



Carabid beetle and spider assemblages along a forested urban–rural gradient in southern Finland

Diane Alaruikka^{1,*}, D. Johan Kotze², Katja Matveinen² & Jari Niemelä²

¹*Finnish Museum of Natural History, P.O. Box 17, Pohj. Rautatiekatu 13, FIN-00014, University of Helsinki, Finland*

²*Department of Ecology and Systematics, P.O. Box 65, Viikinkaari 1, FIN-00014, University of Helsinki, Finland*

**Author for correspondence (e-mail: diane.alaruikka@helsinki.fi; phone: +358-9-19128860; fax: +358-9-19128843)*

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Abstract

To investigate the effects of urbanization on carabid beetles (Carabidae) and ground dwelling spiders (Araneae) a study was completed along a 20 km urban–rural forest gradient in the Helsinki–Espoo area of southern Finland. To study changes in assemblage structure, abundance and species richness, these taxa were collected in the year 2000 using pitfall traps, which had been placed in four forest sites within each of the urban, suburban and rural zones. We expected to find changes in the abundances and species richnesses in the two taxa across the urban–rural gradient, but did not find any. Our second and third hypotheses, stating that generalist species and small-bodied species should gain dominance along the gradient from rural to urban sites, were partly supported as carabid specialists were more characteristic of suburban and rural environments whereas generalists were more likely to be collected from rural areas compared to suburban or urban sites. Furthermore, medium to large-sized carabid individuals were more likely to be collected in the rural sites compared to urban forests. We found no evidence for significant changes in spider abundance or species richness across the urban–rural gradient in relation to body size or habitat specialization. We suggest that urbanization does not have significant effects on the total abundances and species richnesses in these two taxa. However, individual species responded differently to urbanization, and there were significant differences in the specialization and body sizes of carabids across the gradient.

Introduction

Urbanization is increasing worldwide. It is predicted that by the year 2025 the worldwide urban population will double, and that in the United States the urban population will be 80% of the total population (McDonnell & Pickett 1990; Anthrop 2000). Increasing population brings about changes in the urban environment that are collectively called ‘urbanization’.

Urbanization refers to the process of converting countryside landscapes into city or town landscapes (McDonnell *et al.* 1997; Anthrop 2000). There

are many definitions of a city, but for the purpose of this paper it suffices to characterize urban areas as having the following features: (a) high human population densities, (b) highly developed areas with business, industrial and residential components, (c) degradation, alteration, modification and fragmentation of natural habitats (due to high anthropogenic disturbances), (d) warmer temperatures (~2–3°C) than in the surrounding suburban and rural areas (urban heat island effect), and (e) higher numbers of exotic, invasive, accidental and generalist floral and faunal species (Thiele 1977; McDonnell & Pickett 1990; Morris 1992; Guntenspergen & Levenson 1997;

McDonnell *et al.* 1997; Chudzicka & Skibinska 1998; Niemelä 1999a; Anthrop 2000).

A disturbance gradient from urban through suburban to rural environments is an effective framework for studying the effects of urbanization on ecological systems (McDonnell & Pickett 1990; McDonnell *et al.* 1997; Niemelä *et al.* 2000). Indeed, studies of the effects of urbanization using urban–rural gradients have been completed for plants (Tonteri & Haila 1990; Guntenspergen & Levenson 1997), birds (Blair 1996), reptiles (Germaine & Wakeling 2001), and some arthropod groups (Vepsäläinen & Wuorenrinne 1978; Chudzicka & Skibinska 1998; Miyashita *et al.* 1998; Blair 1999; Gibbs & Stanton 2001). In many studies, species showed varying responses to the effects of urbanization along urban–rural gradients leading to community level changes (McDonnell & Pickett 1990; Niemelä 1999b). Some species exhibited favourable responses to urbanization and they thrived in urban environments, while others avoided cities. Manmade or modified habitats created new havens for many exotic and generalist species, while many native and specialist species reacted negatively and have disappeared from these areas (Eversham *et al.* 1996; Chudzicka & Skibinska 1998).

The objective of this study is to gain understanding of the effects of urbanization by comparing carabid beetle (Carabidae) and spider (Araneae) assemblages along an urban–rural forest gradient. This study is part of the GLOBENET project whose objective is to study the effects of urbanization on biodiversity, using urban–rural gradients in different cities around the world (Niemelä *et al.* 2000). The following hypotheses were tested in our study. First, we predict abundances and species richnesses of carabids and spiders to decrease with disturbance (here urbanization), i.e. from rural to urban forest sites (Gray 1989). This has been shown for carabid beetles in Edmonton (Canada), Helsinki (Finland) (Niemelä *et al.* 2002), and Hiroshima City (Japan) (Ishitani *et al.* accepted). It has, however, been shown that for carabid beetles, more disturbed sites are poor in forest specialists, but rich in open habitat species (Niemelä *et al.* 2002). Therefore, we extend this hypothesis by predicting that more disturbed sites (here urban and suburban) would be poor in forest specialist carabids and spiders, but rich in generalist and open habitat species and individuals. Second, we predict that the more anthropogenically disturbed urban areas are characterized by smaller-sized carabids and spiders compared to the lesser disturbed suburban and rural sites (see Blake *et al.* 1994; Ribera *et al.* 2001).

