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ORIGINAL PAPER

Effects of habitat edges and trampling on the distribution of ground beetles (Coleoptera, Carabidae) in urban forests

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Abstract Urban forest patches are generally small with highly contrasting edges bordering non-forest habitat, landscape features that increase with urbanisation. These forest patches are also subject to high human foot traffic resulting in trampling and other user disturbances that affect their quality as habitat for invertebrates. We studied the effects of these factors on carabid beetles in urban forests in the cities of Helsinki (Finland) and Edmonton (Canada). In both cities, the structure of carabid assemblages was affected by trampling intensity and distance to the forest edge. Moderate intensity of trail use was associated with increased beetle captures, especially in Edmonton. The effects on individual species were apparent in Edmonton but harder to demonstrate in Helsinki where forest specialist species may have been largely extirpated already. We suggest that these differences result because there has been a long history of fragmentation of urban forest patches in Helsinki, species loss from such patches is gradual, and understorey vegetation structure constrains human foot traffic in forest patches more in Edmonton than it does in Helsinki.

Keywords City · Fragmentation · Recreational · Urban woodlands · Wear

Introduction

Urban remnant forests worldwide are highly fragmented and used extensively for recreation (Liddle 1997; Arnberger 2006; Carreiro et al. 2008). Where the goal is to keep such urban habitat patches as natural and biodiverse (see Kowarik 2011) as possible, effective guidelines for their management should flow from comparative ecological research (Dennis and Ruggiero 1996; Niemelä 2000; Lehvävirta and Kotze 2009). Studies of insect assemblages can help us objectively assess the 'naturalness' of such habitats and monitor how this value changes over time and with degree of human impact (Niemelä and Kotze 2009; Magura et al. 2010). Urban forest patches, especially in the boreal zone, have sharp habitat edges and dense networks of maintained trails and other paths (Hamberg et al. 2008) resulting from off-trail traffic. Despite the ecological importance of such features, basic ecological information about associated within-patch responses of urban invertebrates is scarce.

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Compared to interiors, forest edges are generally characterised by more variable light, temperature and wind conditions, and are consequently drier (Chen et al. 1993; Murcia 1995; Laurance 1997). Thus, open-habitat insect species as well as some generalists are characteristic of edge habitats (Spence et al. 1996; Matlack and Latvaitis 1999; Magura et al. 2001; Taboada et al. 2004). Forest edges may also be more fertile, at least in boreal cities (see Hamberg et al. 2008, 2009; Malmivaara-Lämsä et al. 2008). This may additionally affect the vegetation and microclimatic conditions at edges, and consequently influence the fauna associated with particular vegetation types. Although a considerable amount of research has been done on carabid beetles at habitat edges (e.g., Spence et al. 1996; Heliölä et al. 2001; Taboada et al. 2004; Koivula et al. 2004; Sroka and Finch 2006), and in urban environments in general (Grandchamp et al. 2000; Fujita et al. 2008; Niemelä and Kotze 2009), less is known about how carabids respond to forest edges in urban areas. Lehvävirta et al. (2006) and Gaublomme et al. (2008) showed that forest generalist species occur more frequently at urban forests edges than in interiors in Helsinki (Finland) and Brussels (Belgium), respectively. Furthermore, carabid catches seem to increase at the edges of urban buckwheat shrub systems in California, USA (Bolger et al. 2000) and oak-sycamore woodlands in Birmingham, UK (Sadler et al. 2006). Small urban forest patches, especially those dissected by trail systems, may take on the characteristics of edge habitats, slowly changing the species pool that originally existed there.

Recreational use of urban forests is frequently associated with a dense network of planned and unplanned footpaths on the forest floor. These and the access they promote lead to disturbance and small-scale fragmentation of the vegetation, and to erosion of the humus layer and even the mineral soil (Florgård 2000; Littlemore and Barker 2001; Malmivaara et al. 2002; Ikeda 2003; Sadler et al. 2006). Other effects of paths can also be observed in urban forest patches, e.g., soil compaction, moisture and nitrogen (and fertility) decrease off paths in urban forests, while pH either increases or decreases with distance from paths (Godefroid and Koedam 2004; Malmivaara-Lämsä et al. 2008). Cover and species richness of understorey vegetation are affected up to 10 m, and possibly further, off these paths (Godefroid and Koedam 2004; Hamberg et al. 2008).

Little information exists about the effects of footpaths on the ground-dwelling fauna in urban forests, as represented by carabid beetles. At the scale of forest stands, Grandchamp et al. (2000) suggest that trampling affects the carabid beetle community only slightly, but Lehvävirta et al. (2006) documented dramatic effects of trampling at the species level. Although Sadler et al. (2006) were not able to separate the effects of trampling from other urban stressors, their results also suggest that carabid beetle assemblages are sensitive to trampling. Collectively, the studies above suggest that carabid beetle assemblages are impacted by recreational pressures in urban environments in ways that make them less similar to assemblages of patches not exposed to recreational activity.

In this paper, we investigate the general hypothesis that carabid beetle assemblages respond to edge effects (distance from the forest edge) and trampling (distance from paths and levels of wear of these paths) as they occur in urban forest patches (see Hamberg et al. 2008). We predicted a gradient of response to edge and trampling effects, from negative for populations of forest and hygrophilous carabid species to positive for open-habitat and xerophilous populations. Additionally, we explored the responses of carabid beetles to a set of vegetation and environmental variables obtained from studies that form part of the 'Edges and Trampling' project on invertebrates, flora and soils of urban forests (see Isaksson 2004; Hamberg et al. 2008, 2009; Malmivaara-Lämsä et al. 2008). Finally, we assessed the generality of carabid responses through a comparison of results obtained from similar intercontinental studies in two northern cities, Helsinki, Finland and Edmonton, Canada.

Methods

Study areas and sampling design

The study was performed using the main urban forest types in Helsinki and Edmonton, two boreal cities with similar sized human populations, but different histories of human occupation. Forest edges were defined as the outermost line connecting trunks of mature trees. South to west facing edges were chosen for the study to maximise the potential effects of the edge (Ries et al. 2004; Hylander 2005). All edges investigated were more than 10 years old and bordered developed areas, such as buildings, roads or paved areas, but not parks. Patches that had been thinned recently or were situated on slopes were excluded from investigation. In Helsinki, 33 mesic forest patches dominated by Norway Spruce (*Picea abies*) (*Myrtillus* type, Cajander 1926; Kuusipalo 1996) were selected. The dominant trees in these patches were >85 years old. In Edmonton, 20 patches of Trembling Aspen (*Populus tremuloides*) stands were selected. The canopy-dominant trees in these patches were >60 years old. In both cities, forest patches were either bounded by urban infrastructure or a different habitat type.

