The effects of trampling on assemblages of ground beetles (Coleoptera, Carabidae) in urban forests in Helsinki, Finland

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Abstract. The occurrence of carabid beetles in relation to trampling was examined in urban forest sites located in the city of Helsinki, southern Finland. The degree of wear of the forest floor was assessed and used as a measure of trampling intensity. In particular, we examined the following predictions: (1) carabid diversity should decrease with increasing trampling intensity, (2) mean body size of the dominating carabid species should decrease with increasing trampling intensity, and (3) opportunistic species should gain dominance in severely trampled sites. In total, 1,326 beetles representing 27 species were captured. The first prediction was not supported, as there was no correlation between species richness or Hill's N2 diversity index and trampling intensity. However, there was a positive correlation between number of carabids captured and trampling intensity of the site. The second hypothesis gained some support, as there was a marginally significant negative correlation between body size and trampling intensity. The hypothesis that opportunistic species should gain dominance in severely trampled sites was supported as one species was very dominant (*Pterostichus melanarius*, 60.0%) in the heavily trampled sites, while there were two equally and less dominant species in the less trampled sites. Individual species did show different responses to the effects of trampling, and the most sensitive forest species may not survive in the heavily trampled sites. We conclude that at the community level (e.g., species richness, diversity), the effects of trampling on carabids in urban forests are subtle, but impacts are pronounced for some sensitive species.

Keywords: Carabidae, trampling disturbance, urbanisation

Introduction

Urbanisation, the conversion of rural land to urban land (McDonnell *et al*., 1997), is as old as civilisation, but its effects on the environment have become more pronounced during the last decades as cities have grown (Davis, 1978; McDonnell *et al*., 1997). Increased human population in cities and the associated disturbances, such as trampling in urban green areas, is a threat to many habitats causing extinction of some species (Niemelä, 1999). However, human disturbance also creates new conditions for species (Davis, 1978), and these altered habitats can maintain a high species diversity, even including rare species (Frankie and Ehler, 1978; Niemelä, 1999, 2000). Furthermore, the specific conditions of urban habitats, such as high degree of disturbance, lead to modification of the original species composition

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(Czechowski, 1982). If we want to understand how biodiversity is affected by urbanisation, it is important to study the response of organisms to human-caused disturbance and to evaluate which processes are relevant in urban habitats. This understanding could provide a framework for sustainable management of urban habitats.

Carabids are appropriate bioindicators, as they are ecologically and taxonomically well known, species-rich, abundant and are sensitive to human disturbance (Niemelä *et al*., 2000). Characteristics of carabid beetles in various habitats have been well studied (Parmenter and MacMahon, 1984; Gaston and Lawton, 1988; Rushton *et al*., 1989; Loreau, 1992), and carabids are known to be sensitive to environmental variation, especially to changes in vegetation caused by various factors, such as forestry (Niemelä *et al*., 1994) and urbanisation (Niemelä *et al*., 2002). Thus carabids are commonly used as ecological indicators for conservation monitoring (Eyre and Luff, 1990; Luff, 1996; Brown, 1997; New, 1998).

In this study, we examine carabid assemblages in forested areas in the city of Helsinki, southern Finland, in relation to trampling intensity of the sites. Our aim is to assess whether the three responses of community structure to stressors, suggested by Gray (1987, 1989), apply to carabid communities in urban forests affected by different levels of trampling: (1) diversity of species communities should decrease with increasing trampling intensity, (2) mean body size of the dominating species should decrease with increasing trampling intensity (see also Blake *et al*., 1994), and (3) opportunistic species should gain dominance in severely trampled sites.

Material and methods

Study sites and carabid sampling

Fourteen study sites were selected from 10 forest areas in the northeastern part of the city of Helsinki, southern Finland (*ca*. 60°N). However, site 2 had to be abandoned, as too many traps were constantly destroyed. Therefore 13 sites were used in the analyses (Table 1).

