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Research article

Effects of undergrowth removal and edge proximity on ground beetles and vascular plants in urban boreal forests

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Abstract

Urban forests are regularly managed for human safety and esthetic reasons, but they are crucial habitat for many species. Removals of undergrowth occur commonly in these forests, yet the ecological consequences of these operations are poorly understood. We sampled ground beetles (Coleoptera, Carabidae) and vascular plants along 20-m edge gradients in Finnish urban forests, in five stands treated 0.5–2.5 years earlier with undergrowth removal and in five untreated stands. We hypothesized that undergrowth removal and edge proximity would benefit opportunistic and open-habitat species, whereas shady-habitat species would be affected negatively. (1) Regarding carabids, diversity and evenness indices, open-habitat species and *Carabus nemoralis* responded positively, and forest species, *Leistus terminatus* and *Pterostichus oblongopunctatus* responded negatively, to the undergrowth removal. Regarding plants, generalists, *Maianthemum bifolium*, *Rubus saxatilis* and *Sorbus aucuparia* responded positively, and forest species, *Geranium sylvaticum*, *Oxalis acetocella* and *Vaccinium myrtillus* responded negatively, to the undergrowth removal. (2) Edge proximity had little effect on both plants and carabids. However, open-habitat carabids were less abundant and less speciose, and the plants *Oxalis acetocella*, *Trientalis europaea* and *Rubus saxatilis* had higher cover, 10–20 m from than right at the edge. (3) Plant (but not carabid) community responded to the undergrowth removal but not to the edge proximity. When managing urban forests, we recommend an avoidance of undergrowth removals at sites that host rare or threatened forest-associated flora and fauna.

Key words: abundance, Carabidae, community, edge effect, management, species richness

Introduction

Urban areas currently host 54% of the Globe's human population, and the proportion may reach 68% by 2050 (United Nations 2018). This trend is made possible by, e.g. increasing intensification of land use and the spread of urban areas (Seto, Guneralp, and Hutyra 2012). These in turn result in loss and fragmentation of earlier contiguous habitat and alterations in biodiversity (McDonnell et al. 1997; Whitford, Handley, and Ennos 2001; Grimm et al. 2008). At a patch level, urban species communities generally contain fewer species and different dominance structure, compared with communities in rural areas (Niemelä et al. 2011). This pattern results from such stressors as pollutants and land use, characteristic for urban environments (McDonnell et al. 1997; Forman 2008).

Urban forests bear many values. For humans, they provide many ecosystem services, such as plant pollination, ground and surface water protection, particle filtering from the air, and noise reduction (Forman 2008; Salo 2015). Urban people commonly appreciate esthetic and recreational values of these

forests (Tyrväinen, Silvennoinen, and Kolehmainen 2003; Chiesura 2004; Kabisch, Qureshi, and Haase 2015). Moreover, from a biodiversity perspective, these forests provide habitat and dispersal routes for many species (Niemelä et al. 2011). Urban areas can also host rare and threatened species (e.g. Alvey 2006; Jones and Leather 2012; Ives et al. 2016). Biodiversity surveys in cities world-wide support this view; Finnish examples include Kurtto (2002), Savola (2012) and Ellermaa (2018). However, quite often the urban spread also produces 'more of the same': urban areas are particularly favorable for opportunistic generalists, disturbance tolerant species and cosmopolitan species (McKinney 2006, 2008; Sadler et al. 2006).

Even if urban forests can be considered important from many viewpoints, their preservation competes with economics (construction projects, urban spread) and their ecological quality is often compromised by such factors as edge effects or trampling. Generally, these factors tend to negatively impact species that are associated with mature forests, and benefit opportunistic species and others that occupy well-exposed habitats, such as meadows (e.g. Littlemore and Barker 2002; Malmivaara, Löfström, and Vanha-Majamaa 2002; Magura, Tóthmérész, and Molnár 2008; Malmivaara-Lämsä et al. 2008; Kotze et al. 2012). Moreover, management of urban forests is common, not necessarily for economic but for safety or aesthetic reasons (e.g. Hamberg, Löfström and Häkkinen 2012). Undergrowth removal, for instance, is a routine operation in these forests, yet its ecological effects are poorly understood except, perhaps, on soil quality and tree growth. With undergrowth we refer to trees and bushes that have not reached the canopy-tree layer, thus exclude floor- and field-layer vegetation.