Finally, we explore the possibility that these two taxa respond in a similar way to the urbanization gradient. Although carabids and spiders follow different life histories, they do occupy and exploit a similar resource base and, therefore, might respond similarly to disturbance, given that this disturbance gradient has a similar effect on their environment. Alternatively, because of the possibility of direct interactions between these primary predacious groups (Lövei & Sunderland 1996), it is difficult to predict the outcome of this hypothesis.

Methods

Study area and sampling design

Helsinki (60°10'N, 24°56'E), has a human population of about 500 000 and covers an area of approximately 185 km². To the west of Helsinki lies the suburban city of Espoo with a population of about 200 000 and covers an area of 312 km² (Tonteri & Haila 1990; Anonymous 2000).

Four urban forest sites, within the city of Helsinki, four suburban sites within the eastern-central part of Espoo, and four rural sites located within the northwestern part of Espoo, near Nuuksio National Park were selected. The sites comprise an approximately 20 km long urban to rural gradient. *Myrtillus* – type coniferous forest (Cajander 1949) dominated by Norway spruce (*Picea abies*) cover the study sites (see also Niemelä *et al.* 2002). Each of the areas immediately surrounding the individual pitfall traps were similar in floral composition. Ground cover vegetation included *Vaccinium myrtillus*, *V. vitis-idaea*, *Luzula pilosa*, *Festuca ovina*, *Pteridium aquilinum* and various moss species. Urban areas were heavily trampled compared with the suburban and rural sites. For example, urban trampling averaged 32.85 m² per 300 m², while suburban and rural trampling averaged less than 1 m² per 300 m² (Venn *et al.* 2002). Detailed information for each of the sites is found in Venn *et al.* (2002).

Ten pitfall traps were placed approximately 10 m apart, in a transect line, within each of the four urban, suburban and rural forest sites. Each transect line was approximately 50–100 m from the nearest forest edges. A total of 120 pitfall traps (40 pitfall traps in each disturbance regime) were in operation from the 3rd of May to the 11th of September 2000. Each pitfall trap consisted of a 65 mm (mouth diameter) plastic cup, which was placed in the ground with its mouth level with the soil surface. The pitfall traps were half

filled with a 50% aqueous propylene-glycol solution, which acted to kill and preserve the catch and were emptied monthly. Brown, 10 × 10 cm² roofs were placed a couple of centimetres above each pitfall trap to keep excess leaf litter, forest debris and rain water out of the traps.

Carabid beetles were identified to species level using standard keys (Lindroth 1985; 1986) by DA, and spiders were identified by Timo Pajunen (Finnish Museum of Natural History, Helsinki).

Carabid beetle and spider species were placed into one of the following three habitat affinity categories based on the literature (see Appendices 1 and 2) and Matveinen (in prep): forest species (species which are found predominately in forest areas), open habitat species (species which occur predominately in open habitats), and generalist species (species which occur in both forest and open habitats).

Data analyses

Hierarchical cluster analyses, based on Bray–Curtis similarity matrices (%), were used to compare the species assemblages for the two taxa along the urbanization gradient. This analysis compares the similarity of species assemblages at different sites, based on the number of species and individuals collected.

A nested analysis of variance was used to test our first prediction that abundance and species richness of carabids and spiders decreased with urbanization. The nested ANOVA approach was followed, as we were primarily interested in differences across the urbanization gradient (main effect), but also in the variation within the 12 sites. Data were transformed to approximate normality (see Table 1) to comply with the parametric test assumptions. From the mean squares in the ANOVA tables we estimated the variance components (as values and as percentages) between traps, sites and the urban–rural gradient (Sokal & Rohlf 1995). This was done to illustrate the amount and proportion of variation at each of the levels in the ANOVA models.

To test the predictions that urban areas are characterized by fewer specialists, and by smaller-sized individuals and species, we used a generalized linear model (GLM) approach. Four GLMs were performed (a carabid abundance, carabid species richness, spider abundance and spider species richness GLM). The abundance response variables were log-transformed and the analyses were performed under the assumption of normality. The species richness analyses were not transformed and the analyses were performed under the assumption of a Poisson distribution. The explanatory variables, listed below, were included via a canonical link function. Factors included in the models were the urban–suburban–rural

Table 1. Results of the nested ANOVA to examine the prediction that urban areas have significantly lower carabid and spider abundance and species richness than rural areas.

Taxon	Source of variation	df	MS	<i>F</i>	<i>P</i>	Var	%
<i>Carabids</i>							
Abundance	Gradient	2	6.188	2.063	=0.183	0.080	10.3
	Sites	9	2.998	6.850	<0.001	0.256	33.1
	Error	108	0.438			0.438	56.6
Species	Gradient	2	60.008	3.926	=0.059	1.118	20.5
	Sites	9	15.283	4.907	<0.001	1.217	22.3
	Error	108	3.115			3.115	57.2
<i>Spiders</i>							
Abundance	Gradient	2	1.654	0.334	=0.725	−0.083	—
	Sites	9	4.956	5.659	<0.001	0.408	31.8
	Error	108	0.876			0.876	68.2
Species	Gradient	2	18.308	1.348	=0.308	0.118	1.5
	Sites	9	13.583	1.828	=0.071	0.615	7.5
	Error	108	7.431			7.431	91.0

This analysis was performed at the trap level with sites (12) nested in the gradient factor. Var – estimated variance component, % – variance component expressed as a percentage.