Sites were selected on the basis of similarity of vegetation. Most sites were located in separate forest areas, except for sites 3, 4, and 5, which were in one forest area, and sites 7 and 8, which were in another (Table 1). The forests were mesic, *Myrtillus*-type in the Cajanderian classification and of natural origin. They were dominated by pine (*Pinus sylvestris*), spruce (*Picea abies*), birch (*Betula* spp.) or a mixture of them. Herbs and grasses, such as *Vaccinium* spp. dominated the field layer. The soils of the sites are podsol-type soils typical for boreal coniferous forests. However, owing to effects of trampling, soils have been compacted and altered in the most heavily disturbed sites.

The sizes of the 10 forest areas within which the 14 sites were located varied from one to over a hundred hectares. The distinct forest stands within the forest areas in which the sampling sites were located ranged from 0.02 to 4.02 ha. When stands were located within larger forest areas, stand size was determined from forest survey maps.

There are differences in the sites as regards their location in relation to residential areas, roads, and other physical structures (Table 1), which may affect carabid communities in addition to the level of wear. However, these effects appear to be of minor importance in relation to the overriding effects caused on vegetation and the ground by trampling by

Table 1. Description of study sites 1–14 (site number 2 had to be abandoned because of continuous disturbance of the traps), their classification into three trampling intensity classes (low [≤ 100 units], intermediate [$100 < x \leq 300$], and high [>300 units]), and brief descriptions of the characteristics of the sites.

Site	Trampling	Intensity	Characteristics
1	397	High	Near blocks of flats, ± 200 m from a busy street. Moist and contains some garbage. Situated by rocks and fields.
3	270	Intermediate	500 m from nearest street, divided into two by a large trail.
4	54	Low	Large trails and many rocks. Dry. Less than 500 m from street.
5	102	Low	A remote site. Moist with ferns. Next to a dog walking area. Contains garbage.
6	55	Low	Surrounded by agricultural fields. Remote and moist.
7	302	Intermediate	Close to sport grounds and fields. Situated on a hill.
8	179	Intermediate	Beside a block of flats. Close to a street.
9	194	Intermediate	Close to houses and blocks of flats. Next to a highway. Moist with a high density of young trees.
10	220	Intermediate	Isolated, humid forest. Close to an infrequently used road and a housing area.
11	186	Intermediate	In a housing area near a kindergarten. 100 m from a busy road. Moist ground.
12	53	Low	Most remote site, ± 1 km from nearest road. Moist ground.
13	762	High	Near a school. Next to a field and houses.
14	566	High	In a housing area with streets on either side of this site. Plenty of rubbish.

humans. We developed a measure of trampling intensity that can be used to quantify the level of such human-caused disturbance in urban forests. Trampling intensity was determined by measuring the surfaces of trails in three randomly selected plots of 100 m² per site. Four trail-wear classes were used (Lehvävirta, 1999): 1 = visible effects of trampling, vegetation damaged, but only a little reduced in cover; 2 = visible effects of trampling, vegetation damaged and reduced in cover, but not completely worn out, sometimes stones and tree roots uncovered; 3 = little or no vegetation left on the trail, but humus layer not worn out, sometimes stones and tree roots uncovered; and 4 = bare mineral ground or a deep trail dug by trampling, no vegetation left, often stones and tree roots uncovered. Trampling intensity was determined by multiplying trail area with trail-wear class so that busier trails were given more weight. Thus trampling intensity ranges from 0, when there are no trails in the site, to 1200, when the entire area of the three plots (300 m²) is bare mineral ground (trail-wear class 4) (Table 1).

Ten pitfall traps (plastic cups 65 mm in diameter), partly filled with a propylene–glycol and water mixture (1:1) as a preservative, were placed in each site. Traps were set flush with the ground surface, 10 m apart. A square brown cover was placed 2–3 cm above each trap to prevent dilution of the liquid by rain and to make traps less visible. Trapping started on 6 May 1999 and ended on 20 August 1999. During this time, traps were emptied four times. Carabid beetles were identified by using keys in Lindroth (1985, 1986).

Data analyses

To examine the prediction that diversity should decrease with increasing trampling intensity, we calculated the Spearman rank correlation between site-specific trampling intensity values and the following three measures: (1) Standardised number of carabid individuals. The number of individuals had to be standardised by sampling effort, since some traps were lost during some trapping periods. (2) Standardised (rarefied) number of carabid species. Rarefaction is a statistical method for estimating the expected number of species of a random subsample drawn from a larger sample (Simberloff, 1978; Magurran, 1988). (3) Hill's N2, the reciprocal of Simpson's index as a diversity measure, which equates the probability that two individuals drawn at random from an infinitely large community belong to the same species (Ludwig and Reynolds, 1988).

