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Urbanization effects on carabid diversity in boreal forests

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Abstract. Carabid abundance, species richness and diversity were compared along an urban-rural gradient in Helsinki, Finland. Increased urbanization was found to result in significant reductions in species richness, though the reductions in abundance and diversity were not statistically significant. Forest habitat-specialist species were scarce in rural sites and virtually absent from urban and suburban sites. There was no evidence of higher diversity at intermediate disturbance levels (suburban sites), as predicted by the intermediate disturbance hypothesis. Species with flight ability and the ability to utilize open habitat were more predominant in urban and suburban sites. Flightless species were more predominant in rural and suburban sites. Carabid abundance data were sufficient to reveal the negative impact of urbanization, so similar studies could be conducted in regions where carabid taxonomy is poorly known. Species composition patterns do, however, provide invaluable information. To conclude, if biodiversity is to be maintained in urban areas, priority must be given to the provision of those habitat features which are essential for sensitive species, such as decaying wood and wet microhabitats. These must be incorporated into urban green networks in particular, if biodiversity and species other than common generalists are to benefit from them.

INTRODUCTION

Anthropogenic modification of landscapes and associated landscape change which pertains to a city or town, i.e. urbanization, causes major changes to the ecosystem. Differences in a number of variables, such as temperature (Bornstein, 1968), acidity, soil hydrophobicity, utilizable carbon and nitrogen levels (McDonnell et al., 1997), deposition of heavy metals (Hynninen, 1986) and other pollutants (Herrmann & Hübner, 1984; Väisänen, 1986), changes in fungal biomass, bacterial flora, leaf-litter decomposition rates (McDonnell et al., 1997), fragmentation and edge effect (Löfström et al., 1999), all contribute to the effect of urbanization. In addition, the highly significant physical covering of potential habitat with asphalt and cement causes direct loss of habitat.

This urbanization effect tends to result in a highly affected core at the heart of the city, surrounded by irregular rings of decreasing urban developement (Dickinson, 1996). The core area of the city often contains patches of natural land which are similar in physiognomic appearance to their rural counterparts but are generally more fragmented, polluted, warmer and drier. Furthermore, core areas are most affected by intense recreational use and often contain exotic species (Gilbert, 1989; Kostel-Hughes, 1995; Kostel-Hughes et al., 1996). In response to this long and probably incomplete catalogue of changes affecting urban green space, it would be surprising if there were no concomitant effects on species composition.

On a global scale, urbanization is resulting in a vast amount of habitat loss and modification, particularly in regions where there is pressure from a rapidly growing human population. In Finland, as in much of Europe, although the human population is not increasing significantly, there is an ongoing migration from rural areas to the cities (Wahlström et al., 1996). This results in increased construction, traffic and pollution, thus increasing the impact on natural areas within and adjacent to these cities. Intense recreational pressure also often has a major impact on such natural areas, resulting in environmental changes (Lehvävirta, 1999). The aesthetic and recreational value of urban green areas is generally appreciated by urban planners and many sites are also preserved for their conservation value. Not surprisingly though, forest patches within urbanized areas are considerably different from their more rural counterparts.

The principal of sampling along a gradient (Whittaker, 1967), for investigating the effects of environmental factors upon ecosystems has been applied to urban-rural gradients (Klausnitzer & Richter, 1983; McDonnell & Pickett, 1990, 1993; McDonnell et al., 1997).

According to Connell's (1978) intermediate disturbance hypothesis, highly disturbed sites, and undisturbed sites, have lower diversity than sites with intermediate levels of disturbance. This hypothesis has been found applicable to a number of different ecosystems (Marone, 1992; Aronson & Brecht, 1996), though other studies have shown that it is not universally applicable (Schwilk et al., 1997; Wiegand et al., 1997).