Carabid abundance values were log-transformed while Spider abundance values were square root transformed to approach approximate normality. Species richness data did not need to be transformed. Only adults were used in the Spider analysis. Negative variance component values were set to zero in the % calculation.

gradient (USR), site (nested in the gradient factor), specialization (carabids were divided into specialists and generalists, SG; spiders were divided into forest, generalist and open habitat species, FGO), body size and guilds (see Appendices 1 and 2). Carabids and spiders were divided into three body size classes, carabids – small (<7 mm), medium ($7 < x < 14$) and large (>14 mm); spiders – small (<2.5 mm), medium ($2.5 < x < 5$) and large (>5 mm). Spider guilds were divided into web builders and hunters based on the literature (Appendix 2).

Results

We collected 26 carabid species (2764 individuals) and 85 spider species (2763 individuals) across the Helsinki urban–rural gradient (Appendices 1 and 2). The catch numbers were rather low (0.17 carabid or spider individuals/trap/day), but consistent with results from other boreal forest studies (Niemelä *et al.* 1986; 1988; Koivula *et al.* 1999).

Occurrence of carabid beetles across the urban–rural gradient

The number of carabid individuals increased from the urban sites (537 individuals) through the suburban sites (905 individuals) to the rural sites (1322 individuals). Species richness was highest in the suburban sites (24 species), while urban sites (18 species) and rural sites (17 species) had a lower species richness. Overall, the most abundant species captured was *Calathus micropterus* (31% of the total carabid catch), followed by *Pterostichus melanarius* (16%). *C. micropterus* was the most commonly collected carabid in urban and suburban sites, while *P. melanarius* was the most abundant carabid in rural sites.

The hierarchical cluster analysis showed that carabid assemblages did not separate according to their location along the urban–suburban–rural gradient, but that urban sites 1, 2 and 4, suburban sites 2 and 3, and rural sites 1 and 2 grouped together (Figure 1A).

The nested ANOVA revealed that there were no significant changes in carabid abundance or species richness across the urban–rural gradient (Table 1; Figure 2). However, there were more species in suburban and rural sites, compared to urban sites, at the 6% risk level. Carabid abundance and species richness showed significant variation at site level, with the largest proportion of variation observed at site and trap level (Table 1).

A number of factors interacted significantly with carabid abundance and species richness, and indeed

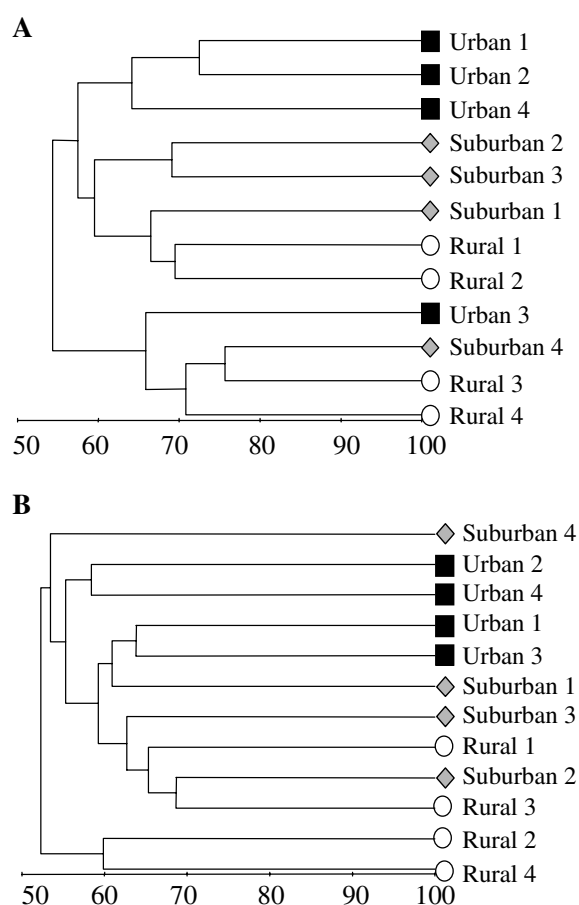


Figure 1. Hierarchical cluster trees based on Bray–Curtis similarity indices (%), one each for carabids (A) and spiders (B).

with spider abundance and species richness (Table 2). The effects that are, however, important here are the ones that interacted significantly with the gradient factor (USR), as our hypotheses dealt with changes across the urban–suburban–rural gradient. Results from the generalized linear model showed that changes in carabid abundance across the urban–rural gradient depended on whether the beetle was a generalist or a specialist, and on the size of the individual (Table 2). Specialist individuals were more likely, although statistically not significantly at the 5% Type I risk level ($p = 0.066$) to be caught in suburban and rural environments but, surprisingly carabid generalists were more likely to be collected from rural than either urban or suburban environments (Figure 3A). Large- and medium-sized individuals were more likely ($p = 0.006$), to be collected from rural environments and least likely to be collected from urban environments (Figure 3B). In terms of carabid species richness, we found no significant gradient interaction.

