (Niemelä 2000). This scarcity of urban ecological research may be due to the lower value that many ecologists and the public place on urban environments as compared to more pristine environments (see references in Niemelä 2000). This view is exacerbated by the perception that urban areas mainly host generalist and exotic species, species not considered important in regional diversity.

Urban green areas are, however, important from both an ecological and sociological point of view. Like islands, urban environments contain habitat and species combinations not typically found in the surrounding areas (Frankie and Ehler 1978). Urban ecological research is also valuable in that these environments can be compared with the surrounding rural environment, thereby improving our understanding of the effect of humans on nature. A good example is that of air pollution. Ranta (2001) showed that the decrease in mean annual SO_2 concentration in the city of Tampere (Finland) was followed by a rapid recolonisation of lichens on tree trunks. Although sites outside the city still had twice as many lichen species as within the city, this study shows that the health of the urban environment of Tampere has increased substantially since the 1970s.

A way to gauge anthropogenic effects on nature is to study ecosystem structure and function along urban-rural gradients (McDonnell and Pickett 1990). Urban areas are characterised by densely populated, developed and often highly disturbed city centres, surrounded by areas of decreasing development and habitation (Dickinson 1966). Although some studies have shown that

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urban-rural gradients are complex to quantify (see McDonnell et al. 1997, Natuhara et al. 1999, Germaine and Wakeling 2001), the gradient is nevertheless intuitively obvious – most people know what is meant by urban, suburban and rural. This gradient also provides a unique opportunity for scientists to collaborate, as urban-rural gradients are characteristic of many cities around the world.

In 1998, an international collaborative effort to search for anthropogenic impacts on biodiversity was initiated. The project, called Globenet (Niemelä et al. 2000, 2002), applies the gradient approach across urban-rural gradients, using a common methodology and a common invertebrate taxon (carabid beetles). The project focuses on the predictions of Gray (1989). First, that carabid abundance and species richness will decrease with an increase in disturbance (urbanisation). This was shown for carabid beetles in Edmonton (Canada) and Helsinki (Finland), but not in Sofia (Bulgaria) (Niemelä et al. 2002). Second, that the mean body size of the carabid assemblage should decrease with increasing disturbance. In other words, the likelihood of collecting a small-bodied individual (or species) is higher in urban compared to rural sites. Blake et al. (1994) showed that within grasslands, carabid body size decreased as management intensity increased, and Ribera et al. (2001) showed that carabid beetles were smaller in highly managed habitat in Scotland compared to those in less managed sites. This hypothesis was also supported by data collected across an urban-rural gradient in Sofia and Helsinki, but not in Edmonton (Niemelä et al. 2002). Third, we expect to see little change in the number of habitat generalists across the gradient, but do expect to find fewer forest specialists in the urban forests compared to forests in the surrounding rural environment. For example, it should be more likely to collect a carabid beetle specialist (individual or species) in rural compared to urban sites.

In this paper we examine these hypotheses in the Japanese city of Hiroshima.

Materials and methods

Study area and collecting technique

Carabid beetles were collected across an urban-suburban-rural gradient in Hiroshima City in Japan (Fig. 1). Hiroshima City is built on the delta of River Ota. Rapid urbanisation occurred during the 1960s, and today the city is highly populated with over 1 100 000 inhabitants at a density of 1515 km^{-2}. Four sites were selected in the urban area of Motoujina, four in the suburban area of Takedayama, and four in the rural area of Gongenzan (Fig. 1). Urban Motoujina is dominated by secondary forests of broad-leaf evergreen trees (*Quercus glauca* Thunb. ex Murray, *Cartanopsis cuspidate* (Thunb. ex Murray), *Machilus thunbergii* Sieb. et Zucc.). This preservation area is used for recreational purposes. The suburban Takedayama study area is also dominated by secondary forest of broad-leaf deciduous trees (*Quercus serrata* Thunb. ex Murray, *Quercus variabilis* Blume) and pine trees (*Pinus densiflora* Sieb. et Zucc.). This study area is bordered by a motorway (to the west) and a railway (to the east), and is characterised by a longstanding industrial site and residential areas. Rural Gongenzan is characterised by secondary forest of broad-leaf deciduous trees (*Quercus serrata* Thunb. ex Murray, *Alnus sieboldiana* Matsumura), and is used for hiking and for the observation of wildlife.