The aim of this study is to investigate the effects of urbanization upon carabid diversity along an urban-rural gradient and, in particular, to answer the following questions: a) are there any significant differences in the carabid assemblages of urban, suburban and rural sites, particularly regarding species richness, abundance and community composition, b) how do the different carabid

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Appendix 1. Features of the 12 forest sites, and their surroundings, which could affect carabid population dynamics. Distance is measured from an arbitrary point in the city centre. Width of forest indicates those sites which are most affected by edge effects, as some large patches of forest (e.g. U2 and U3) were in the form of long, narrow strips. Trampling is the total area of paths or heavily trampled ground contained in three 100 m^2 squares (i.e. per 300 m^2). Connectivity indicates if and how the sites are connected to extensive areas of forest cover. Adjacent open vegetation indicates whether there are significant, large patches of open land adjacent which may be advantageous to those species which also thrive in such habitat. Urban open land is heavily disturbed open land, which provides a similar resource for just a few of the hardiest generalist species. Nuuksio is an area of c. 70 000 ha of forest, part of which is a national park. U, S and R indicate urban, suburban and rural sites 1–4.

Site	Size	Distance from city centre	Width of forest	Trampling	Connectivity to extensive forest	Adjacent open vegetation	Urban open land: gardens, wasteland, etc.
	ha	km	m	m^2			
U1	20	2	390	46.80	–	–	5 ha villa gardens, 3 ha sports complex and carpark
U2	440	1	670	36.79	300–500 m wide strip	–	Flats with playgrounds, stables
U3	440	1.5	350	44.60	300–500 m wide strip	–	30 ha industrial site, rocky
U4	3.8	4.5	63	3.20	300 m from Central Park	–	Housing & roads
S1	4	9	133	0	–	40 ha fields	–
S2	4	11	140	0	–	2 ha road construction site	30 ha industrial site
S3	88	14.5	840	0	–	60 ha	Suburban housing & motorway
S4	50	12.5	140	3.15	Corridor to 350 ha & on to Nuuksio	70 ha	20 ha suburban housing & motorway
R1	11	16	260	0	Very narrow corridor to Nuuksio	60 ha	2 ha sawmill
R2	10	17	980	0	Corridors to Nuuksio	8 ha	Few houses with large gardens
R3	70 000	18	–	0	Extensive forest	–	–
R4	70 000	18.5	–	3.92	Extensive forest	–	–

species' attributes and site characteristics influence these results and c) do the predictions of Connell's intermediate disturbance hypothesis (1978) hold true for carabid communities along an urban-rural gradient?

Carabid beetles (Coleoptera: Carabidae) were selected because they are easy to collect and preserve, taxonomically and ecologically well known, include sensitive specialist and less sensitive generalist species and have been recommended by a number of authors (Thiele, 1979; Blake et al., 1994; Langor et al., 1994).

This study is part of the "Globenet" programme (Global Network for Monitoring Landscape Change), which is an international initiative to develop appropriate mechanisms for the global investigation of the impact of urbanization on ecosystems (see Niemelä et al., 2000 and http://www.helsinki.fi/science/globenet).

MATERIALS AND METHODS

Study sites

The urban-rural gradient comprised of a transect from central Helsinki (60°10′N, 24°56′E) to northern Espoo (60°17′N, 24°38′E) in southern Finland (hemiboreal vegetation zone, Ahti et al., 1968), covering a distance of approximately 20 km. Twelve sites along the gradient were selected for this study: Four urban, four suburban and four rural. Urban sites were located within the core of the city of Helsinki, with busy roads, densely populated and industrial sites adjacent. Rural sites were in areas with minimal human population, only light traffic and no nearby industrial sites, and suburban sites were intermediate between these two extremes (Appendix 1). The forest stands in which the study sites were located were spruce dominated (*Picea abies* L.), with *Myrtillus* - type vegetation (Cajander, 1949). The age of the dominant spruce trees was estimated to be in excess of 80 years. Other site characteristics are shown in Appendix 1.

Pitfall trapping

Whilst there are complications to be considered, pitfall-trapping is the best means currently available for sampling carabid communities (Greenslade, 1964; Thiele, 1979; Spence & Niemelä, 1994). We placed ten pitfall traps (mouth diameter = 65 mm) at least 10 m apart in an irregular line at each site. The traps were sunk into the ground, their mouths flush with the surface. Approximately 40 ml of a propylene-glycol solution (1:1 aqueous) was used in order to kill and preserve the trapped arthropods. Plastic covers were placed a few centimeters over the traps to avoid dilution of the glycol by rainfall.

The traps were emptied on a monthly basis during one growing season (May-September 1998). Carabids were identified to species using Lindroth (1985, 1986) and spiders (Araneae) were reserved for possible use in subsequent studies.