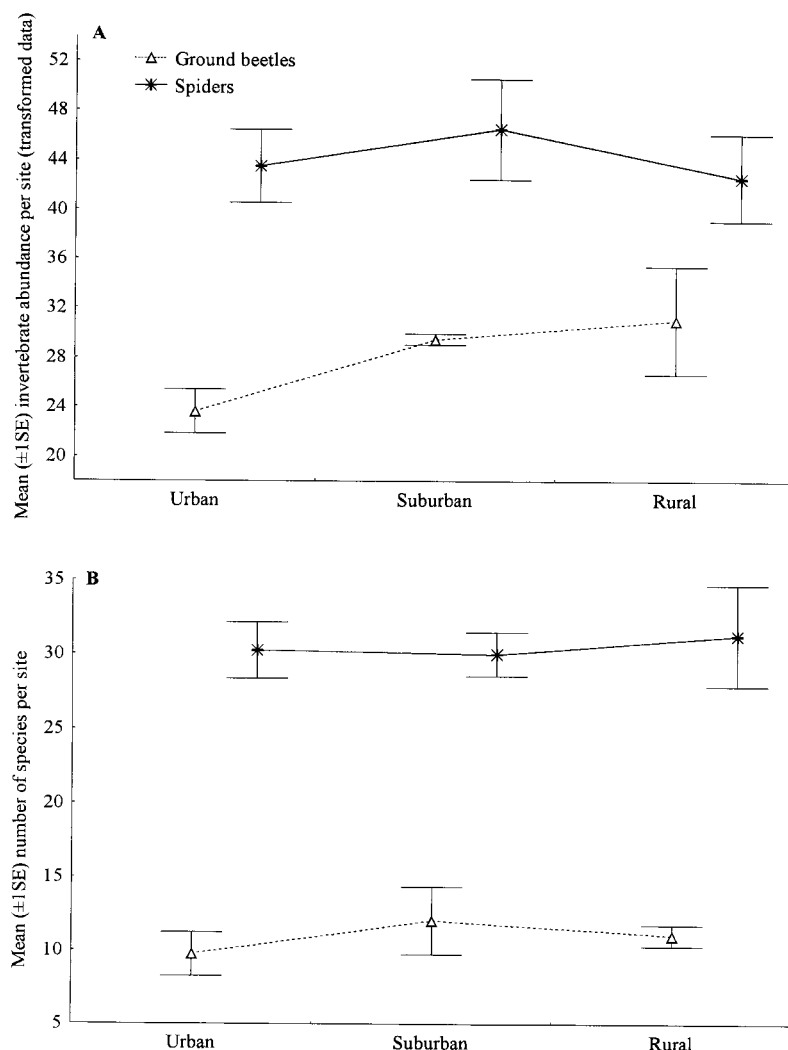


Figure 2. Carabid and spider abundance (A) (transformed values, see Table 1) and species richness (B) changes across the urban–suburban–rural gradient.

Occurrence of spiders across the urban–rural gradient

Species richness of spiders was surprisingly similar across the gradient (urban sites 59 species, suburban 55 species and rural 56 species). Numbers of individuals were somewhat higher in the suburban sites (997 individuals) than in the urban sites (907 individuals) or in the rural sites (859 individuals). Overall, the most abundant species collected was *Leptyphantes tenebricola* (27% of the total spider catch), followed by *L. alacris* (6%). *L. tenebricola* was the most abundant species captured in urban, suburban and rural sites.

In the hierarchical cluster analysis the branching off for most of the spider sites occurred between 60% and 70% (Figure 1B). There was some degree of grouping

of the spider assemblages of the sites according to their location along the gradient. Urban sites 2 and 4, and 1 and 3 grouped together, so did rural sites 2 and 4. Suburban site 4 showed the least amount of similarity in assemblage structure to the other sites.

We found little evidence to support our hypothesis of a decreased spider abundance and species richness with urbanization (Table 1; Figure 2). There was, however, significant variation in spider abundances at site level (Table 1). Most of the variation in the spider ANOVA models are at site (abundance test) and trap (abundance and species richness tests) levels (Table 1).

The spider GLMs produced no significant interaction with the gradient factor (Table 2). Various spider characteristics interacted significantly with one another. For example, the abundance of spiders of a

Table 2. Results of the generalized linear models to test two hypotheses. First, that the likelihood of collecting a large individual (or species) is higher in the rural environment compared to the urban environment. And second, that the likelihood of collecting a specialist individual (or species) is higher in the rural environment compared to the urban environment.

Parameter	df	SS	MS	Ratio	<i>p</i>	SS	MS	Ratio	<i>p</i>	
	<i>Carabid individuals</i>					<i>Carabid species</i>				
USR	2	4.990	2.495	2.495	0.111	0.902	0.451	0.451	0.644	
Body size	2	0.181	0.090	0.090	0.914	0.186	0.093	0.093	0.912	
SG	1	14.135	14.135	14.135	0.001	5.693	5.693	5.693	0.028	
USR × site	9	9.252	1.028	1.028	0.456	9.028	1.003	1.003	0.472	
USR × body size	4	20.288	5.072	5.072	0.006	5.349	1.337	1.337	0.294	
USR × SG	2	6.363	3.181	3.181	0.066	1.224	0.612	0.612	0.553	
Body size × SG	2	86.639	43.320	43.320	<0.001	22.470	11.235	11.235	<0.001	
Higher order interactions	31	35.017	3.090	—	ns*	17.662	2.012	—	ns*	
Residual	18	11.703	0.650			8.914	0.495			
Total	71	188.566	2.656			71.428	1.006			
	<i>Spider individuals</i>					<i>Spider species</i>				
USR	2	0.049	0.025	0.025	0.976	0.136	0.068	0.068	0.934	
Body size	2	9.922	4.961	4.961	0.011	70.850	35.425	35.425	<0.001	
FGO	2	109.754	54.877	54.877	<0.001	293.863	146.931	146.931	<0.001	
Guilds	1	12.427	12.427	12.427	<0.001	105.098	105.098	105.098	<0.001	
USR × site	9	4.868	0.541	0.541	0.837	3.824	0.425	0.425	0.915	
USR × body size	4	0.883	0.221	0.221	0.926	4.147	1.037	1.037	0.398	
USR × FGO	4	1.329	0.332	0.332	0.855	5.080	1.270	1.270	0.295	
USR × guilds	2	0.347	0.174	0.174	0.841	3.506	1.753	1.753	0.184	
Body size × FGO	4	26.101	6.525	6.525	<0.001	29.145	7.286	7.286	<0.001	
Body size × guilds	2	117.475	58.737	58.737	<0.001	216.491	108.245	108.245	<0.001	
FGO × guilds	2	59.035	29.517	29.517	<0.001	48.869	24.434	24.434	<0.001	
Higher order interaction	133	38.783	2.538	—	ns*	86.283	7.178	—	ns*	
Residual	48	82.329	1.715			4.650	0.097			
Total	215	463.301	2.155			871.942	4.056			