We placed 10 pitfall traps (10 m apart) at each site, resulting in a total of 120 traps across the urban-rural gradient in compliance with the Globenet programme protocol (Niemelä et al. 2000, 2002, <www.helsinki.fi/science/globenet/>). The traps were 85 mm in mouth diameter and 135 mm deep. We placed a plastic square plate (150 × 150 mm) above each trap to prevent rainwater and excess plant material from entering the traps. Collecting started 30 April 2001 and traps were visited every 15 d until 1 October 2001.

Statistical analyses

We used cluster analysis with Bray-Curtis Similarity Index to examine differences in the structure of carabid assemblages between the twelve sites across the urban-rural gradient. The aim of the cluster analysis is to find natural groupings of sites such that sites within a group are more similar to each other than to sites in different groups (Clarke and Warwick 1994).

Biotic distinctness between sites was calculated using a complementarity index (Colwell and Coddington 1994):

$$C_{jk} = \left(\frac{\sum_{i=1}^{S_jk} |X_{ij} - X_{ik}|}{\sum_{i=1}^{S_jk} \max(X_{ij}, X_{ik})} \right) \times 100$$

where X_{ij} and X_{ik} are the presence-absence values for carabid species i in list j and list k. Complementarity (C_{jk}) varies from 0 (when the species lists are identical) to 100% (when the species lists are completely different) (Colwell and Coddington 1994). We compared species lists from urban and suburban sites, from urban and rural sites and from suburban and rural sites.

Using trap-specific data, we employed a nested analysis of variance to test for differences in carabid abundance and species richness between sites and across the urban-rural gradient. The Scheffé unplanned comparisons test was used to investigate differences among means, resulting from the ANOVAs (Sokal and Rohlf 1995). Visual inspection of the data (using normal