Pitfall traps (diameters 65 and 110 mm, depths 70 and 80 mm in Helsinki and Edmonton, respectively) were used to estimate activity-density of the carabid beetles collected (see Thomas et al. 1998). Traps were placed at least 10 m apart to reduce the possibility of spatial correlation of samples (Digweed et al. 1995). Additionally, we tested for spatial autocorrelation of pitfall trap samples by fitting a continuous random walk of order 2 along each transect (Lindgren and Rue 2008) using the INLA library in R (Rue et al. 2009), but model estimates and standard errors changed little when a spatial component was added (results not shown). Plastic roofs were placed 3–4 cm above the traps to prevent litter and rainwater from entering the traps, and a propylene-glycol:water solution (1:1) with a drop of detergent was used to kill and preserve the beetles in the traps. As we aimed to investigate the possible effects of both habitat edges and trampling (defined as wear on forest paths and distance from the paths), we placed the traps adjacent to and further away from paths showing varying levels of use at varying distances from forest edges (see Fig. 1 in Hamberg et al. 2008).

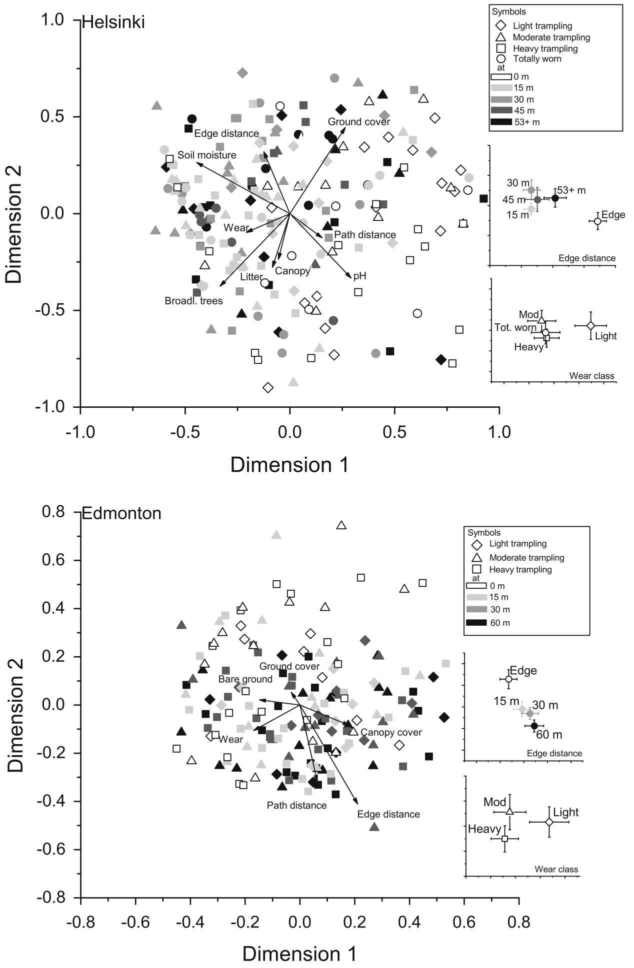

Fig. 1 Two-dimensional GNMDS ordinations of 194 (Helsinki, Finland) and 160 (Edmonton, Canada) pitfall traps placed at the edge towards the urban forest interior and at different distances from paths of varying trampling intensity. Helsinki and Edmonton insert plots: centroids and SE of edge distance and wear classes

The following levels of use were applied to reflect trampling intensity on paths in this study (Lehvävirta 1999): (1) Low—visible effects of trampling, vegetation damaged but only slightly reduced in cover; (2) Moderate—visible effects of trampling, vegetation damaged and reduced in cover, but not completely eliminated; (3) Heavy—generally no vegetation on the path, humus layer still evident but rocks and tree roots sometimes uncovered; (4) Totally worn—very thin and patchy humus layer, no vegetation remaining and bare mineral soil, rocks and tree roots often uncovered. Trampling intensity class 4 occurred in Helsinki but was not evident at any of the sites studied in Edmonton.

In Helsinki, a total of 206 traps were placed in 33 patches at varying distances (0–108.5 m) from forest edges, and next to and up to 11.2 m from forest paths affected by different trampling intensity. Replication depended on availability and not all combinations of edge distance and trampling intensity were present in each forest patch. Ideally, for example, a single patch could have had four edge samples, one each for low, moderate, heavy and totally worn paths. In reality, none of the forest patches had sampling points at all combinations of edge distance and path trampling intensity. Therefore 33 patches were sampled in Helsinki to ensure sufficient replication through an incomplete block design. In Edmonton, a total of 160 traps were placed in 20 separate forest patches that were at least 50 m apart and in four different areas (>10 km apart). Unlike Helsinki, work in each patch in Edmonton focused on only one path, classified as representing low, moderate or heavy trampling. In each patch, traps were placed next to and 10 m from the path at 0 m (edge), 15, 30 and 60 m from the patch edge.

In Helsinki, continuous trapping started on 4 Jun 2003 with traps visited five times until 22 Sep 2003. In Edmonton it started on 31 May 2003 with traps visited three times until 2 Sep 2003. The resulting data included 1030 records in Helsinki (22,454 trap-days) and 480 records in Edmonton (13,544 trap-days). Carabids collected were identified using keys in Lindroth (1961–1969, 1985, 1986).

Within the framework of research performed in the 'Edges and Trampling' project, a suite of vegetation and environmental variables were measured around each pitfall trap (for detailed descriptions on how these variables were measured, see Isaksson 2004; Hamberg et al. 2008; Malmivaara-Lämsä et al. 2008). Of these measured variables, six [canopy cover (%), vegetation cover (%), litter cover (%), soil moisture (%), broadleaf trees (%) and pH] and three [canopy cover (%), vegetation cover (%) and bare ground (%)] were recorded in the Helsinki and Edmonton datasets, respectively (see Table 1 and Appendix 1 in Electronic supplementary material) to explore the factors which influenced responses of beetle assemblages to the urban environment.