To examine the hypothesis that mean body size of the dominating species should decrease with increasing trampling intensity, the parameter WML (weight median length) was calculated (Blake *et al*., 1994). First, species were listed from the largest body-length to the smallest using the arithmetic mean. Body length data for each species were taken from Lindroth (1985, 1986). Thereafter, species were divided into 2-mm size classes, the first class including beetles of 2–4 mm and the last one those of 24–26 mm. For each size class, length was converted into weight (W) using the following formula: weight $= 0.03069 \times \text{length}^{2.63885}$ (Jarišik, 1989). Biomass for each size class was calculated by multiplying W by N (total number of individuals within a weight class). From this product, the percentage of biomass of each class was calculated as well as the cumulative percentage of biomass. WML is the size of the 50% value of this cumulative biomass (Blake *et al*., 1994). Spearman rank correlation was used to assess the relationship between trampling intensity and WML.

To examine the hypothesis that opportunistic species should gain dominance in severely trampled sites, species rank-abundance relationships (Magurran, 1988) were established for three disturbance levels; high trampling (three sites, trampling intensity exceeding 300 units), intermediate trampling (six sites, trampling intensity $100 < x \leq 300$), and low trampling (four sites, trampling intensity ≤ 100 units) (Table 1).

Finally, the relationship between the occurrence of individual carabid species and trampling was investigated. Species were divided into forest and open habitat species according to Lindroth (1985, 1986) to assess whether habitat association of the species is related to how well they tolerate trampling effects. Mean abundance and species richness of open and forest habitat species were compared among the three trampling levels using Kruskal–Wallis ANOVAs. Furthermore, the relationship between dispersal ability (the ability to fly) and three trampling levels was investigated using Kruskal–Wallis ANOVAs. Species were divided into those that can fly (long-winged and dimorphic species) and those that cannot (short-winged species) (Lindroth 1985, 1986).

Results

A total of 1,326 carabid individuals belonging to 27 species were captured. The number of individuals ranged between 41 and 285 per site, and that of species between 8 and 15 (Table 2). The most abundant species were *Pterostichus melanarius* (29.6% of total catch),

Table 2.   Carabid species captured in this study.