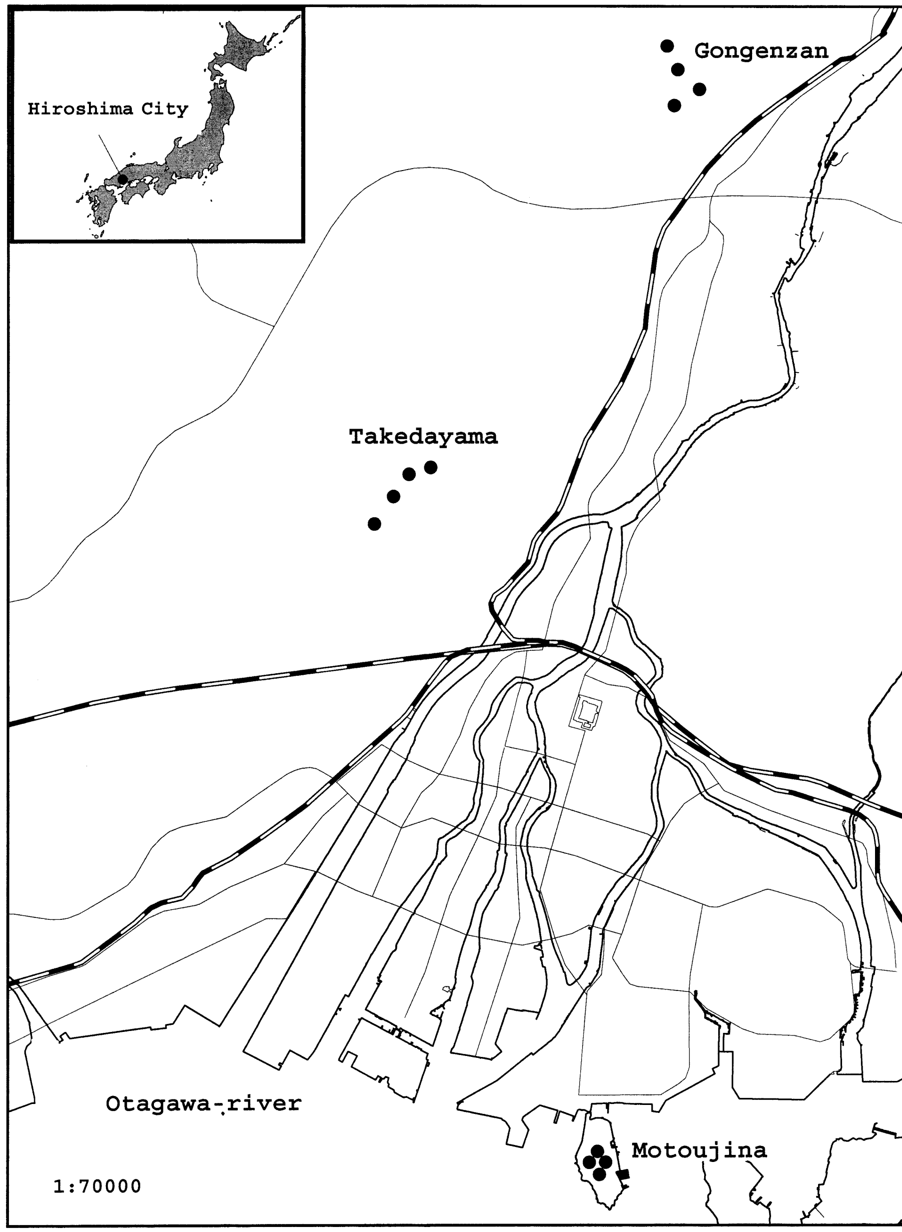

Fig. 1. Map of the study area.

probability plots) suggested that the abundance data should be square-root transformed to approach normality. Species richness data did not need to be transformed.

To test whether larger bodied individuals and species are more likely to occur in the rural surroundings than the urban environment, and to test whether forest specialist individuals and species are more likely to occur in the rural surroundings, we used the generalised linear model (GLM) method. Two GLMs were performed at site level (twelve sites), one on carabid abundance, and one on species richness. Abundance data approached normality after log transformation and the analysis was performed under the assumption of normality. Species richness was not transformed and was performed under the assumption of a Poisson distribution. Factors included in the models were the urban-suburban-rural gradient (U_S_R), site (nested in the gradient factor), beetle specialisation (S_G, forest specialists and habitat generalists, respectively), and body size which was grouped into three size classes; small (5–14.99 mm), medium (15–24.99 mm) and large (25–35 mm). Abundance and species richness were divided into two specialisation categories (S_G), and three size categories (small, medium, large) resulting in 72 degrees of freedom [(2 × 3) × 12 sites].

Results

Overall, 1627 individuals representing 26 carabid and the closely related brachinid species (hereafter collectively called carabids) were collected across the urban-rural gradient in Hiroshima City (Table 1). The urban sites yielded the lowest number of individuals (287) and species (13), while the rural sites yielded the highest numbers (882 individuals and 23 species). Overall, *Carabus japonicus chugokuensis* was the most abundant species collected, making up 26% of the total catch, followed by *Synuchus nitidus* (21%). Urban sites were dominated by *Lesticus magnus* (42% of urban catch) and *Synuchus cycloderus* (30%). Suburban and rural sites were dominated by the same two species: *Synuchus nitidus* (27% in suburban and 22% in rural sites) and *Carabus japonicus chugokuensis* (24% in suburban and 35% in rural sites). The two most dominant species made up a higher proportion of the catch in urban sites (72%) compared to the suburban (51%) or rural (57%) sites, supporting one of Gray's (1989) propositions that more disturbed sites are characterised by one or a few very dominant species, more so than in less disturbed sites.

According to the cluster analysis, carabid assemblage structure of the urban sites was substantially different from suburban and rural sites (Fig. 2). Urban sites clustered to the other sites at 45% similarity. Suburban and rural sites were more alike, but rural sites 1, 3 and 4 separated at 71% similarity from the other suburban and rural sites (Fig. 2). Complementarity values were consistent with the cluster analysis results in that the urban sites showed lower similarity with suburban and rural sites. Urban and suburban sites shared 10 species, with a complementarity value (C_{jk}) of 58%. Urban and rural sites shared 12 species with a C_{jk} of 50%. Suburban and rural sites shared 18 species with a C_{jk} of 31% indicating lower complementarity (i.e. higher similarity) than between urban and suburban or urban and rural sites.

Carabid abundance and species richness changed significantly across the urban-rural gradient. Within site variation was low, but between sites variation (i.e. urban to suburban to rural) was high (Table 2). Both abundance and species richness were low in urban sites, but significantly higher in suburban sites and highest in rural sites (Fig. 3).