Table 1 Summary statistics of the vegetation and environmental variables measured in urban forest patches in Helsinki (Finland) and Edmonton (Canada)

	Mean	SD	Range	Correlate with		
				Edge distance	Wear class	Path distance
Helsinki						
Canopy cover (%)	74.30	29.14	0–100	−0.028 (0.686)	0.005 (0.940)	−0.019 (0.788)
Vegetation cover (%)	45.28	27.66	0.10–139.2	0.268 (<0.001)	−0.010 (0.891)	−0.056 (0.426)
Litter cover (%)	85.29	18.76	15–100	−0.236 (<0.001)	−0.011 (0.872)	0.024 (0.730)
Soil moisture (%)	32.31	10.30	8.29–53.37	0.466 (<0.001)	−0.041 (0.555)	0.079 (0.260)
Broadleaf trees (%)	49.38	33.16	0–100	−0.277 (<0.001)	−0.067 (0.340)	0.008 (0.913)
pH	4.41	0.42	3.67–5.88	−0.510 (<0.001)	0.065 (0.350)	−0.040 (0.565)
Edmonton						
Canopy cover (%)	63.49	18.80	3.13–97.40	0.287 (<0.001)	−0.063 (0.429)	0.229 (0.004)
Vegetation cover (%)	83.48	32.66	0–166.50	0.138 (0.082)	−0.160 (0.043)	0.050 (0.532)
Bare ground (%)	19.82	20.35	0–87.50	−0.005 (0.950)	0.240 (0.002)	0.096 (0.230)

Correlations (Spearman's rho and *P* values) of these variables with distance from the edge, path wear class and distance from the path are also given

Statistical analyses

Global Non-metric Multidimensional Scaling (GNMDS, vegan 1.15-3 package; Oksanen et al. 2009) in R (R Development Core Team 2009) was used to investigate relationships of the edge, trampling and the vegetation and environmental variables measured (Table 1) with the assemblage structure of carabid beetles at both sites. The Bray-Curtis coefficient was used as a dissimilarity measure and permutation tests were used in the vector fitting procedure. GNMDSs presented here were run for each city using all of the variables measured in that city. Similar results, not presented here, were obtained for GNMDSs run with a more restricted set of common variables [edge distance, trampling class, distance from paths, canopy cover (%) and vegetation cover (%)] measured in both cities.

Generalised linear mixed models were used to test our statistical hypotheses, using the glmmPQL function in the MASS package of R (Venables and Ripley 2002). The most frequently collected species ($\geq$50 individuals) were analysed individually, and data about the remaining species of lower activity-density were analysed as groups defined by expected habitat association (see Table 2).

The basic model for both countries included (1) distance from the forest edge as a factor, (2) path wear as a factor, (3) distance from the path as a continuous variable in Helsinki (0.45–11.2 m from the path edge) or a factor in Edmonton (next to and 10 m from the path), (4) forest patch as a random factor (to deal with the dependency of sampling points within a forest patch), (5) collecting visit as a fixed factor (reflecting the time of the season) and (6) log number of trapping days as an 'offset term' to account for trap losses in the field. Although continuous, samples in Helsinki were grouped into six edge distance classes to achieve a more effective comparison with the Edmonton data (i.e., 0 m class = traps placed from 0 to 7.5 m from the edge, 15 m class = traps at 7.6–22.5 m,…, 60 m class = traps at 52.6–67.5 m, and 75 m class = traps at 67.6–108.5 m from the edge). Path wear classes, as explained above, were low, moderate, heavy and totally worn in Helsinki, and low, moderate and heavy in Edmonton. Sampling error of the beetle catch (response variable) was modelled with a negative binomial error distribution (White and Bennetts 1996; O'Hara and Kotze 2010).

Additional GLMMs were run to explore the effects of vegetation and environmental variables on beetle activity-density. These models included the six 'core' (i.e., common) variables from both cities (see above), and the additional variables as outlined in Table 1. As these variables have different units of measurement they were standardised to zero mean and unit variance in order to evaluate their relative contributions to the beetle response (Schielzeth 2010).

Patches from which no individuals of a particular species or species group were collected were excluded from the GLMM analyses for that species or group (see the 'frequency' column in Table 2), as for these patches the reason for a zero catch of the focal species is most likely a stand level factor, while we focused on factors internal to stand level. Trap losses, generally due to disturbance by humans or wildlife, at different times during the activity period of these seasonal beetles can have considerable effects on activity-density estimates and were corrected by including an offset term for the number of trapping days per visit in the models, as described above. Traps were lost on 40 occasions in Helsinki (3.9% loss) and on 44

Table 2 Means, standard errors of means, minimum and maximum catch of the carabid species collected in urban woodlands in Helsinki ($n = 33$) and Edmonton ($n = 20$)

Species	Size (mm)	Wing form	Total catch	Mean catch	SE	Min.	Max.	Freq.
Helsinki (Finland)								
Amara brunnea FM(d)	5.2–6.8	M	234	7.31	1.07	1	26	32
Carabus hortensis FD(m)	22–28	B	80	4.71	0.79	1	11	17
Calathus micropterus FD(m)	6.5–8.8	B	718	23.16	2.96	1	59	31
Pterostichus oblongopunctatus FD(m)	9.5–12.6	M	175	6.25	1.01	1	19	28
Notiophilus biguttatus FD[a]	5–6	D	10	1.25	0.25	1	3	8
Group FM			66	3.47	1.01	1	17	19
Group GM			86	4.53	1.56	1	30	19
Pterostichus melanarius GD(m)	12–18	D	161	6.71	1.52	1	28	24
Pterostichus niger GM(d)	15–20.5	M	372	14.31	5.11	1	134	26
Group OD			43	2.87	0.55	1	7	15
All 28 species			1,945	58.94	7.95	2	252	33
Edmonton (Canada)								
Agonum retractum FM	6–8	D	585	29.25	6.28	3	108	20
Calosoma frigidum FM	17–27	M	166	9.22	2.33	1	36	18
Calathus ingratus F(g)D(m)	7–11	D	1,525	76.25	13.73	9	294	20
Platynus decentis F(g)M	9–14	M	1,143	57.15	9.17	13	146	20
Agonum gratiosum GM	6–9	M	70	5.00	2.21	1	32	14
Pterostichus pensylvanicus GM	10–12	D	480	24.00	5.52	2	88	20
Group FT			30	2.14	0.33	1	5	14
Group GM			35	3.89	1.06	1	11	9
Pterostichus adstrictus GD(m)	10–13	M	179	8.95	1.27	1	22	20
Pterostichus melanarius GD(m)	12–18	D	526	27.68	7.28	1	115	19
Synuchus impunctatus G(o)D	9–11	D	184	10.22	1.52	2	27	18
Group GD			63	3.94	1.16	1	19	16
Group OM			35	2.19	0.37	1	5	16
Group OD			49	3.27	0.63	1	8	15
All 27 species			5,070	253.5	36.23	82	783	20