Environmental factors

We assessed the amount of trampling at each site as a crude measure of disturbance on the forest floor by taking three, 100 m^2 squares along each transect. The area of paths and any other eroded patches which lie within each of these squares, was recorded.

Other environmental factors such as size of forest patch, amount of edge, distance from extensive forest, area of adjacent fields/open land and extent of urbanized land were assessed using the Greater Helsinki recreational map (see Appendix 1).

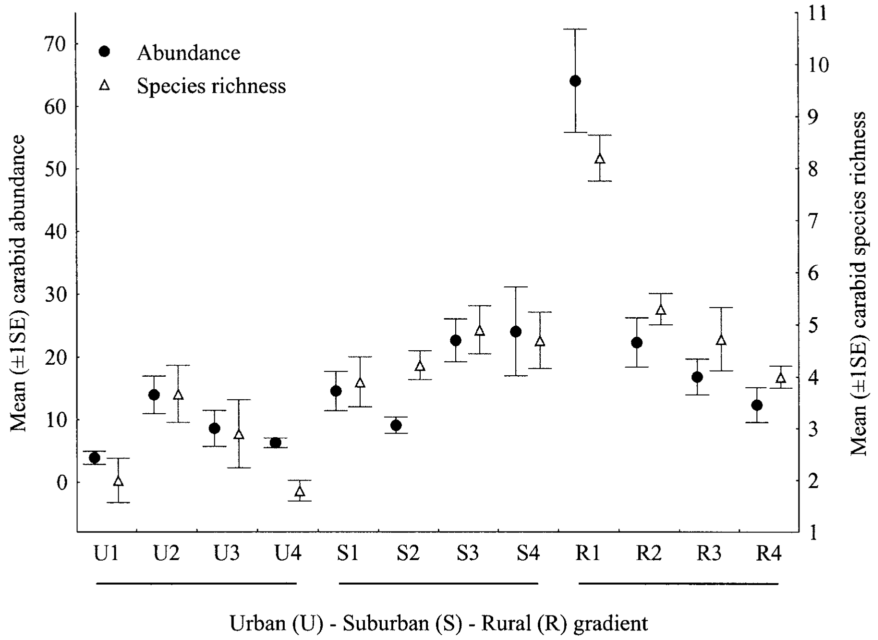

Fig. 1. Carabid species richness and abundance along the urban-rural gradient. Urban (U1-4), suburban (S1-4) and rural (R1-4) sites are indicated along the horizontal axis.

Data analyses

A nested ANOVA was used to analyze data of carabid abundance and species richness per trap and per site. The hypothesis that urbanization has an effect upon carabid abundance and/or species richness was tested across the three levels of urbanization: urban, suburban and rural. Data were log (X + 1) transformed to achieve approximate normality for both abundance and species richness. Pearson's correlation coefficient was used to examine the degree of correlation between abundance and species richness. In addition, we calculated the Brillouin diversity index for each site.

TABLE 1. Nested ANOVA table showing the effect of urbanization on (a) carabid abundance, (b) species richness and (c) abundance with site R1 removed. Abundance and species richness data were log (x + 1) transformed to comply with parametric test assumptions. The analyses were performed at the trap level with the 12 sites (11 in 'c') nested in the gradient factor. Var - estimated variance component, % - variance component expressed as a percentage (see Sokal & Rohlf, 1995).

Effect	df	SS	MS	F ratio	P	Var.	%
a) **Abundance**							
Urbanization level	2	5.037	2.519	3.884	0.061	0.047	27.2
Sites	9	5.837	0.649	9.680	<0.001	0.058	33.8
Error	108	7.236	0.067			0.067	39.0
Total	119	18.110					
b) **Species richness**							
Urbanization level	2	1.658	0.829	8.888	0.007	0.018	41.4
Sites	9	0.840	0.093	5.038	<0.001	0.007	16.9
Error	108	2.000	0.019			0.019	41.7
Total	119	4.497					
c) **Abundance (–R1)**							
Urbanization level	2	2.913	1.456	3.952	0.064		
Sites	8	2.948	0.369	5.185	<0.001		
Error	99	7.036	0.071				
Total	109	12.897					

Ordination by Principal Component Analysis (PCA) was used to compare the similarity of the carabid assemblage at each site and to examine the significance of different species characteristics. Species that were collected from one site only and only one individual, were excluded from this analysis.