As with the nested ANOVAs, the GLMs showed that both carabid abundance and species richness changed significantly across the urban-rural gradient (Table 3). Concerning abundance, there was a significant interaction between carabid body size and specialisation across the urban-rural gradient (U_S_R × Body size × S_G in Table 3) indicating that differences in carabid abundance across the gradient depend on both beetle size and specialisation (Fig. 4). Urban environments were mainly characterised by small-sized forest specialists and medium-sized habitat generalists. In contrast, suburban and rural environments were characterised by medium-sized forest specialists and small-sized habitat generalists. Large-sized forest specialists were absent from the urban environment, but were collected in suburban and rural surroundings (Fig. 4). Concerning species richness, we detected no significant effect of urbanisation on either body size or habitat specialisation (Table 3).

Discussion

Our results support the main predictions made in this study. First, carabid abundance and species richness increased significantly across the Hiroshima City gradient, from a low in urban environments to a high in rural environments. Second, urban environments were characterised by smaller-sized carabid individuals while it was more likely to collect larger-sized individuals in the rural environments. Moreover, the likelihood of collecting a specialist carabid was higher in suburban and rural sites, compared to urban sites. The second and third predictions, however, were not applicable to carabid species richness.

Assemblage structure, abundance and species richness changes across the gradient

Urbanisation had a marked effect on carabid assemblage structure. In particular, urban areas were considerably different from suburban and rural areas, as was shown by cluster analysis. The main reason for this difference is the absence of the large-sized forest specialist *Carabus japonicus chugokuensis* (the most numerous carabid in this study) from urban areas. A similar distinctive division between forest and urban sites was detected by Tonteri and Haila (1990) using a two-way indicator-species analysis (TWINSPAN classification) on vegetation data in Helsinki and its surroundings. Furthermore, Niemelä et al. (2002) found a similar pattern for carabid beetles in Helsinki. This pattern is, however, not universal as little discrimination between urban, suburban and rural sites was found for carabid assemblages in Edmonton (Canada) and Sofia (Bulgaria) (Niemelä et al. 2002). Interestingly, carabid assemblage changes along the urban-to-rural gradient in Helsinki and Hiroshima City are rather similar, although the biogeographical location of the two cities is quite different.

Table 1. Carabid beetles collected across urban-rural gradients in Hiroshima City, Japan. Body size in mm. Specialisation categories: S – forest specialists, G – habitat generalists. U1 – urban site 1, U2 – urban site 2, etc.

	Beetle characteristics		Urban				Suburban				Rural				Total
	Size	Specialisation	U1	U2	U3	U4	S1	S2	S3	S4	R1	R2	R3	R4	
Anisodactylus tricupsidatus Morawitz, 1863	13.2	S			1		1	1	2	1	3		1	1	11
Carabus dehaanii dehaanii Chaudoir, 1848	26.2	S					3	3	3		5	4	4	2	24
Carabus japonicus chugokuensis (Nakane, 1961)	21.1	S					32	29	21	30	90	93	60	70	425
Carabus yaconinus yaconinus Bates, 1873	28.9	G					1								1
Chlaenius abstersus Bates, 1873	14.2	G					1				1	4	1	3	10
Chlaenius micans (F., 1792)	15.9	G					1	2					1		4
Chlaenius naeviger Morawitz, 1862	14.3	G	3	4	3	1	27	23	5	34	38	28	36	47	249
Damaster blaptoides blaptoides Kollar, 1836	35.0	G	4	2	2	4					2	1			15
Diplocheila zeelandica (Redtenbacher, 1868)	25.0	G	1		1		1	1	1		5	3	4	8	25
Epomis nigricans (Wiedemann, 1821)	20.2	G										1			1
Haplochlaenius costiger (Chaudoir, 1856)	22.7	G	1	1		1							1		4
Harpalus griseus (Panzer, 1797)	11.8	G					2		2		5	4	4	4	21
Harpalus tridens Morawitz, 1862	12.2	G		1				1		1	4		2	1	10
Leptocarabus kyushuensis (Nakane, 1860)	30.5	G					2		2			1			5
Lesticus magnus (Motschulsky, 1860)	24.4	G	30	33	31	27	3	5	4		1	1	1		136
Panagaeus japonicus Chaudoir, 1861	11.1	S											1		1
Planetes puncticeps Andrewes, 1919	12.4	S					1		1			1			3
Pterostichus polygenus Bates, 1883	8.6	S		1			1	1		1		1	1	1	7
Synuchus arcuaticollis (Motschulsky, 1860)	9.0	S							3			2			5
Synuchus congruus (Morawitz, 1862)	8.2	S								2					2
Synuchus cycloderus (Bates, 1873)	12.0	S	25	21	13	27	11	6	5	5	10	14	25	22	184
Synuchus dulcigradus (Bates, 1873)	9.0	S		4	2	6	4	3	5	2	15	10	9	7	67
Synuchus nitidus (Motschulsky, 1861)	15.5	S	6		5	2	31	46	22	24	51	21	58	68	334
Trigonognatha cuprescens Motschulsky, 1857	15.6	S					10	6	9	11	4	6	4		50
Trigonotoma lewisii Bates, 1873	16.8	S	2	2	2			1	2						9
Brachinus scotomedes Redtenbacher, 1868	14.0	S	6	1	4	7					2		1	3	24
Number of individuals			78	70	64	75	132	128	87	111	236	195	214	237	1627
Number of species			9	10	10	8	17	14	15	10	15	17	18	13	26
Summary (individuals/species)			(287/13)				(458/21)				(882/23)				