Abbreviations: USR – Urban–suburban–rural gradient; SG – specialist and generalist (carabids); FGO – forest habitat; generalist and open habitat species (spiders); ns = not significant.

*All higher order interaction *p* values are larger than 0.320, except for two higher order interactions in the *Spider species* analysis (USR × body size × FGO, *p* = 0.213; USR × body size × guilds, *p* = 0.166). Only adults were used in the Spiders analyses.

particular body size class depended on whether they are forest, generalist or open habitat individuals or whether they are hunters or web builders (Table 2). Although interesting, none of these significant interactions were important in testing our urbanization hypotheses.

Discussion

Effects of urbanization of carabid and spider assemblages

The main results of this study can be summarized as follows:

1. The abundances and species richnesses of the two taxa studied were not significantly different across the Finnish urban–rural gradient. However, there was significant variance at the site level for the abundances in both taxa and for carabid species richness.

2. For carabid abundance, specialization and body size were found to have significant effects across the gradient. However, for species richness no significant interactions were found. Furthermore, no significant interactions were detected for spider abundance or species richness in relation to specialization and body size across the gradient.
3. Some significant differences were found in the responses of both taxa to urbanization. Carabids showed a significant effect in relation to specialization and body size across the gradient, but spiders did not. Carabid specialists were more characteristic of suburban and rural environments, whereas generalists were more likely to be collected from rural areas compared to suburban or urban sites. Furthermore, medium- to large-sized carabid individuals were more likely to be collected in the rural sites compared to urban forests.

Our study did not reveal any major effects of urbanization on carabid and spider assemblages. Other studies,

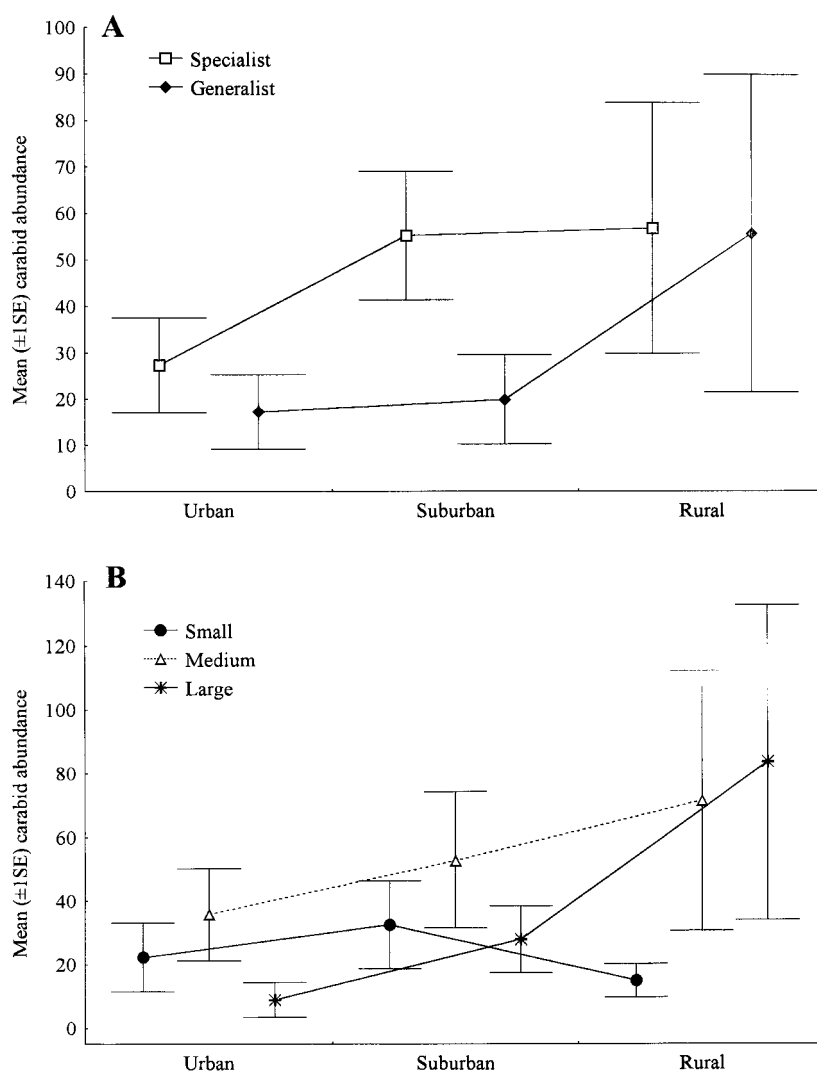


Figure 3. The nearly statistically significant gradient \times specialization and statistically significant gradient \times body size interactions found in the GLM analyses, in terms of carabid abundance (see Table 2). These results show that specialist individuals are more characteristic of suburban and rural environments, and surprisingly, that carabid generalists are more likely to be collected from rural, compared to urban or suburban sites (A), and that it is more likely to collect medium- and large-sized carabid individuals in rural compared to urban environments (B).