| Species name	High trampling			Intermediate trampling						Low trampling			
	1	13	14	3	7	8	9	10	11	4	5	6	12
Agonum fuliginosum (Panzer, 1809)							1						
A. mannerheimii (Dejean, 1828)		1											
Amara brunnea (Gyllenhal, 1810)	3	2	4	4	1	1	5	16	2	4	2		1
A. communis (Panzer, 1797)	3				2		8	4		3	14		
Badister bullatus (Schrank, 1798)	1			1							1		
B. lacertosus (Sturm, 1815)			1							1			
Bembidion lampros (Herbst, 1784)					1			1					
Calathus erratus (Sahlberg, 1827)							2						
C. melanocephalus (L., 1758)		6	14	1	1		1		1	1			
C. micropterus (Duftschmid, 1812)	3	21	41	9	9	17	17	27	43	10	30	16	6
Carabus hortensis (L., 1758)			1	5	8	3		2	28	2	22	21	6
C. nemoralis (Müller, 1764)	12	10	1	7	9	11	1		1		4	2	
C. violaceus (L, 1758)												3	6
Cychrus caraboides (L., 1758)			1	1					1	1			2
Harpalus quadripunctatus (Dejean, 1829)	1	2					2	1	1			1	
H. rufipes (Degeer, 1774)					1								
Leistus ferrugineus (L., 1758)			1				3		1				
Notiophilus palustris (Duftschmid, 1812)			1			1	1		2				
Patrobus atrorufus (Ström, 1768)	5						2	1					
Pterostichus melanarius (Illiger, 1798)	4	157	185	2	9	4		19	2	6	4		1
P. niger (Schaller, 1783)	3	3	9	1	1	4	17	3		7	4	2	14
P. oblongopunctatus (F., 1787)	10	35	26	6	7	3	20	85	36	3	7	1	5
P. strenuus (Panzer, 1797)	8	1		2	1	4	5	3	3	4	3	1	
P. vernalis (Panzer, 1796)	1												
Syntomus truncatellus (L., 1761)												1	
Synuchus vivalis (Illiger, 1798)				1	2								
Trechus secalis (Paykull, 1790)				3	13	1	2						
Total number of individuals	54	238	285	43	65	49	87	162	121	42	92	47	41
Standardised number of individuals	54	251	292	43	81.3	57.7	87	162	127	42	92	47	42.1
Total number of species	12	10	12	13	14	10	15	11	12	11	11	8	8
Rarefied number of species	11.2	5.9	5.9	12.6	11.4	9.4	11.4	7.0	7.0	10.9	9.1	7.5	8.0
Hill's diversity measure	8.6	2.2	2.2	9.7	8.6	5.4	7.2	3.1	3.8	8.6	5.2	3.2	5.6
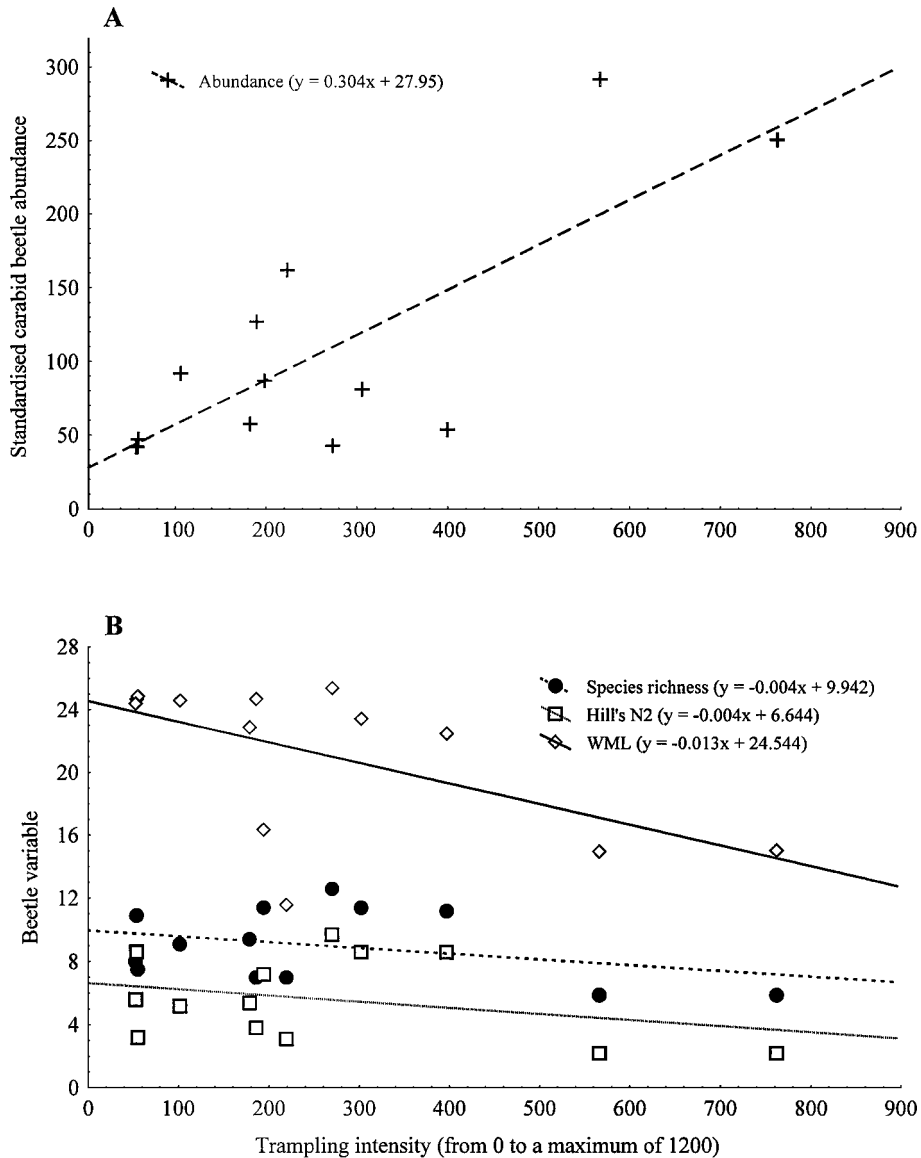
Figure 1. Correlations between trampling intensity and standardised carabid abundance (**A**), and between trampling intensity and rarefied species richness, Hill's N2 diversity measure, and WML (**B**).