The species characteristics used were flight ability and the ability to utilize open habitat, which were taken from Lindroth (1985, 1986 and 1992), Thiele (1977) and Kinnunen (1999) (see Appendix 3). Species were considered to be capable of dispersal by flight if either of the former authorities had confirmed, or strongly suggested, ability to fly and, in the case of dimorphic or polymorphic species, if part of the population in this region was known to be capable of flight (Lindroth, 1992). Some macropterous species are therefore considered as flightless.

RESULTS

Response of carabid abundance and species richness to urbanization intensity

A total of 2203 individuals and 25 species were collected (Appendix 2). Most of the abundant species, in particular *Pterostichus melanarius*, *P. niger*, *P. oblongopunctatus* and *Carabus hortensis*, were markedly less abundant in the urban sites than the rural sites. One of the most abundant species, *Calathus micropterus*, however, appeared to be equally abundant across the three regions.

The nested ANOVA revealed a highly significant effect of urbanization along the gradient for species richness (Table 1). For abundance the effect was just outside the 5% confidence interval and abundance was highly correlated with species richness (Pearson correlation coefficient: $r = 0.848$). Both abundance and species richness were low in the urban sites and high in the rural sites, particularly site R1 (Fig. 1). These ANOVA models explained a high proportion of the variance in the data. Because rural site R1 had a conspicuously high value for abundance (641 individuals), the ANOVA was repeated