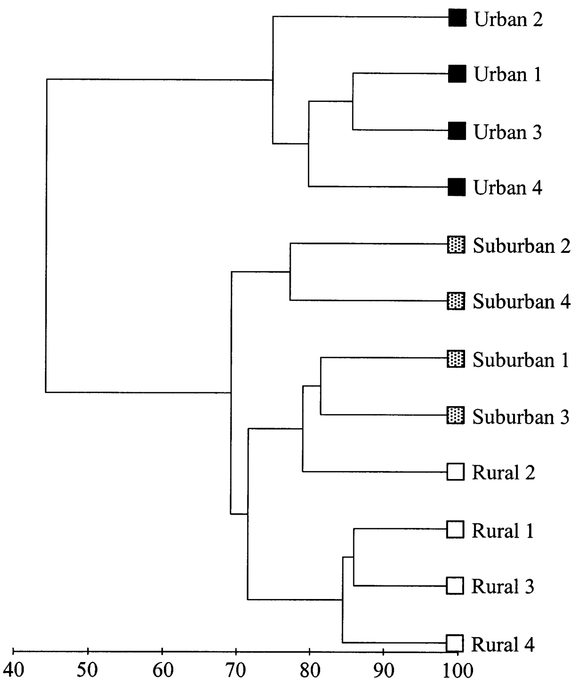

Fig. 2. Cluster analysis dendrogram (using the Bray-Curtis Similarity Index) showing differences in carabid assemblage structure across the urban-rural gradient. Urban sites were distinctly different from both suburban and rural sites (45% similarity).

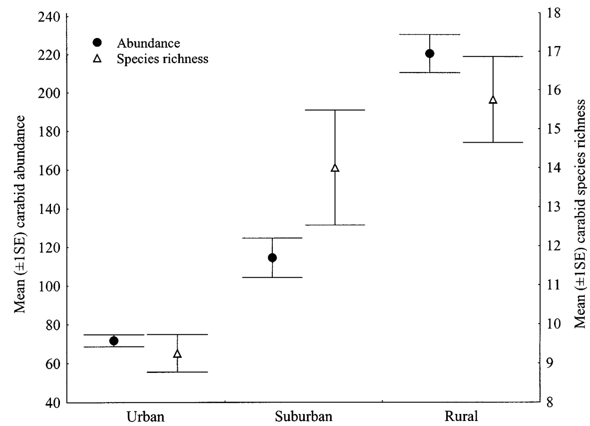

Fig. 3. Carabid abundance and species richness differences across the Hiroshima urban-suburban-rural gradient. The ANOVA tests indicate significant differences across the urban-rural gradient, and subsequent post-hoc comparisons tests (Scheffé tests) revealed that for both abundance and species richness, the urban sites were significantly different from the suburban and rural sites and that the suburban sites were significantly different from the rural sites. Note that this figure is constructed at the site level, while the ANOVA test was performed at the trap level.

This study and the one by Niemelä et al. (2002) show that even within the same group of organism (carabid beetles), there is considerable variation in response to urbanisation. The most obvious reason for this is that cities differ in terms of their spatial structure and configuration, their degree of development and age, and importantly, their level and degree of human disturbance. For example, cities with a stark difference in human disturbance between urban areas and the surrounding rural environment, will most likely have significant differences in carabid assemblage structure between these areas as carabids are thought to be good environmental indicators (Ishitani 1996, Niemelä 1996, Lövei and Sunderland 1996, McGeoch 1998, Rainio and Niemelä 2003).