however, have found that urbanization has significant effects on various taxonomic groups. For example, urbanization was found to have a negative effect on bird species diversity (Blair 1996; 1999), lizard abundance and species richness (Germaine & Wakeling 2001), ant assemblages (Vepsäläinen & Wuorenrinne 1978), carrion beetles (Gibbs & Stanton 2001), carabid beetles (Niemelä *et al.* 2002) and shrub species richness (Tonteri & Haila 1990). However, not all studied taxa showed a negative response to urbanization, as was demonstrated for understory plant assemblages along an urban–rural gradient in Milwaukee, USA (Guntenspergen & Levenson 1997). Here, herb and

shrubs species diversities did not change significantly across the gradient.

Carabids did not respond to the disturbance gradient as we expected them to. The overall abundances and species richnesses did not show significant differences in less disturbed suburban and rural sites, as had been shown earlier (Niemelä *et al.* 2002; Ishitani *et al.* accepted). However, carabid species richness was found to show a response to the gradient at the 6% Type I risk level so we cannot completely rule out the possibility that there is a true response. As in Niemelä *et al.* (2002) the more disturbed sites (urban) were poorer in forest specialists, but contrary to our

hypothesis, generalists were most abundant in the rural, that is the least disturbed sites. Also, trampling intensity at the sites should be studied further as it has been shown that carabids respond negatively to severe trampling, which may be characteristic of some urban forests (Grandchamp *et al.* 2000). Perhaps the level of trampling disturbance in our study sites was not intense enough to cause major changes in the carabid assemblages.

We did not find any significant differences for the overall spider abundances at the gradient level. The reason might be that spiders are not strictly specialized in their habitats, although they seem to have an optimal habitat (Huhta 1965; Palmgren 1972, Palmgren & Biström 1979; Väisänen & Biström 1990). However, we found a significant effect at the site level. Spiders might be more affected by the small-scale habitat structure than the large-scale variation (urbanization gradient). For example, the web builders are affected by the structure of the vegetation (Huhta 1971; Palmgren 1972) as they need suitable places for their webs. We suggest that further studies should use several sampling methods because pitfall traps catch only those individuals that are active at the ground level (Huhta 1971). Web builders, which composed most of the pitfall trap catch, are basically only active at the ground level when they have to move their webs because of some disturbance (Leclerc 1991).

Body size and disturbance

It has been suggested that the disturbance level of an area is associated with the body-size distribution of carabid species (Blake *et al.* 1994; Lövei & Sunderland 1996; Brändle *et al.* 2000). Blake *et al.* (1994) found that there was a negative correlation between degree of disturbance and body size of carabids. Also, Gibbs & Stanton (2001) using an urban–rural gradient, found a higher abundance of smaller-bodied compared with larger-bodied carrion beetles in the more highly fragmented urban forests. Our study results seem to concur with the above studies as large- and medium-sized carabid individuals were more likely to be collected from the rural forests and least likely to be collected from the urban forests.

Conclusions

Although our study did not reveal any major effects of urbanization on carabid and spider assemblages, a

more detailed investigation of the landscape features along the gradient would be beneficial and may help to explain the trends observed here. We suggest that further research is needed concerning forest connectivity, stand size, age and isolation in each of the urban, sub-urban and rural zones. Further research is also needed to examine the human disturbance intensity in each of the sites along the gradient. As carabids and spiders responded differently to the disturbance gradient when specialization was concerned, we suggest a multi-taxa approach to be used also in further studies.

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Appendix 1. Carabid beetles collected across the urban (U), suburban (S) and rural (R) gradient. Body size and habitat affinities are also given (data obtained from Lindroth 1985; 1986; Thiele 1977).