Species and species groups are listed a priori from most forest/hygrophilic (top) to most open/xerophilic (bottom) per city. Statistics are based on the number of woodlands (Freq.) from which the species were collected. Species are classified into Forest (F), Generalist (G), Open habitat (O), Moist habitats (M) and Dry habitats (D). Habitat affinities are not always certain, and lowercase letters in parentheses indicate alternative affinities. [a] *N. biguttatus* was not analysed due to low numbers. FT: all low-density forest species (Canada only). Wing forms (*M* macropterous, *B* brachypterous, *D* dimorphic) are also given. Finland: Group FM: *A. obscurum*, *B. bullatus*, *C. glabratus*, *C. caraboides*, *D. fenestratus*, *H. quadripunctatus*, *L. terminatus*. Group GM: *L. pilicornis*, *N. palustris*, *P. assimilis*, *P. atrorufus*, *P. diligens*, *P. nigrita*, *P. strenuus*, *S. pumicatus*, *T. micros*, *T. secalis*. Group OD: *C. melanocephalus*, *C. nemoralis*, *H. affinis*, *L. ferrugineus*. Canada: Group GM: *A. sordens*. Group GD: *A. placidum*, *C. chamissonis*, *C. nemoralis*, *P. foveocollis*. Group OM: *A. affine*, *A. thoreyi*, *C. maeander*, *P. septentrionis*. Group OD: *A. cupreum*, *A. cupreolata*, *A. obesa*, *A. thoreyi*, *C. calidum*, *C. cribricollis*, *H. fuliginosus*. Group FT: *H. fulvilabris*, *P. mannerheimii*

occasions in Edmonton (9.2% loss), translating to losses of 926 (4.1% loss) and 1,232 (9.1% loss) trap-days.

Results

Twenty-eight (1,945 individuals) and 27 (5,070 individuals) carabid beetle species were collected from Helsinki and Edmonton, respectively (Table 2). Despite lower sampling effort in Edmonton, overall species diversity was similar between the cities and beetles were notably more abundantly collected in Edmonton. *Calathus micropterus* dominated the Helsinki dataset (36.9% of the total catch), followed by *Pterostichus niger* (19.1%), *Amara brunnea* (12.0%) and *Pterostichus oblongopunctatus* (9.0%). In Edmonton, *Calathus ingratus* (30.1%) and *Platynus decentis* (22.5%) dominated the catch, followed by *Agonum retractum* (11.5%) and the introduced European species *Pterostichus melanarius* (10.4%).

The GNMDS ordinations suggested that distance from the forest edge and trampling intensity affected composition of carabid beetle assemblages in both Helsinki and Edmonton (Fig. 1). In particular, assemblages immediately at the edge differed notably from those further in the

Table 3 Maximum correlations (*r*) of vectors in the GNMDS ordination configurations of pitfall trap samples next to and further away from paths at various distances from urban woodland edges in Helsinki, Finland (194 traps) and Edmonton, Canada (160 traps)

Helsinki variable	*r*	*P*	Edmonton variable	*r*	*P*
Canopy cover (%)	0.024	0.196	Canopy cover (%)	0.082	0.001
Vegetation cover (%)	0.106	<0.001	Vegetation cover (%)	0.015	0.478
Litter cover (%)	0.089	<0.001	Bare ground (%)	0.023	0.307
Soil moisture (%)	0.094	<0.001			
Broadl. trees (%)	0.104	<0.001			
pH	0.112	<0.001			
Edge distance	0.085	0.001	Edge distance	0.128	<0.001
Wear class	0.044	0.035	Wear class	0.025	0.283
Path distance	0.017	0.367	Path distance	0.095	0.001

forests, and assemblages sampled along lightly trampled paths differed from those along paths of higher trampling intensities. Although many were significant, correlations of single environmental variables with the structure of beetle assemblages were generally weak (Table 3). The carabid assemblages in Helsinki correlated most strongly with pH, vegetation cover (%) and broadleaf trees (%). In Edmonton, the beetle assemblage correlated strongest with distance from the edge and distance from the path, two variables of central interest in this study.

In Helsinki, there was no clear pattern of edge sensitivity or affinity for individual carabid species and species groups (Fig. 2a, b; Table 4; see also Appendix 2 in Electronic supplementary material). Nonetheless, data for *C. micropterus*, *Carabus hortensis* (forest species), and *P. niger* (a hygrophilic generalist) suggested some edge sensitivity. In Edmonton, some beetles classified as generalists or open-habitat species, or as being associated with drier habitats, were more abundantly collected at the edges, in accordance with our a priori hypotheses (Fig. 2c, d; Table 4; Appendix 3 in Electronic supplementary material). These included *P. melanarius* and the GD (generalist-dry) and OD (open habitat-dry) species groups. However, increased captures near the edge for *Agonum gratiosum* and *Pterostichus pensylvanicus* (hygrophilic generalists), *A. retractum* (a hygrophilic forest species) and *C. ingratus* (a species of uncertain habitat and moisture affinity) are more difficult to explain in terms of microhabitat affinity. Two species were highly sensitive to the edge. *Platynus decentis* is a hygrophilic, forest habitat or generalist species, but *Synuchus impunctatus* is characterised as a xerophilic generalist or open-habitat species.

Beetles in Helsinki appeared to be insensitive to path trampling intensity (except for *P. niger*), and all forest-associated species were insensitive to distance from the paths (Fig. 3a, b; Table 4; Appendix 2 in Electronic supplementary material). However, the generalist and open-habitat species and groups showed a predictable pattern, with more GM (generalist-moist) individuals collected further from the paths and fewer OD (open habitat-dry) individuals collected further from the paths (Fig. 3b). Carabid catches in Edmonton reflected these habitat features in a fairly predictable way (Fig. 3c, d; Table 4; Appendix 3 in Electronic supplementary material). For example, most species displayed higher activity-density in the vicinity of intermediately trampled paths compared to little and heavily trampled paths (Fig. 3c), and there was a gradient of response to distance from the paths; forest-to-generalist and/or hygrophilic species were collected more frequently away from the paths, while open habitat-to-generalist and/or xerophilic species were more frequent next to the paths, as predicted (Fig. 3d).

Responses of beetles captured in Helsinki to the six environmental variables measured were highly variable (Appendices 2 and 4 in Electronic supplementary material). Overall, pH, soil moisture (%), vegetation cover (%) and litter cover (%) had the largest general effects on beetle activity-density in these forests (see Table 1 for variable details). The effects of higher pH on individual species were particularly remarkable, and mostly positive. For example, across the range of pH values in this study (Table 1), a one unit increase in pH resulted in a three and twofold increase in the predicted number of individuals of *P. oblongopunctatus* and *P. melanarius* respectively, and *P. niger* decreased by a quarter (calculation for *P. oblongopunctatus*: exp(coefficient/SD of pH) = 3.12; see Appendices 2 and 4 in Electronic supplementary material and Table 1). There was a slight trend that hygrophilic species, associated with forest or more generalist in habitat use, increased in activity-density with % soil moisture while species associated with dryness decreased as soil moisture (%) increased, as expected. For example, *P. melanarius* decreased by a third in activity-density in Helsinki with a 10% increase in soil moisture (exp(coefficient/SD of soil moisture × 10) = 0.62). Canopy cover (%) and broadleaf trees (%) affected these beetles minimally.