Calathus micropterus (18.8%), and *Pterostichus oblongopunctatus* (18.4%). The proportion of each of the next eight species was less than 8% each, and the abundances of the remaining 16 species were less than 0.7% each.

There was a positive correlation between the standardised number of individuals and the trampling intensity (Spearman $r_{s} = 0.621$, $p = 0.024$) (figure 1A), which was caused by
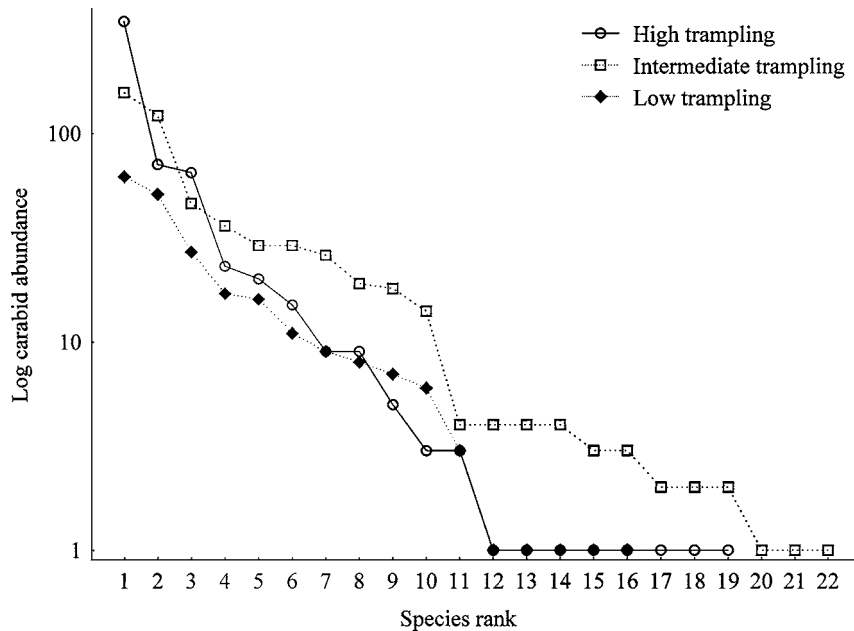
Figure 2.   Rank-abundance distribution of the carabid species in the three trampling intensity categories.

the high abundance of the species *Pterostichus melanarius* in the severely trampled sites. However, the prediction that diversity should decrease with increasing trampling intensity was not supported by our data, as there was no statistically significant correlation between trampling intensity and rarefied species richness ($r_s = -0.116$, $p = 0.706$) or Hill's N2 diversity index ($r_s = -0.185$, $p = 0.544$) (figure 1B).

The hypothesis that mean body size of the dominating species should decrease with increasing trampling intensity gained some support, as there was a marginally significant negative correlation between trampling intensity and WML ($r_s = -0.549$, $p = 0.052$) (figure 1B).

The hypothesis that opportunistic species should gain dominance in severely trampled sites species was supported (figure 2). In the highly trampled sites, the rank–abundance curve is steeper than in the other two trampling classes. This is caused by the high dominance of *Pterostichus melanarius* (60.0%) in the highly trampled sites, while there were two equally and less dominant species in the less trampled site classes: *Pterostichus oblongopunctatus* (29.8% of the catch) and *Calathus micropterus* (23.1%) in the intermediate class, and *C. micropterus* (27.9%) and *Carabus hortensis* (22.9%) in the low trampled sites. However, the highest number of rare species was captured in the highly trampled sites, the lowest number in intermediately trampled sites (figure 2).