Carabid species	U	S	R	Size	Habitat affinity
<i>Agonum fuliginosum</i> (Panzer)	1	0	2	6.65	F (moist areas)
<i>A. obscurum</i> (Herbst)	11	2	8	5.80	F (moist areas)
<i>Amara brunnea</i> (Gyllenhal)	31	157	26	6.00	F
<i>Calathus erratus</i> (Sahlberg)	0	2	0	10.15	O
<i>C. melanocephalus</i> (L.)	1	1	0	7.40	O
<i>C. micropterus</i> (Duftschmid)	195	340	319	7.65	F
<i>Carabus glabratus</i> (Paykull)	0	12	12	26.00	F
<i>C. hortensis</i> (L.)	3	68	60	25.00	F
<i>C. nemoralis</i> (Müller)	6	15	10	24.00	G (parks, gardens)
<i>Cychrus caraboides</i> (L.)	0	2	4	16.50	F
<i>Dromius fenestratus</i> (F.)	0	1	0	6.10	F (arboreal)
<i>Harpalus quadripunctatus</i> (Dejean)	0	0	6	10.75	F
<i>Leistus ferrugineus</i> (L.)	6	1	0	7.25	G
<i>L. terminatus</i> (Hellwig in Panzer)	4	2	1	7.00	F
<i>Notiophilus biguttatus</i> (F.)	3	3	3	5.50	F
<i>Patrobus assimilis</i> (Chaudoir)	1	2	1	8.90	G
<i>P. atrorufus</i> (Ström)	17	2	13	8.55	F
<i>Pterostichus diligens</i> (Sturm)	0	5	0	6.00	G (wet habitats)
<i>P. melanarius</i> (Ill.)	11	37	404	15.00	G (parks, gardens)
<i>P. niger</i> (Schaller)	51	87	175	17.75	F
<i>P. nigrita</i> (Paykull)	1	1	x 0	10.80	G (wet habitats)
<i>P. oblongopunctatus</i> (F.)	63	74	198	11.05	F
<i>P. strenuus</i> (Panzer)	1	8	0	6.60	G
<i>Trechus secalis</i> (Paykull)	131	76	80	3.75	G
<i>T. rivularis</i> (Gyllenhal)	0	6	0	4.60	F (peaty areas)
<i>T. rubens</i> (F.)	0	1	0	5.75	G
Number of individuals	537	905	1322		
Number of species	18	24	17		
Totals (individuals/species)	2764/26				
At trap level:					
Mean no. of individuals	13.4	22.6	33.1		
Standard error	2.53	2.39	5.24		
At site level:					
Mean no. of individuals	134.3	226.3	330.5		
Standard error	34.72	10.55	162.78		

F – forest habitat species; O – open habitat species; G - generalist species.

Appendix 2. Spiders collected across the urban (U), suburban (S) and rural (R) gradient. Body size and habitat affinities are also given (data obtained from Saaristo 1971; Roberts 1987; 1996; Kronestedt 1990; Heimer & Nentwig 1991; Matveinen, in prep.).

Spider families & species	U	S	R	Body lengths		Habitat affinity	Guild
				Female	Male		
(1) Agelenidae							
<i>Cryphoea silvicola</i>	7	5	27	2.75	2.75	F (moss, tree trunks)	W
(2) Araneidae							
Juveniles	0	1	0				W
(3) Clubionidae							
Juveniles	1	0	0				
<i>Clubiona lutescens</i>	2	1	0	7.00	5.00	G (moist habitats)	H
<i>C. subtilis</i>	0	1	3	3.75	2.75	O (bogs)	H

Appendix 2. (Continued)

Spider families & species	U	S	R	Body lengths		Habitat affinity	Guild
				Female	Male		
(4) Gnaphosidae							
Juveniles	1	4	2				
<i>Haplodrassus cognatus</i>	0	0	1	8.00	8.00	F	H
<i>H. signifer</i>	1	0	0	8.50	7.00	G	H
<i>H. soerenseni</i>	6	18	10	6.50	5.00	F	H
<i>Zelotes clivicolus</i>	2	0	0	5.00	5.00	G	H
(5) Hahniidae							
<i>Hahnia pusilla</i>	3	0	6	1.40	1.40	G (bogs)	W
(6) Linyphiidae							
Juveniles	73	47	55				
<i>Agyreta cauta</i>	0	2	1	2.30	1.95	G (bogs, meadows)	W
<i>A. conigera</i>	28	57	39	2.05	1.95	F (moss)	W
<i>A. ramosa</i>	2	19	23	2.25	2.13	F (moist habitats)	W
<i>A. subtilis</i>	0	2	20	2.25	2.20	F	W
<i>Allomengea scopigera</i>	119	37	0	4.75	4.20	F (moist habitats)	W
<i>Bathyphanes gracilis</i>	1	0	0	2.20	1.75	O (bogs, meadows)	W
<i>B. parvulus</i>	15	6	0	2.25	1.90	O (bogs, meadows)	W
<i>Bolyphanes alticeps</i>	0	1	2	4.00	3.50	G	W
<i>Centromerus arcanus</i>	30	53	28	2.00	2.25	F (bogs)	W
<i>C. sylvaticus</i>	3	0	0	3.25	2.60	G	W
<i>Ceratinella brevis</i>	7	4	3	2.00	1.90	G	W
<i>Cnephalocotes obscurus</i>	0	1	0	1.80	1.65	G (bogs, meadows)	W
<i>Dicymbium tibiale</i>	1	19	9	2.35	2.25	F	W
<i>Diplocentria bidentata</i>	8	6	12	2.00	1.80	F	W
<i>Diplocephalus latifrons</i>	8	13	5	1.75	1.75	F	W
<i>D. picinus</i>	2	5	0	1.70	1.55	F	W
<i>Diplostyla concolor</i>	8	66	12	2.60	2.40	F	W
<i>Erigonella hiemalis</i>	11	2	0	1.70	1.50	O	W
<i>Gonatium rubellum</i>	2	2	2	3.10	2.65	F	W
<i>Gongylidium rufipes</i>	4	0	0	3.15	2.75	F	W
<i>Helophora insignis</i>	1	1	0	3.75	3.40	F	W
<i>Lepthyphantes alacris</i>	31	59	89	2.95	2.55	F	W
<i>L. angulatus</i>	0	2	1	2.05	2.05	G (bogs, meadows)	W
<i>L. angulipalpis</i>	4	4	4	2.35	2.35	F	W
<i>L. cristatus</i>	1	1	0	2.40	2.25	F (bogs)	W
<i>L. mengei</i>	0	1	0	1.90	1.75	F	W
<i>L. pallidus</i>	2	2	0	1.95	1.80	F	W
<i>L. tenebricola</i>	256	219	275	2.70	2.70	F	W
<i>Macrargus rufus</i>	23	16	19	4.05	3.63	F	W
<i>Maro lehtineni</i>	1	0	0	1.30	1.05	F	W
<i>Maso sundevalli</i>	0	0	1	1.55	1.50	F	W
<i>Micrargus apertus</i>	0	3	1	1.95	1.75	F	W
<i>M. herbigradus</i>	2	0	0	1.70	1.60	G	W
<i>Microneta viaria</i>	8	51	7	2.75	2.75	F	W
<i>Minyriolus pusillus</i>	2	0	1	1.23	1.18	F	W
<i>Neriere clathrata</i>	2	0	0	4.35	4.10	F	W
<i>N. montana</i>	0	0	1	5.90	5.50	F	W
<i>N. peltata</i>	0	1	0	3.25	2.85	F	W
<i>Pityohyphantes phrygianus</i>	0	3	1	5.00	4.50	F	W
<i>Pocadicnemis pumila</i>	0	0	1	1.95	1.80	G (bogs, meadows)	W
<i>Poecilonea variegata</i>	1	0	1	2.20	2.08	F	W
<i>Porrhomma pallidum</i>	2	4	7	1.90	1.85	F	W
<i>Tapinocyba pallens</i>	37	36	15	1.60	1.60	F	W
<i>Tapinopa longidens</i>	2	2	1	3.50	3.40	F	W
<i>Thyreostenius parasiticus</i>	0	1	0	1.60	1.60	F	W
<i>Troxochrus nasutus</i>	0	1	0	1.85	1.00	F	W