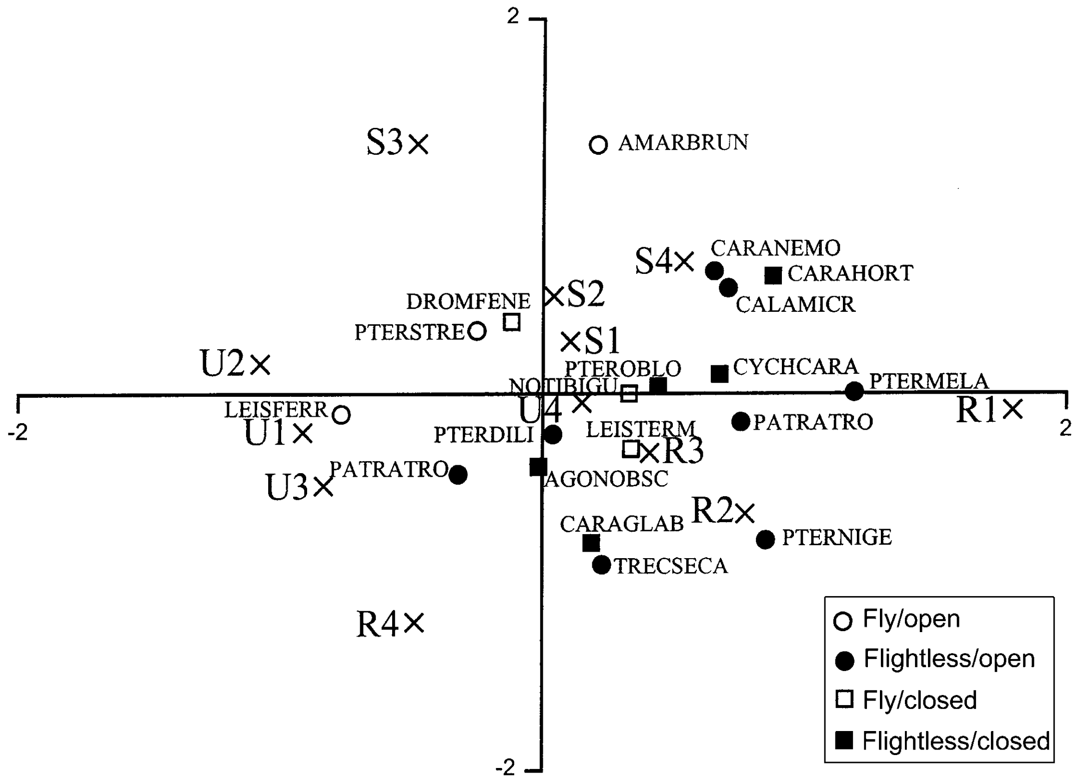

Fig. 2. PCA ordination of carabid species distributions with regard to site. *Pterostichus niger* favours rural, *Amara brunnea* suburban and *Leistus ferrugineus* urban sites. Species which are close to the origin are less affected by urbanization intensity. The carabid species are marked to indicate those which are capable (fly) or incapable (flightless) of flight and those which are (open) or are not (close) able to utilize open habitat. Species which are able to fly and utilize open habitat favour the suburban and urban sites, whereas most flightless species, open habitat species in particular, preferred rural and suburban sites. All of the species which were predominant in urban sites were open habitat species. The key to the abbreviations used for the scientific names is in Appendix 2. Urban, suburban and rural (U, S and R) sites are marked with a cross (X).

excluding this site, though this had a negligible effect on the result.

Diversity was lowest at urban site U4 and highest at rural site R3. Mean diversity was highest in the rural and lowest in the urban area (Table 2), and a Kruskal-Wallis ANOVA revealed a marginal trend of decreasing diversity with increasing urbanization intensity (Kruskal-Wallis test statistic = 4.769, $p = 0.092$).

The PCA of the carabid data (Fig. 2) showed distinct clustering of the sites, with clear separation according to urbanization intensity. The cumulative percentage of variance explained by the first two axes of the ordination were 39.3% and 56.1% respectively. Separation of the sites occurred in three different directions within two-dimensional space. The urban sites separated negatively along the X-axis, the suburban sites positively along the Y-axis and the rural sites towards positive X and negative Y.

The incorporation of relevant species characteristics into the PCA (Fig. 2) showed that species which are able to fly and utilize open habitat (e.g. *Amara brunnea*, *Leistus ferrugineus* and *Pterostichus strenuus*), were relatively more abundant in urban and suburban sites, whereas flightless species (e.g. *Pterostichus niger*, *Carabus nemoralis*, *C. hortensis*), were restricted to rural and suburban sites. Open habitat species were predominant in the urban sites.

TABLE 2. Brillouin diversity index for each site, including the mean values for each area.

Site	Urban	Suburban	Rural
1	1.34	1.43	1.62
2	1.49	1.67	1.56
3	1.58	1.47	1.77
4	0.72	1.52	1.55
Mean	1.28	1.52	1.63

DISCUSSION

Effects of urbanization upon carabid communities

Our results indicate that urbanization has a negative effect upon carabid species richness and abundance. Both species richness and abundance were markedly reduced in the urban sites compared to the other two levels, although the abundance effect along the gradient was not statistically significant at the 5% risk level. Mean diversity also decreased with increasing urbanization (rural > suburban > urban). Our hypothesis that urbanization has a strong, negative effect upon carabid communities in boreal forests is thus supported.

The ordination results showed a complex pattern, though the sites grouped reasonably well according to

Appendix 2. Numbers of carabids caught from sites U1-4 (urban), S1-4 (suburban) and R1-4 (rural) for each species. The abbreviations are those used in the ordination figure.