The occurrence of forest and open-habitat species was not associated with trampling intensity. Numbers of forest carabid individuals and species were not significantly different across the three trampling intensity levels (individuals: $\chi^2 = 0.61$, $p = 0.74$, species: $\chi^2 =$

Table 3. The six most abundant species and the five species occurring in most sites. A = abundance, S = number of sites occupied by the species, M = sites number where the species was most abundant with symbols indicating high (h), intermediate (i) or low (l) trampling of the site, L = sites where the species was least abundant, N = sites where the species was absent.

Species name	A	S	M	L	N	Species characteristics (Lindroth 1985, 1986)
Pterostichus melanarius	393	11	13 h 14 h		6 l 9 i	Very eurytopic; in parks, gardens, forest edges, and light woods; open and not too dry ground; favoured by human disturbance.
Calathus micropterus	249	13	11 i 14 h	1 h 12 l		Light, warm, and dry forests, also in shaded places in open country; among litter and moss, moderately dry ground; often in company with *Pt. oblongopunctatus*.
Pterostichus oblongopunctatus	244	13	10 i	6 l		Eurytopic woodland species; light stands; moderately dry soil.
Carabus hortensis	98	10	5 l 6 l 11 i		1 h 13 i 9 i	Typical forest species; humus-rich, rather dry soil.
Pterostichus niger	68	12	9 i 12 l		11 i	Characteristic of woodland; humus-rich, rather moist soil.
Amara brunnea	45	12	10 i		6 l	Shady habitats, open forests, also found in open country; among mosses and leaves.
Pterostichus strenuus	35	11	1 l 9 i		12 l 14 h	Characteristic species of the litter layer of damp deciduous forest on clayey, mull-rich soil, also in shaded sites in open country.
Trechus secalis	16	4	7 i			Moist, rather shaded sites, in woodland as well as in open country in rich meadows; under dead leaves and other debris, mostly on soil rich in humus.
Carabus violaceus	9	2	6 l 12 l			Eurytopic species; prefers light forests, also to a lesser extent in shady habitat in open country; rather dry soil rich in humus.

2.76, $p = 0.25$). Similarly, the number of individuals and species of open-habitat species were not significantly different across trampling intensity levels (individuals: $\chi^2 = 1.78$, $p = 0.13$; species: $\chi^2 = 2.29$, $p = 0.32$). However, the habitat requirements of individual species correspond well with their occurrence across the trampling classes. Table 3 lists the five most abundant species and the six species occurring in most sites with their ecological characteristics and habitat requirements.

There were no differences between the number of individuals ($\chi^2 = 3.63$, $p = 0.16$) or species ($\chi^2 = 0.14$, $p = 0.93$) of flying species among the three trampling intensity levels. Similarly, there were no differences in the number of individuals ($\chi^2 = 0.11$, $p = 0.95$) of nonflying species, but there were significantly fewer nonflying species in the low trampling sites than in the other trampling intensity categories ($\chi^2 = 6.90$, $p = 0.03$).

Discussion

Our results showed that in urban forests human disturbance in the form of trampling had some effects, but no profound effects, on carabid communities. As a consequence, the hypotheses of community response to stress proposed by Gray (1987, 1989) and applied here to urban forests with varying degrees of trampling disturbance were only partly supported.

The proposition of decreasing diversity with increasing stress (trampling in our study) was not supported. We detected no relationship between species richness or diversity and trampling intensity. Furthermore, there was a positive correlation between the number of carabid individuals and trampling intensity, which was caused by the high abundance of one species, *Pterostichus melanarius*, in the severely trampled sites. The dominance of this species was also reflected in the species abundance patterns (see below). Interestingly, this European species has been introduced to North America and is the most common carabid species in the Canadian city of Edmonton (Niemelä and Spence, 1991, 1994), which suggests that it has successfully adapted to urban habitats across the northern temperate-boreal zone.