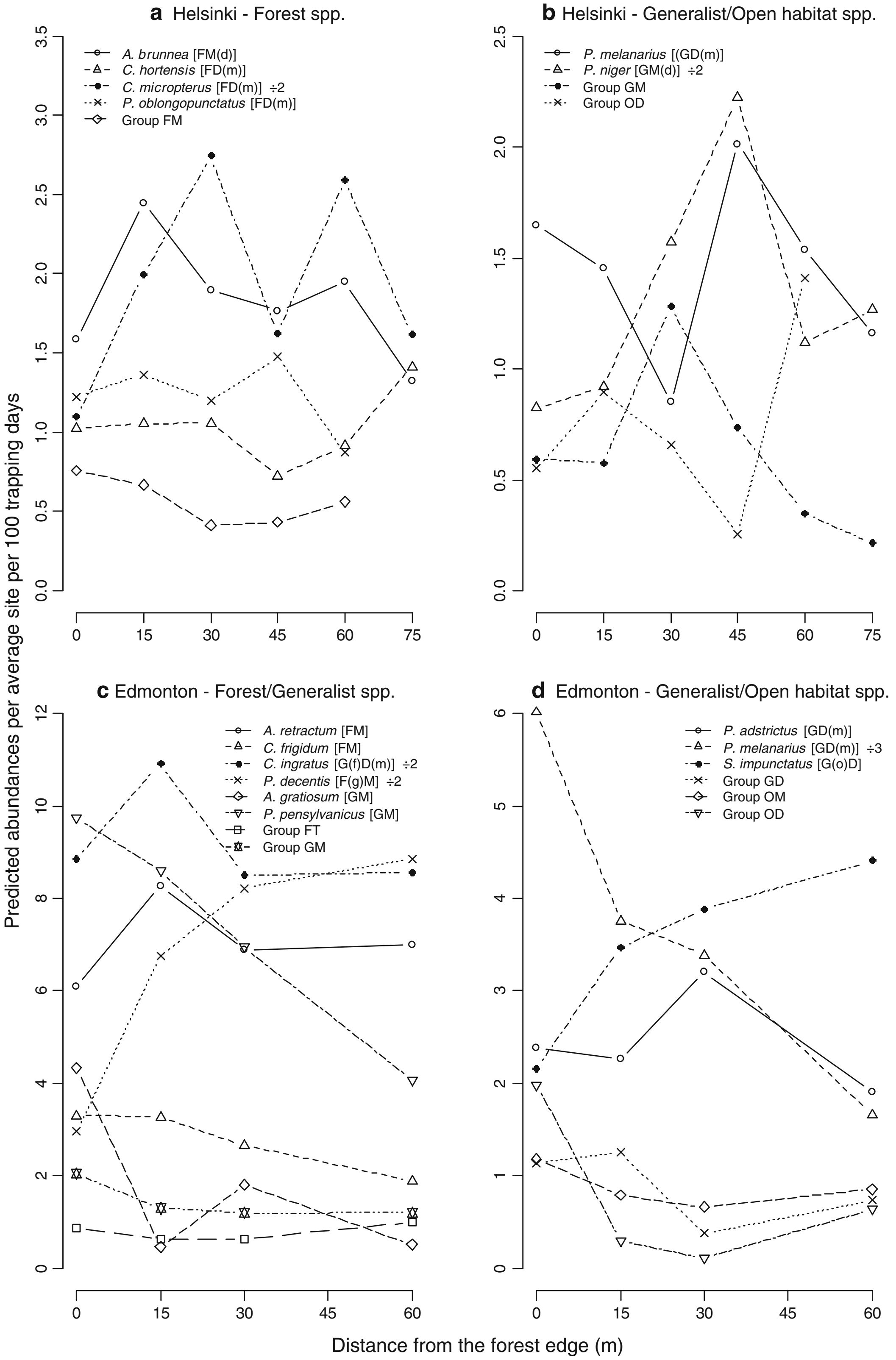

Fig. 2 Carabid beetle responses to distance from the urban forest edge in Helsinki (**a** forest and moisture/dryness associated species, **b** generalist/open habitat, moisture/dryness associated species) and Edmonton (**c** forest/generalist and moisture associated species, **d** generalist/open habitat, moisture/dryness associated species). The activity-density of certain species were divided by a factor for graphical purposes (see values after some species names)

Table 4 Generalised Linear Mixed Model results for species and species groups collected from Helsinki and Edmonton