Furthermore, the gradient from urban to rural is not likely to be a simple, unimodal gradient reflecting human population numbers and the associated levels of disturbance in green areas only, but rather a complex one where many factors (temperature, moisture, edaphic factors, pollution etc.) interact (McDonnell et al. 1993). These factors, together with possible changes in species interactions along the gradient, are likely to be different in different cities, which could lead to differences in beetle response across the different urban-rural gradients. For example, in this study the urban sampling areas were all situated on a site that can be considered an island (even though the site is connected to the mainland), complicating the gradient comparison even further. Finally, insect populations can fluctuate considerably between years (Wolda 1978, 1992, Den Boer 1981) making generalisations based on single-year studies across these gradients difficult.

Table 2. Nested ANOVA showing differences in carabid abundance and species richness across the urban-suburban-rural gradient and between the twelve sites selected. Abundance data were square root-transformed to apply with parametric test assumptions. Species richness data did not need to be transformed. ns = not significant. % – the variance component expressed as a percentage of the sum of their variances (see Sokal and Rohlf 1995).

Parameter	Source of variation	DF	MS	F	p	Variance component	%
Individuals	Gradient	2	43.734	79.066	<0.001	1.080	57.8
	Sites	9	0.553	0.702	0.706	−0.023	
	Error	108	0.788			0.788	42.2
Species	Gradient	2	87.058	30.165	<0.001	2.104	43.9
	Sites	9	2.886	1.080	0.383	0.021	0.4
	Error	108	2.671			2.671	55.7

Table 3. Generalized linear model results. This analysis was performed to test two hypotheses. First, that the likelihood of collecting a specialist individual (or species) is higher in the rural environment compared to the urban environment. And second, that the likelihood of collecting a large individual (or species) is higher in the rural environment compared to the urban environment. Abbreviations: U_S_R – urban-suburban-rural gradient (factor), S_G – forest specialists and habitat generalists (factor).

Factor	DF	Deviance	Deviance ratio	F	p
Abundance					
U_S_R	2	9.156	4.578	4.578	0.025
Body size	2	46.773	23.387	23.387	<0.001
S_G	1	5.037	5.037	5.037	0.038
U_S_R × body size	4	2.469	0.617	0.617	0.656
U_S_R × S_G	2	8.185	4.093	4.093	0.034
Body size × S_G	2	15.892	7.946	7.946	0.003
U_S_R/site	9	2.803	0.311	0.311	0.961
U_S_R/site × body size	18	3.570	0.198	0.198	0.999
U_S_R/site × S_G	9	0.315	0.035	0.035	1.000
U_S_R × body size × S_G	4	41.775	10.444	10.444	<0.001
Residual	18	4.458	0.248		
Total	71	140.434	1.978		
Species richness					
U_S_R	2	7.687	3.844	3.844	0.041
Body size	2	30.824	15.412	15.412	<0.001
S_G	1	3.382	3.382	3.382	0.082
U_S_R × body size	4	1.137	0.284	0.284	0.884
U_S_R × S_G	2	1.927	0.964	0.964	0.400
Body size × S_G	2	11.839	5.919	5.919	0.011
U_S_R/site	9	2.870	0.319	0.319	0.958
U_S_R/site × body size	18	10.057	0.559	0.559	0.887
U_S_R/site × S_G	9	1.812	0.201	0.201	0.991
U_S_R × body size × S_G	4	7.253	1.813	1.813	0.170
Residual	18	5.629	0.313		
Total	71	84.417	1.189		

The individuals (response) variable was log transformed to approach approximate normality. The species (response) variable did not need to be transformed, and the distribution of species followed a Poisson distribution. In both analyses we used a Canonical link function.

Both carabid abundance and species richness decreased significantly with increased urbanisation. This result is in agreement with what was postulated by Gray (1989), and with what has been found for carabid beetles in Helsinki and Edmonton (Niemelä et al. 2002), and for lizards in Tucson, Arizona (Germaine and Wakeling 2001). Niemelä et al. (2002) argued that this pattern is possibly a result of several factors including the unfavourability of urban environments to specialist species. This possibility is discussed below.