Species	Abbreviation	U1	U2	U3	U4	S1	S2	S3	S4	R1	R2	R3	R4	Total
Amara brunnea (Gyllenhal, 1810)	amarbrun	3	2	2	2	4	10	65	62	7	0	12	0	169
A. eurynota (Panzer, 1797)	amareury	0	0	0	0	0	0	1	0	0	0	0	0	1
Agonum fuliginosum (Panzer, 1809)	agonfuli	0	0	0	0	0	0	0	0	0	0	0	1	1
A. mannerheimii (Dejean, 1828)	agonmann	0	0	0	0	0	0	0	0	0	0	1	0	1
A. obscurum (Herbst, 1784)	agonobsc	0	0	2	0	0	0	0	0	0	0	7	0	9
A. thoreyi Dejean, 1828	agonthor	0	0	0	0	0	0	0	0	0	0	0	1	1
Calathus micropterus (Duftschmid, 1812)	calamicr	22	52	30	49	76	25	59	63	84	37	53	35	585
Carabus glabratus Paykull, 1790	caraglab	0	0	0	0	0	0	0	2	0	2	1	5	10
C. hortensis Linneus, 1758	carahort	0	0	3	1	24	18	17	22	25	20	11	2	143
C. nemoralis Müller, 1764	caranemo	0	3	0	0	16	4	8	0	16	2	0	0	49
Cychrus caraboides (Linneus, 1758)	cychcara	0	0	0	0	1	0	0	0	1	0	0	0	2
Dromius fenestrius (Fabricius, 1794)	dromfene	0	1	0	1	0	0	0	1	0	0	0	0	3
Leistus ferrugineus (Linneus, 1758)	leisferr	1	0	1	1	1	0	0	0	0	0	0	0	4
L. terminatus (Hellwig *in* Panzer, 1793)	leisterm	0	0	1	0	0	0	0	0	1	0	0	0	2
Notiophilus biguttatus (F., 1779)	notibigu	2	2	2	0	1	0	5	0	8	1	0	2	23
Patrobus assimilis Chaudoir, 1844	partassi	0	0	6	0	0	0	0	0	0	0	01	0	7
P. atrorufus (Ström, 1768)	patratro	0	0	2	0	0	0	0	0	94	0	0	0	96
Pterostichus diligens (Sturm, 1824)	pterdili	1	0	1	0	1	0	0	0	1	0	0	0	4
P. melanarius (Illiger, 1798)	ptermela	0	34	0	0	4	7	0	73	316	78	22	0	534
P. niger (Schaller, 1783)	ptemige	6	6	0	0	15	7	0	6	32	44	56	29	201
P. oblongopunctatus (Fabricius, 1787)	pteroblo	6	28	9	8	2	14	73	11	45	30	16	33	275
P. strenuus (Panzer, 1797)	pterstre	1	9	0	1	0	0	2	0	0	0	1	0	14
Synuchus vivalis (Illiger, 1798)	synuviva	1	0	0	0	0	0	0	0	0	0	0	0	1
Trechus rubens (Fabricius, 1792)	trecrube	0	0	0	0	0	0	0	0	0	0	1	0	1
T. secalis (Paykull, 1790)	trecseca	0	1	30	0	1	0	1	1	11	2	4	16	67
Total number of individuals		43	138	89	63	146	85	231	241	641	216	186	124	2203
Total number of species		9	10	12	7	12	7	9	9	13	9	13	9	25

urbanization level. The only exceptions were sites U4 and R4. U4 is the smallest and most isolated of the urban patches but it grouped closely to the rural and suburban sites. There was considerably less trampling here compared to the other three urban sites (Appendix 1), suggesting that the intensity of recreational pressure could be a significant factor in determining the carabid assemblage of urban sites. R4, the most remote of the rural sites and set within extensive forest cover, grouped surprisingly closely to the urban sites. This site was the only rural site in which trampling was detected (Appendix 1), which further supports the suggestion that disturbance due to recreational use could be the explaining factor. Indeed, Grandchamp et al. (2000) found that trampling affects carabid communities in a similar way to that suggested in this study.

There are several possible explanations for the lower carabid diversity in the urban sites. McDonnell et al. (1997) have shown that leaf-litter decomposition proceeded significantly faster at urban sites and that carbon and nitrogen processing proceeded to very stable forms, from which they were unavailable for re-utilization. This result implies that the cycling of the two most important nutrients in ecosystems, upon which whole food chains depend, could have been replaced by sinks which, whilst not destroying them, effectively remove these nutrients from the food chain. This could account for the dramatic reduction in carabid species richness and abundance in urban sites reported in this study.

Species characteristics and the urban habitat

Consideration of individual species trends supports the suggestions that:

1. Urbanization has a negative impact upon the abundance of even the most abundant species, with the single exception of *Calathus micropterus*
2. Forest specialist species do not thrive in areas which are affected even by quite moderate levels of urbanization, and
3. The species which are more abundant in urban sites are generalist species and species of open habitat (*Leistus ferrugineus* and *Patrobus atrorufus*), capitalizing on the altered conditions of this disturbed habitat.

A major component of anthropogenic impact upon boreal forests is habitat fragmentation (Andrén, 1997; Hanski, 1999). The forest cover of the study region has become highly fragmented, particularly during the latter

APPENDIX 3. Carabid species characteristics which could affect dispersal ability and recolonization prospects. Details of wing morphology are shown, as definite knowledge of flight ability is unavailable for many species. Fields refers to the ability of species to utilize agricultural land, dry/wet indicates hygrophilia. U/R shows preference for rural or urban areas, with (U) indicating possible preference for the urban environment (Thiele, 1977, Lindroth, 1985, 1986, 1992; Kinnunen, 1999).