	Interc.	Distance from the edge (m)					Trampling				
		15	30	45	60	75	Interm.	Heavy	Tot. worn	Path dist*	Theta
Helsinki											
Amabru											
Estim.	−5.777	0.433	0.178	0.107	0.206	−0.180	0.230	0.245	0.055	0.011	26.505
P	**<0.001**	**0.024**	0.465	0.757	0.456	0.785	0.326	0.257	0.831	0.779	
Carhor											
Estim.	−5.887	0.025	0.029	−0.350	−0.117	0.318	0.055	0.194	0.329	−0.016	1,374
P	**<0.001**	0.947	0.943	0.533	0.795	0.442	0.877	0.571	0.341	0.868	
Calmic											
Estim.	−4.263	0.599	0.916	0.392	0.858	0.387	−0.011	0.133	−0.010	−0.029	1.653
P	**<0.001**	**0.003**	**<0.001**	0.151	**<0.001**	0.332	0.952	0.449	0.960	0.504	
Pteobl											
Estim.	−3.117	0.109	−0.021	0.187	−0.339		0.115	−0.107	−0.021	−0.002	12.305
P	**<0.001**	0.648	0.946	0.658	0.318		0.675	0.698	0.945	0.978	
Group FM											
Estim.	−3.862	−0.123	−0.606	−0.560	−0.297		0.230	0.061	0.513	−0.030	2,451
P	**<0.001**	0.780	0.140	0.242	0.406		0.531	0.886	0.168	0.667	
Group GM											
Estim.	−4.887	−0.030	0.769	0.213	−0.532	−1.005	0.147	0.097	−0.453	0.319	6.583
P	**<0.001**	0.935	**0.034**	0.676	0.248	0.232	0.766	0.846	0.392	**0.009**	
Ptemel											
Estim.	−3.893	−0.127	−0.664	0.199	−0.070	−0.352	−0.045	−0.017	−0.186	0.047	3.405
P	**<0.001**	0.593	0.111	0.683	0.871	0.590	0.872	0.953	0.677	0.680	
Ptenig											
Estim.	−6.288	0.112	0.646	0.994	0.305	0.430	−0.110	−0.458	−0.443	0.061	3.260
P	**<0.001**	0.598	**0.002**	**0.003**	0.267	0.214	0.582	**0.037**	**0.049**	0.235	
Group OD											
Estim.	−4.367	0.475	0.172		−0.785	0.933	−1.024	−0.722	−0.318	−0.163	2,151
P	**<0.001**	0.306	0.758		0.494	0.317	0.064	0.125	0.487	0.264	
Edmonton											
Anoret											
Estim.	−3.974	0.306	0.123		0.139		1.175	0.552		0.904	0.759
P	**<0.001**	0.166	0.583		0.534		**0.027**	0.253		**<0.001**	
Calfri											
Estim.	−3.121	−0.010	−0.217		−0.565		−0.293	−0.243		0.429	1.162
P	**<0.001**	0.975	0.519		0.114		0.684	0.706		0.082	
Caling											
Estim.	−2.565	0.209	−0.039		−0.033		0.833	0.518		0.181	1.265
P	**<0.001**	0.172	0.803		0.834		0.062	0.211		0.099	
Pladec											
Estim.	−2.593	0.828	1.024		1.099		0.283	−0.237		0.525	1.009
P	**<0.001**	**<0.001**	**<0.001**		**<0.001**		0.543	0.593		**<0.001**	
Agogra											
Estim.	−4.305	−2.247	−0.875		−2.138		2.379	1.165		−0.653	0.406
P	**<0.001**	**<0.001**	**0.034**		**<0.001**		**0.048**	0.250		0.069	
Ptepen											
Estim.	−2.144	−0.125	−0.338		−0.873		0.458	−0.185		−0.450	0.888
P	**<0.001**	0.577	0.142		**<0.001**		0.375	0.707		**0.008**	

Table 4 continued

	Interc.	Distance from the edge (m)					Trampling				
		15	30	45	60	75	Interm.	Heavy	Tot. worn	Path dist*	Theta
Group FT											
Estim.	−5.579	−0.333	−0.307		0.143		0.827	1.071		0.234	1,361
P	**<0.001**	0.531	0.564		0.760		0.292	0.172		0.519	
Group GM											
Estim.	−4.897	−0.456	−0.535		−0.527		1.488	0.252		0.171	0.191
P	**<0.001**	0.507	0.440		0.443		0.053	0.720		0.731	
Pteads											
Estim.	−3.525	−0.055	0.294		−0.225		−0.211	0.355		−0.194	0.489
P	**<0.001**	0.870	0.356		0.508		0.607	0.348		0.404	
Ptemel											
Estim.	−3.930	−0.470	−0.575		−1.291		2.218	0.893		−0.408	0.678
P	**<0.001**	0.058	**0.021**		**<0.001**		**0.002**	0.136		**0.029**	
Synimp											
Estim.	−6.612	0.473	0.586		0.712		−0.028	−0.408		−0.829	0.849
P	**<0.001**	0.110	**0.044**		**0.013**		0.956	0.403		**<0.001**	
Group GD											
Estim.	−5.027	0.092	−1.101		−0.438		0.769	0.552		−0.328	2.517
P	**<0.001**	0.769	**0.012**		0.221		0.352	0.490		0.206	
Group OM											
Estim.	−7.972	−0.402	−0.577		−0.327		0.597	0.114		0.362	2.130
P	**<0.001**	0.406	0.250		0.483		0.286	0.835		0.312	
Group OD											
Estim.	−3.870	−1.905	−2.855		−1.137			0.278		−0.944	0.412
P	**<0.001**	**<0.001**	**<0.001**		**0.005**			0.443		**0.008**	

Significant *P* values are in bold face. See Table 2 for full species names and Appendices 2 and 3 in the Electronic supplementary material for full model details. In Helsinki, the intercept includes plots at the edge at paths of low trampling intensity. Path dist* is a continuous variable. In Edmonton, the intercept includes plots at the edge next to paths of low trampling intensity. Path dist* here is a two-level factor. The 'Distance from the Edge' and 'Trampling' variable coefficients represent contrasts to the factor levels in the intercept. Theta is the aggregation value with lower values indicating a higher degree of aggregation. Initially these models included two environmental variables shared by the two cities [canopy cover (%) and understorey vegetation cover (%)]. Results from these models (not shown) were similar to results including all vegetation and environmental variables measured from the cities, which are presented in the Electronic supplementary material

In Edmonton, most beetle populations responded positively to an increase in canopy cover (%) and negatively to an increase in bare ground (%); response to vegetation cover (%) was more variable (Appendices 3 and 5 in Electronic supplementary material). However, overall responses of the species to these variables were relatively small, with a few exceptions.

Discussion

Carabid beetle assemblages in urban woodlands of Helsinki and Edmonton responded to edge and trampling effects in remarkably similar ways. Those sampled immediately at habitat edges differed from those more than 10 m into forest patches, but the structure of assemblages at all non-edge forest locations in both cities did not vary much. Furthermore, the areas of lightly trampled paths hosted assemblages different from those with higher trampling intensities. Our results suggest that the effects of edges and trampling can be predicted to the extent that a change at the community level can be expected, but the exact and species specific directions of change are more difficult to predict.

Patterns of overall assemblage response were not simply associated with strong responses by individual species. In Helsinki, there was little interpretable response of individual species and groups with similar habitat affinity. In Edmonton, however, many species and habitat affinity groups responded as we had hypothesised. A lack of strong species-specific responses to these disturbance factors in Helsinki might reflect a general localised loss of species negatively impacted by these disturbances that has resulted from a much longer history of urban effects than in Edmonton (see Niemelä et al. 1994). This would be consistent with the much lower overall catch rates observed in Helsinki.