In this article, we compare urban boreal forests where undergrowth had recently been removed to similar forests where undergrowth had been retained. Our data consist of ground beetles (Coleoptera, Carabidae; hereafter 'carabids') and vascular plants sampled at different distances from edges of these forests. North European carabids and vascular plants are ecologically and taxonomically well known, and both respond to micro-habitat variation at different spatial scales (e.g. Niemelä 1997; Reinikainen et al. 2000; Mossberg and Stenberg 2003; Koivula 2011). These qualities make them suitable model organisms for studying biological responses to human impact at spatial scales of within and between stands, which are relevant for urban land-use management. Surprisingly, then, in their review on biodiversity of urban parks, Nielsen et al. (2014) concluded that studies on urban environments seldom bridge between fauna and flora, a core feature of this study.

Research concerning boreal forest management suggests that undergrowth removal can impact carabids and plants. For example, clear-cutting changes the assemblage (hereafter 'community' for convenience) structure of carabids (Niemelä, Koivula, and Kotze 2007) and plants (Jalonen and Vanha-Majamaa 2001; Pykälä 2004; Palviainen et al. 2005; Tonteri et al. 2016) through rapid colonization of open-habitat associated species and increase of succession generalists (Niemelä et al. 1988; Spence et al. 1996; Koivula 2002; Pykälä 2004). If living trees are retained, changes in species composition can be considerably smaller (Bergstedt and Milberg 2001; Macdonald and Fenniak 2007; Work et al. 2010; Johnson, Strengbom, and Kouki 2014), perhaps because of smaller changes in the forest-floor shade and micro-climate (Koivula 2012). Hence the undergrowth removal—studied here—may be expected to affect carabids and plants only little, as the sheltering canopy trees are retained. However, undergrowth removal is often accompanied by removals of tree trunks and branches from the ground, resulting in lower structural variation and altered nutritional conditions in the soil, which in turn potentially impact forest specialists negatively, and succession generalists positively (Palviainen 2005; Nittérus, Åström, and Gunnarsson 2007).

Adjacent habitats exchange energy, species and nutrients across their mutual boundary, and species communities change gradually across a gradient from one habitat to another; these are referred to as edge gradients (Murcia 1995). In this study, the gradients reach from street-side verges toward interior parts of forested patches. These edges are abrupt interfaces between forested patches and artificial surfaces (paved roads, built-up areas etc.), the latter being quite inhospitable for carabids and plants (e.g. Guirado, Pino, and Roda 2006; Prass et al. 2017). In forest-edge gradients, the overall richness and open-habitat associated species may decrease, and shade-demanding species may increase, toward interior forest, as earlier shown for carabids (Heliölä, Koivula, and Niemelä 2001; Magura 2002; Koivula, Hyyryläinen, and Soininen 2004) and plants (Guirado, Pino, and Roda 2006; Hamberg et al. 2008; Vallet et al. 2010).

Here, we propose the following predictions:

1. As communities of carabids and vascular plants in managed boreal and temperate forests largely consist of open-habitat species and succession/canopy-closure generalists (Tonteri 1994; Pykälä 2004; Niemelä et al. 2007; Aavik et al. 2009; Bescond, Fenton, and Bergeron 2011; Duguid and Ashton 2013), we expect the total species richness and diversity of carabids and plants to peak in stands where undergrowth has been removed, and at sampling plots closer to the edge.
2. The abundance and species richness of species requiring shady conditions or closed canopy (hereafter 'forest species' for convenience) should decrease, whereas those of open-habitat associated species (hereafter 'open-habitat species') should increase, following undergrowth removal.
3. The abundance and richness of forest species should increase, and those of open-habitat species should decrease, with increasing distance from forest-patch edge toward interior.
4. If at least some carabids and plants respond to the undergrowth removal and/or edge proximity, then the community structure of these groups should change with these two factors accordingly.

Methods

We selected five study sites, each with two stands 50–200 m apart, distributed over the city of Jyväskylä, Finland (62°14" N, 25°44" E; Fig. 1). Each stand represented Myrtillus or Oxalis-Myrtillus type forest (Cajander 1949). The dominant canopy trees were 60–100 years old Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), aspen (*Populus tremula*) and birches (*Betula pendula* and *Betula pubescens*). The undergrowth—prior to its removal from half of the stands—consisted mostly of birches, aspen, gray alder (*Alnus incana*), rowan (*Sorbus aucuparia*) and alder buckthorn (*Rhamnus frangula*). Forest floor and field vegetation was dominated by *Vaccinium* dwarf shrubs, *Calamagrostis* and *Deschampsia* grasses, and by *Pleurozium*, *Dicranum* and *Hylocomium* mosses.