Species	Wings	Fields	Wet/dry	Gen/ Spec	U/R	Comments
Amara brunnea	Full-winged	+/–	Dry	Generalist	U	Open, deciduous
A. eurynota	Full-winged	Yes	Dry	Atypical	U	Open land
Agonum fuliginosum	Reduced, some full-winged	No	Wet	Specialist	R	Wet woodland, fens
A. mannerheimii	Full-winged, probably non-functional	No	Wet	Very specialized	R	Wet, dark spruce forests
A. obscurum	Usually reduced	No	Wet	Specialist	R	Dark forests, moss, litter
A. thoreyi	Full-winged	No	Wet	Atypical		Forests, fens
Calathus micropterus	Constantly reduced	+/–	Dry	Generalist	U	Warm, dry forests, open
Carabus glabratus	Rudimentary	+/–	Wet	Specialist	R	Dark spruce forests
C. hortensis	Rudimentary	+/–	Dry	Forest		Mixed forests
C. nemoralis	Rudimentary	Yes	Dry	Generalist	U	Light forests, parks, open
Cychrus caraboides	Virtually totally reduced	No	Wet	Atypical		Shady, deciduous forests
Dromius fenestrius	Capable of flight	No	Dry	Atypical		Pine forest canopy
Leistus ferrugineus	Varies, often non-functional	Yes	Dry	Generalist	U	Open, woodland
L. terminatus	Varies, often non-functional	+/–	Wet	Atypical		Hardwood forests
Notiophilus biguttatus	Dimorphic	+/–	Dry	Generalist	U	Forest clearings
Patrobus assimilis	Constantly rudimentary	Yes	Dry/wet	Generalist	U	Open, forests
P. atrorufus	Constantly rudimentary	Yes	Wet	Generalist	U	Alluvial deciduous forests, parks, fields
Pterostichus diligens	Mostly rudimentary, some full-winged	Yes	Wet	Generalist		Swamps, meadows, forests
P. melanarius	Usually rudimentary; some full-winged	Yes	Not too dry	Generalist	U	Open, fields & parks
P. niger	Full, possibly non-functional	Yes	Wet/dry	Generalist		All forests & parks
P. oblongopunctatus	Full-winged, but never flies	+/–	Dry	Generalist	U	Forests, light & dry
P. strenuus	Dimorphic, strong or reduced	Yes	Wet	Atypical	U	Deciduous forests, open
Synchus vivalis	Dimorphic, strong or reduced	Yes	Dry	Atypical	U	Dry, open country
Trechus rubens	Full-winged	Yes	Wet	Generalist		Open, forest, water
Trechus secalis	Constantly reduced	Yes	Wettish	Generalist	U	Woodland, open

half of the 20th century (Wuorenrinne, 1978). The urban and suburban areas of the gradient contain a mosaic of mostly small patches of forest, parks, wasteland and asphalt, the proportion of asphalt and the small size of the forest patches being more marked in more urban areas. The size, width and connectivity data in Appendix 1 give an indication of how much each site is affected by fragmentation and edge effects. Although sites U2 and U3, for example, are situated in a 440 ha patch of forest, the portion of it which lies within the urban region and contains these sites, is in the form of a narrow strip, c. 300–500 m in width. These sites were actually quite species rich, though this was predictably due to the presence of open habitat generalist species and species which are atypical of the spruce forest habitat (Halme & Niemelä, 1993). Edge effects and intense recreational pressure thus appear to counteract the advantages conferred upon these sites by their large size and connectivity with extensive forest.

Communities generally contain a few very abundant species and a comparatively large number of scarce species (Magurran, 1988; Niemelä, 1993). Generalist species usually fall into the former of these groups and specialists mostly into the latter. Thus, even if several specialist species were lost from a community, this would be unlikely to have any discernable effect upon carabid abundance, though species richness should decrease. Despite this, however, a loss of abundance was also evident, although not significantly so. Most of the highly abundant generalist species, e.g. *Pterostichus melanarius*, *P. niger*, *P. oblongopunctatus* and *Carabus hortensis*, which are readily able to utilize even highly disturbed habitat, were less abundant in the urban sites. Thus we can surmise that either urbanization is resulting in a significant loss of resources available or that it is otherwise making the environment more harsh.