Appendix 2. (Continued)

Spider families & species	U	S	R	Body lengths		Habitat affinity	Guild
				Female	Male		
<i>Walckenaeria antica</i>	8	3	6	2.30	2.13	G (dry habitats)	W
<i>W. atrotibialis</i>	2	6	0	2.50	2.25	G (bogs)	W
<i>W. cucullata</i>	8	17	13	2.35	2.20	F	W
<i>W. cuspidata</i>	0	1	1	2.70	2.50	F	W
<i>W. dysderoides</i>	7	4	1	2.00	1.80	F	W
<i>W. nudipalpis</i>	1	0	0	2.90	2.85	G (moist habitats)	W
<i>W. obtusa</i>	1	0	2	3.40	3.00	F	W
(7) Liocranidae							
Juveniles	1	0	0				
<i>Agroeca brunnea</i>	0	0	3	7.50	6.50	G	H
<i>A. proxima</i>	0	0	2	6.50	4.75	G	H
(8) Lycosidae							
Juveniles	22	26	16				
<i>Alopecosa aculeata</i>	0	0	1	9.90	7.50	F	H
<i>A. pulverulenta</i>	1	0	0	8.25	6.50	O	H
<i>A. taeniata</i>	29	36	30	9.60	8.60	F	H
<i>Pardosa lugubris</i>	12	28	11	5.50	4.50	G	H
<i>Pirata hygrophilus</i>	0	12	10	5.75	5.00	G (moist habitats)	H
<i>Trochosa terricola</i>	45	51	26	10.50	8.00	G	H
(9) Mimetidae							
Juveniles	3	1	2				
<i>Ero furcata</i>	4	4	4	2.88	2.63	F	H
(10) Salticidae							
<i>Euophrys erratica</i>	1	0	0	3.50	3.50	On walls, among stones	H
<i>E. frontalis</i>	1	0	0	4.00	2.50	G (bogs)	H
<i>Neon reticulatus</i>	0	0	1	2.50	2.25	F	H
(11) Tetragnathidae							
Juveniles	0	1	1				
<i>Pachygnatha listeri</i>	18	5	3	4.25	3.75	F	W
(12) Theridiidae							
Juveniles	0	0	2				
<i>Crustulina guttata</i>	1	0	0	1.75	1.75	F	W
<i>Euryopsis flavomaculata</i>	0	3	1	3.75	3.00	G (bogs, meadows)	W
<i>Robertus lividus</i>	2	12	11	3.25	3.25	F	W
<i>R. scoticus</i>	1	0	3	2.00	1.88	F (pine bogs)	W
<i>Steatoda bipunctata</i>	0	0	1	5.75	4.50	G (houses, tree trunks)	W
(13) Thomsidae							
Juveniles	3	1	0				
<i>Xysticus audax</i>	0	0	2	7.00	4.00	F	H
<i>X. cristatus</i>	1	0	0	7.00	4.00	O	H
<i>Ozyptila praticola</i>	0	2	0	3.50	2.75	F	H
<i>O. trux</i>	11	2	9	4.50	3.50	G (bogs, meadows)	H
(14) Zoridae							
Juveniles	0	1	0				
<i>Zora nemoralis</i>	3	0	3	4.50	3.50	G	H
<i>Z. spinimana</i>	1	2	9	5.75	4.75	G	H
Total number of individuals	907	997	859				
Total number of species	59	55	56				
Totals (individuals/species)	2763/85						
At trap level:							
Mean no. of individuals	19.7	22.10	19.3				
Standard error	1.43	1.61	1.57				
At site level:							
Mean no. of individuals	197.0	221.0	192.8				
Standard error	26.69	36.91	30.79				

F – forest habitat species; O – open habitat species; G – generalist species; W – web builder; H – hunter spider.