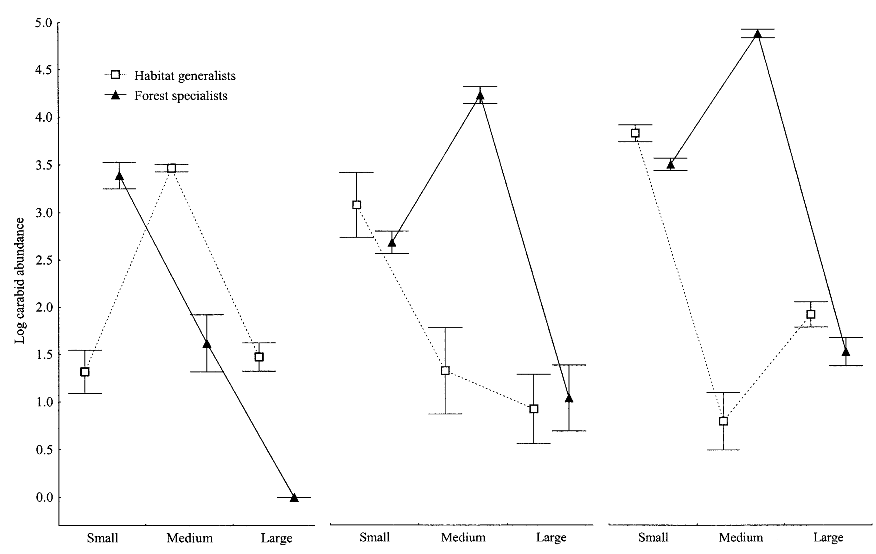

Fig. 4. The significant urban-suburban-rural × body size × specialisation interaction found from performing a GLM on carabid abundance values. This interaction shows that urban areas are characterised by small-sized specialist and medium-sized generalist individuals, while more undisturbed areas are characterised by larger-sized specialist and small-sized generalist individuals.

Evidence in the literature suggests that highly disturbed areas are characterised by smaller-sized carabid (Blake et al. 1994, Ribera et al. 2001) and spider species (Miyashita et al. 1998) than are less disturbed sites. We do not, however, expect this to be true for habitat generalists because of their broad potential resource base, but do expect this pattern for forest specialists. Indeed, no large, and only few medium-sized specialist individuals were collected in urban Hiroshima, while many medium-sized and some large-sized specialist individuals were collected in the suburban and rural sites. In terms of generalist individuals, the city of Hiroshima was characterised by medium-sized beetles, while few medium- and large-sized generalist individuals were collected in suburban and rural sites. These results appear to corroborate the notion that disturbed areas are characterised by small-sized and generalist species. The question then arises: why are small species more tolerant to disturbance? This may be because small-sized carabid species are more often winged than are large-sized species, and therefore small species are more vagile than large species and can colonise and recolonise ephemeral and unstable habitats more easily. However, it is evident that there is a complex interaction between carabid size, degree of generalism and wing-development. In order to study these relationships in detail, exact information about these ecological characteristics of the species is required.

Globenet and generalisations

This study is part of the international Globenet project. The aim of Globenet is to search for common patterns in a single taxonomic group (here carabid beetles) across urban-rural gradients in cities around the world, with urban areas more disturbed anthropogenically than suburban and rural areas (Niemelä et al. 2000). The ultimate goal is to improve our understanding of urban biodiversity patterns and to provide tools for the maintenance of biodiversity in urban areas. In ecology, there is a genuine need for true replicative studies, where research is done in the same system using the same species (Palmer 2000). Although Globenet is not truly replicative (because cities are spatially and temporally different, and the Carabidae is made up of different constituent species in different cities), the programme does aim to search for generalisations. One such generalisation from urbanisation studies done in Edmonton (Canada), Helsinki (Finland) (Niemelä et al. 2002), and now Hiroshima (Japan) is that it appears that carabid abundance and species richness are lower in urban areas than in suburban and rural environments. This generalisation does not, however, hold for Sofia (Bulgaria) where we found that carabid abundance and species richness did not change significantly across the urbanisation gradient (Niemelä et al. 2002).

In the future, the Globenet project will focus on three issues. First, to continue studying carabid abundance and species richness differences across urban-rural gradients in other cities. Second, to develop and test more explicitly the effects of urbanisation on beetle body size and specialisation, as was done in this study. And finally, to operationalise the urban-rural gradient (see Peters 1991), meaning to quantify this gradient in terms of human disturbance. Suggested urbanisation quantification include, area and intensity of habitat wear (see Lehvävirta 1999, Grandchamp et al. 2000), human population density in the vicinity of the sites, percentage of built up area in the vicinity of the sites, or a combination of these.

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