Wet forest habitats, decaying wood and extensive forest cover are scarce in urban areas (Karjalainen, 1991), though can still be found in the rural region. The rarest habitat specialist species caught in this study, *Agonum mannerheimii*, as well as the scarce *A. fuliginosum*, *A. thoreyi* and *Trechus rubens*, are all dependent on such features and were only found from the rural region. *A. mannerheimii,* in particular, is in decline within the Fennoscandian region (Niemelä et al., 1987; Lindroth, 1992, p. 611) and is clearly unlikely to benefit from the protection of urban or suburban sites, unless they possess such features as are required by sensitive habitat specialists. Even less sensitive forest specialist species, such as *Carabus glabratus*, are also quite rare in the more urbanized sites. This supports the suggestion that urban forests are inhospitable places for the forest carabids of the region.

One of the questions which this study set out to answer was whether Connell's (1978) hypothesis of greater diversity at intermediate levels of disturbance applies to the case of carabid diversity along an urbanization gradient. In this study, neither the Brillouin diversity index nor the species richness values support the suggestion of higher diversity in the intermediately disturbed suburban sites. This could be due to the intensity of the negative effect of urbanization, which has been demonstrated in this study.

The urban and suburban areas also contained a couple of species for which there were equally few recordings, *Amara eurynota* and *Synuchus vivalis*. These, however, are not regionally threatened species but are species which are atypical of the hemi-boreal, spruce-forest habitat (Lindroth, 1985, 1986). They are species which generally prefer drier, more open habitat (Appendix 3), apparently taking advantage of the altered conditions of the more urban forest sites. Such areas are thus providing an opportunity for some species to gain access to a new kind of habitat (Eversham et al., 1996) but this is always likely to be at the cost of the most sensitive species, such as *Agonum mannerheimii* and a large number of similarly sensitive species which were not captured in this study (Halme & Niemelä, 1993).

The ability of species to utilize open countryside and to fly might significantly affect different species' persistence prospects in the more urbanized areas. Indeed, the PCA shows that flight-capable species which were able to utilize open habitat (e.g. *Amara brunnea*, *Leistus ferrugineus*) were predominant in urban and suburban areas. These traits are obviously of benefit to species inhabiting areas where the forest cover is more fragmented and interspersed with parks, streets and buildings. Flightless species, on the other hand, were more predominant in rural and suburban sites, as their dispersal between the more isolated urban habitat patches will be handicapped. Accordingly, all of the species which were predominant in urban sites were also those which utilize open habitat. Thus, consideration of species characteristics suggests that flight ability and the ability to utilize open habitat, which are commonly traits of generalist species, confer an important advantage in more urbanized habitats. Flightless species in particular are thus more common in non-urban sites.

Implications for the management of urban forests

It is quite evident that altered environmental conditions are resulting in assemblage changes in urban forests, as exemplified here for carabid beetles. There is also a growing awareness of the need for appropriate strategies for the management of urban green areas, with consideration of specific objectives such as aesthetic, recreational and economic interests, as well as sustainable developement criteria, such as biodiversity and the amelioration of pollution (Gilbert, 1989). This study illustrates the need for the implementation of, and evaluation of, potential measures to improve the biodiversity of urban green space. Measures to improve the quality and connectivity of urban green spaces must be planned in accordance with the needs of the most sensitive species, rather than being content with connectivity elements in the form of strips of lawn or trees. Many of the habitat features of which these sensitive species require in forested regions are well known, such as dead and decaying trees and woody material, as well as wet forest, mature deciduous trees and natural water-channels (Karjalainen, 1991). Attempts are being made to include these into urban green networks but they must also be preserved in, and introduced into, the corridors which connect urban green spaces (Bueno et al., 1995). Without urban green corridors which are planned for and function effectively for sensitive and specialist species, there is little possibility of improving the biodiversity of urban green space. However, as Niemelä (2001) points out, the functioning of ecological corridors is a question of considerable controversy and it is evident that more research is needed on the usefulness of ecological corridors in the urban setting.

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