The hypothesis that mean size of species should decrease with disturbance was supported by our findings, as there was a negative correlation between trampling intensity and WML. Carabid body size has been shown to correlate negatively with trampling intensity, so that heavily trampled sites are dominated by small species and lightly trampled sites by large species (Tietze, 1985; Šustek, 1987, 1992). For instance, Blake *et al.* (1994) showed that carabids in intensively managed grasslands were of smaller body size (WML) than were carabids in less intensively managed sites. Furthermore, Klausnitzer (1983a) found that disturbed urban areas hosted carabids of smaller average body size than did less disturbed sites at the city edge. Similarly, Pearsall and Walde (1995) found that abandoned apple orchards were characterised by the large species of the genus *Carabus*, while managed orchards were dominated by smaller species, such as *Harpalus rufipes* and *Pterostichus coracinus*. In our study, the large *Carabus hortensis* was particularly sensitive to trampling, as has been detected in other studies as well (Halme and Niemelä, 1993). However, *C. nemoralis*, which according to Pearsall and Walde (1995) was found in less disturbed habitats, was quite abundant in our heavily trampled sites.

There are three, mutually nonexclusive explanations for the large-bodied carabid species being more sensitive to disturbance than small-bodied species. First, small-bodied carabids usually have a higher reproductive output than large-bodied species (Grüm, 1984; Lövei and Sunderland, 1996) and are therefore more likely to sustain viable populations in highly disturbed areas, here highly trampled urban forests. Second, larval mortality is considered to be the key factor for adult fluctuations in carabids (Den Boer, 1986). As carabid larvae are soil bound and less mobile than adults (Lindroth, 1992), disturbance of the litter and soil are important in determining their survival and thus adult population size. Large-bodied carabids usually have longer life cycles, particularly longer larval periods, which are more sensitive to soil disturbances than larvae of small-bodied species (Blake *et al.*, 1994). Third, highly trampled urban areas possibly support fewer prey items, or a higher fluctuating food source, which favour small-bodied and often winged species (see Blake *et al.*, 1994).

The numerical dominance of *P. melanarius* in the heavily trampled sites (60% of the sample) supports the prediction that opportunistic species should gain dominance in stressed

environments. This species is a habitat generalist and favours disturbed sites (Lindroth, 1986). Furthermore, it has been introduced from Europe to North America, where is has very successfully invaded urban and other disturbed areas in temperate and boreal regions (Niemelä and Spence, 1991). Similar numerical dominance by one or a few carabid species was reported by Klausnitzer (1983b) in Leipzig (Germany) and Czechowski (1982) in Warsaw (Poland).

Interestingly, climax boreal forests have a similar species-abundance structure with the sites in our study. Boreal forests are dominated by very few carabid species due to the harsh conditions of this habitat (Niemelä, 1993). Thus it appears that conditions in cities and in climax boreal forests favour species that are adapted to stressed environments allowing them to become abundant. This dominance creates a community structure typical for stressed environments.

Although community measures of carabids such as species richness and diversity did not vary consistently with trampling level, examination of the characteristics of individual species suggested that carabids indicate changes in urban forests. The occurrence of species associated with open habitat (*Calathus melanocephalus*, *C. erratus*, *Bembidion lampros*, *Harpalus* spp.) in the intermediate and highly trampled sites is probably caused by the favourableness of this habitat for such species (i.e., openness and scarcity of ground vegetation). Invasion of such species into urban forests from the surrounding grasslands is common and increases with decreasing size of the forest patch (Halme and Niemelä, 1993; Niemelä, 2001). Furthermore, many of the open-habitat species are able to fly (Lindroth, 1985, 1986), enabling them to colonise suitable sites rapidly and perhaps leave unfavourable ones.

Our study showed that some aspects of carabid characteristics, such as average body size of species and flight ability, are associated with trampling in urban forests. However, these responses are subtle and masked by high variation among sites of the same trampling intensity. Furthermore, there are confounding factors that were not measured in this study. Thus inclusion of variables such as history of the site, its physical and biotic characteristics including canopy closure and soil moisture could allow better comparison of the sites. For instance, in a study in Scotland, Blake *et al*. (1996) showed that history and habitat type of the site were more important than management practises such as grazing, cutting, and fertilisation for the composition of carabid communities. One of the important features of urban green areas is their historical uniqueness, which stems from the varying degree of human-induced disturbance resulting in a number of successional paths across habitat patches (Niemelä, 1999). Even adjacent patches may exhibit different succession paths depending on human-use and colonisation history of plants, which is to a great extent determined by chance events (Gilbert, 1989). This historical uniqueness and overwhelming external control of succession is an important feature distinguishing urban habitats from more natural ones (Trepl, 1995) and deserve more research.

Acknowledgments

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