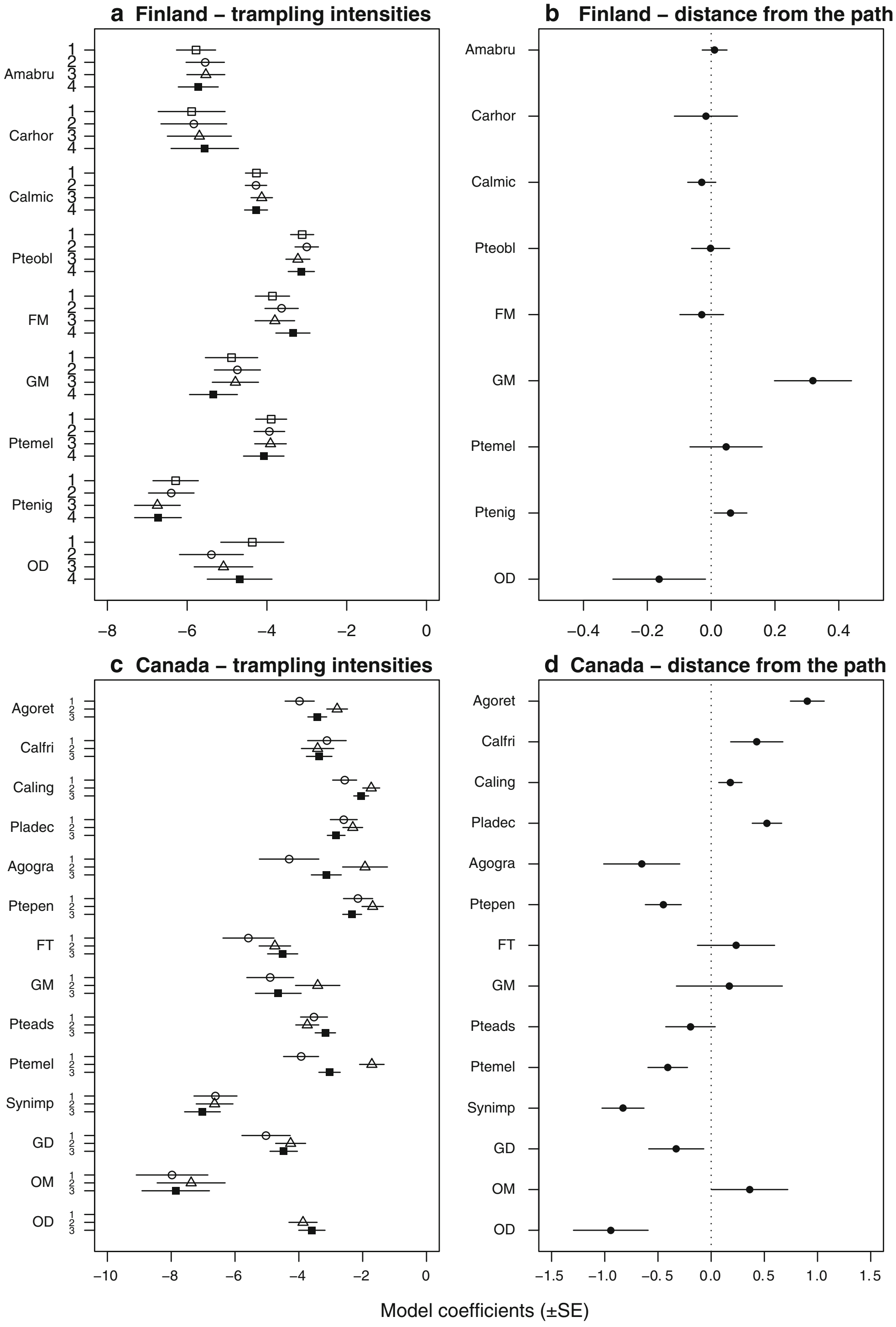

Fig. 3 Carabid beetle responses (model coefficients ± 1SE, see Table 4) to path trampling intensities and distance from the paths in urban forests in Helsinki (*top panels*) and Edmonton (*bottom panels*). Species and species groups are listed a priori from most forest/hygrophilic (*top*) to most open/xerophilic (*bottom*) per city. Trampling intensity plots; *1* lightly trampled path, *2* moderately trampled path, etc. (see text). Species abbreviations consist of the first three letters of the genus and species name. For example, Amabru = *Amara brunnea*. See Table 2 for full species names

Edge effects

The majority of the abundantly collected species, which were mainly classified as forest or generalist species, showed little response to forest edge in this study. Such 'neutral' edge responses are common (Ries et al. 2004; Ries and Sisk 2008), perhaps reflecting, in our case, increased movement of carabid beetles throughout these small urban forests in response to limited resource availability (Wallin and Ekbom 1994). Furthermore, true forest specialist carabid species appear to be missing from urban forests, particularly in Helsinki (see below), thus no clear responses to the edge were observed. Indeed, forest fragmentation results in the loss of habitat and the creation of novel ecological boundaries (see Ewers and Didham 2006), and it seems that patch size confounds the response of carabid species to distance from the edge in urban environments (Lehvävirta et al. 2006). We argue below that due to a longer history of fragmentation in urban environments, and in particular the reduced sizes of forest patches, most forest specialist species have already gone locally extinct in Helsinki, while this process is not as advanced in Edmonton.

Urban forest edges differ from many others in one important respect: the open side of the edge is a hostile environment for many forest organisms (Ries and Sisk 2004; Koivula and Vermeulen 2005; Kupfer et al. 2006). At these abrupt edges (López-Barrera et al. 2005) population dynamics may be primarily influenced by harsh abiotic conditions and human activity, and not much by interactions with species from the surrounding matrix (Rand et al. 2006). Studies from other abrupt edges have shown that species associated with open habitats decrease rapidly from forest edges inwards and seldom penetrated deeper than a few metres into forests (Bedford and Usher 1994; Spence et al. 1996; Kotze and Samways 2001; Heliölä et al. 2001; Koivula et al. 2004). Although open habitat species contribute to the number of carabid species collected from urban forests (Niemelä and Kotze 2009; see also Lövei et al. 2006), they account for few of the individuals collected here (1–2% of collections in either city), and thus are unlikely to influence the population dynamics of the resident forest fauna.

Because specialist species have narrower tolerance limits to the environment than generalist species (Rainio and Niemelä 2003) the lack of strong response to the edge may simply reflect that few of the abundantly collected species are true forest specialists (see also Lehvävirta et al. 2006), particularly in Helsinki where only two forest species (*C. micropterus* and *Carabus hortensis*) increased marginally in density into the forests. In Edmonton, *P. decentis* responded as predicted, while *A. retractum* and *C. ingratus* occurred in high numbers from the edge to the interior. Furthermore, our classification of carabid beetle affinities was broadly based on light and moisture associations (Thiele 1977; Lindroth 1985, 1986), and the results suggest that this classification may not support a predictable response to edges in urban forests. Carabid beetles may respond more strongly to variables not associated with edge effects. For example, even though pH decreased statistically significantly from the edge to the interior in forest patches in Helsinki, the correlation was weak ($r^2 = 0.26$); however, a number of species responded strongly to pH differences (see Appendix 4 in Electronic supplementary material). This result is not surprising as carabid beetles are known to be sensitive to pH changes in the soil (Paje and Mossakowski 1984), and pH receptor cells have been recently discovered on the antennae of carabid species (Merivee et al. 2005; Milius et al. 2006).

In Edmonton, a number of species classified either as open-habitat specialists or xerophilous were most abundantly collected at the edge. These include *P. melanarius*, and species in groups open-habitat/dryness-associated (OD) and generalist/dryness associated (GD). The high activity-density of *P. melanarius* at woodland edges in Edmonton corroborates the hypothesis that edges favour the establishment and spread of some exotic species (Niemelä and Spence 1999; Hickerson et al. 2005). Although *P. melanarius* is widespread in its native Europe, curiously it does not appear to be favoured by edges in Helsinki. This contradiction suggests that edges in areas formerly under continuous forest may provide ecological niche space for species new to the system, even if those species are not necessarily pre-adapted to exploit them (Spence 1990).

Trampling

Clearly carabid beetle assemblages in both Helsinki and Edmonton differed considerably between areas around paths with higher and lower trampling. To our knowledge this is the first study investigating the effects of this particular disturbance on carabid beetles and indeed on epigaeic invertebrates in general, at a small scale. Previous studies of trampling on carabids have been performed at site level and have not considered variation in intensity of disturbance within sites. For example, trampling in urban forests in Helsinki was measured as the percentage of path cover at site level (Grandchamp et al. 2000; Lehvävirta et al. 2006), with both studies showing only subtle and inconsistent responses of either assemblages or particular species. Deer grazing and moose browsing experiments in boreal forests showed that the carabid beetle community composition changed considerably following these disturbances, but these studies did not differentiate the effect of grazing and browsing from the possible effect of trampling (Suominen et al. 2003; Melis et al. 2006, 2007). Livestock grazing experiments have presented similar results (Abensperg-Traun et al. 1996; Cole et al. 2006). Our results on human recreational trampling are in line with those of these studies. However, it is important to note that in our study carabids were not collected on the trampled paths. Thus, our results show that a local response to trampling is seen even in seemingly untrampled vegetation off the paths. This mirrors earlier results about the effects of trampling on vegetation and microbial communities in untrampled vegetation off the paths (Hamberg et al. 2008; Malmivaara-Lämsä et al. 2008) and suggests that human use of urban green space will change the character of biotic assemblages that exist in those sites.

These changes will be registered in terms of increase, decrease or loss of particular species. In Helsinki one species, *P. niger* (the second-most abundantly collected species) clearly decreased in activity-density with increased levels of trampling. Furthermore, six of the nine species/groups analysed in Helsinki were captured less frequently in wear class 4 sites than in wear class 1 sites (see Table 4; Fig. 3). Four of these, *C. micropterus*, *P. oblongopunctatus*, *P. melanarius* and the open-habitat/dryness-associated group, also responded negatively to trampling at sites in a previous study (Lehvävirta et al. 2006).

In Edmonton, responses of individual species to trampling intensity were more apparent. However, the effects were not clearly negative; in fact, for 9 of 14 species/groups analysed, beetles were most abundantly collected in the vicinity of intermediately trampled paths, and 9 species were more abundantly collected in the vicinity of heavily trampled paths than lightly trampled paths. This suggests that some disturbance associated with human footpaths increased beetle catches (see also Digweed et al. 1995) and that moderate to high levels of trampling can have a positive effect on the catch of carabid beetles in some situations and over a spatial scale of a few metres. Additionally, lower microhabitat complexity at highly trampled paths may provide for unobstructed beetle movement (Wallin and Ekbom 1988), and thus a higher catch (but see Nittérus and Gunnarsson 2006).

It is possible that differences observed between Helsinki and Edmonton reflect differences in forest type that, in turn, affect human behaviour. The more open canopy of urban deciduous forest in Edmonton is associated with a dense shrubby understorey including an abundance of thorny plants [e.g. prickly rose (*Rosa acicularis*), buffalo berry (*Shepherdia canadensis*)] and such understories may deter off-trail human excursions (Matlack 1993). Increased beetle activity in the vicinity of trails may result from warmer microclimate in the absence of this dense shrubby layer (e.g., Davies-Colley et al. 2000). In contrast, the more open understorey of coniferous forests in Helsinki may lead to more widespread effects of human foot traffic and thus diminish differences in carabid activity between trails and apparently less travelled areas.

The urban carabid beetle community

Carabid beetle assemblages in boreal forests are typically species poor (Niemelä 1993; Niemelä et al. 1994) and are dominated by a few abundant species (see Niemelä et al. 1988; Niemelä and Spence 1994; Koivula et al. 1999; Koivula 2002; Niemelä et al. 2002; Work et al. 2008; Bourassa et al. 2011). In urban forests in Helsinki and Edmonton, overall species richness is lower than in rural forests, as forest-associated species are not present (Niemelä et al. 2002; Niemelä and Kotze 2009). Because there is a longer history of urban effects in Helsinki, more of these species may have been locally extirpated than in Edmonton. Helsinki's urban forests are dominated by a few characteristic species (e.g., *C. micropterus*, *P. niger*, *A. brunnea*, *P. oblongopunctatus*, *P. melanarius* and *Carabus hortensis*) and assemblages are less diverse than in more natural forest. However, some species (e.g., *Carabus glabratus*, *Notiophilus biguttatus*, *Trechus secalis*, *Cychrus caraboides* and *Leistus terminatus*) more commonly collected from more natural coniferous forests appear to be adversely affected by urbanisation. Three of these species (*C. glabratus*, *T. secalis* and *C. caraboides*) are flightless, and thus likely poor at re-colonising sites after local populations disappear (see Halme and Niemelä 1993). Such species are consequently more vulnerable to local stochastic events in highly fragmented urban landscapes, and may ultimately disappear completely from urbanised Finnish landscapes.

Although such loss is not that evident in Edmonton (but see Bourassa et al. 2011 for evidence of the process), several hygrophilic forest specialists (e.g., *Carabus taedatus, Scaphinotus marginatus* and several *Patrobus* species) are much more commonly encountered in rural aspen forests than at urban sites (e.g. Niemelä et al. 1992). However, there may be enough of these species and other aspen forest specialists (e.g., *A. retractum*) remaining in Edmonton's urban forest patches so that a response to broader canopy influences is detectable. Effective trail management systems may forestall or prevent altogether loss of overall species diversity in Edmonton's urban green spaces.

In summary, our study has shown that the structure of boreal carabid assemblages in urban forest patches of northern Europe and Canada is affected by both trampling and edge effects. Effects on particular species, however, are subtle and variable, and appear to be expressed largely in hydrophilic forest specialists. We suggest that along with increasing time since fragmentation of urban forest patches, forest specialist species common in rural forests become less abundant and may eventually be lost from urban areas.

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