About 45–70% of undergrowth and occasional canopy trees were removed from the other of the two stands at each site during winters 2006/2007 (two stands) or 2008/2009 (three stands). The other stand at each site was left intact at the time of study (Table 1). With 'treatment' we refer to the undergrowth removal

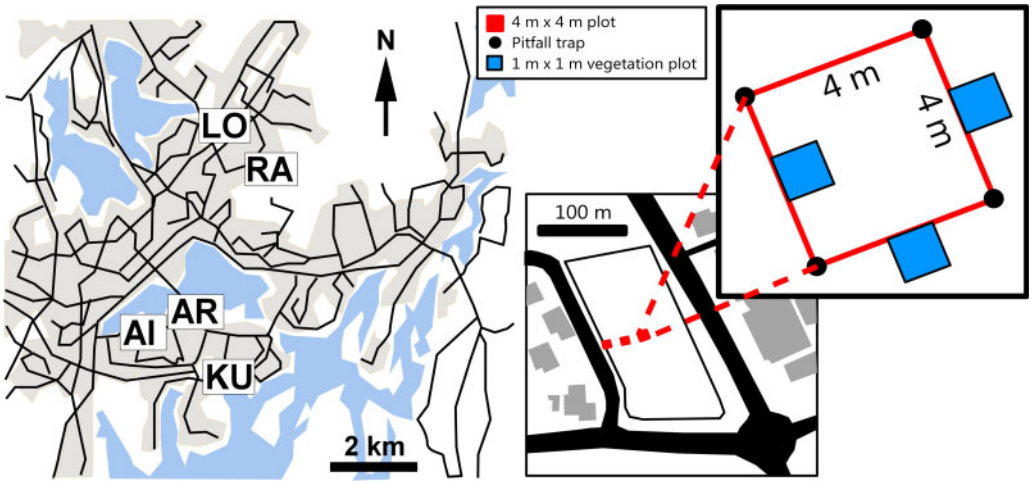

Figure 1: Spatial distribution of five sampling sites, each with two study stands, in the city of Jyväskylä, Finland. Black lines are main roads or streets; light blue patches are lakes; light gray patches show built-up areas (settlement, industrial etc.). The sites are indicated with two-letter codes (compare Table 1). The vignettes show an example study stand (Ainola, untreated) with three sampling stations arranged to an edge-distance gradient from 0 to 20 m toward patch interior, and a sampling station showing the placing of four pitfall traps and three vegetation plots.

Table 1: Structural variables collected from 10 study-forest stands in Jyväskylä, Finland

Variable	AI-UN	AI-TR	AR-UN	AR-TR	KU-UN	KU-TR	LO-UN	LO-TR	RA-UN	RA-TR
Structural variables										
Edge compass direction	NE	SW	S	E	SE	NW	W	W	NW	NW
Treatment winter*		2008/2009		2008/2009		2008/2009		2006/2007		2006/2007
Canopy cover (%)*	83	60	80	50	63	23	57	10	45	35
Canopy-layer trees, age*	65	90	100	100	90	90	85	90	60	55
Trees, volume (m^3/ha)*	104	211	157	218	198	173	224	197	107	183
Trees, n/ha*	440	350	370	340	350	320	540	220	440	340
Understory, n/ha	1400	600	2800	1300	4100	1600	12 800	3600	1500	800
Litter, cover (%)	27.3	16.7	29.8	45.5	25.0	27.8	46.7	14.2	33.3	17.2
Rocks, cover (%)	0.6	0.0	24.5	0.0	15.6	16.1	0.6	2.3	4.0	2.4
Mosses, cover (%)	10.2	5.9	13.3	0.0	9.0	6.9	3.1	2.5	9.6	1.3
Bare ground, cover (%)	3.8	7.3	2.3	1.1	1.3	0.7	0.2	0.2	0.1	0.1
Carabid beetles (mean/sampling station)										
Number of species	8.7	8.7	3.7	9.0	10.7	7.0	4.3	5.7	7.3	6.7
Number of individuals	60.3	29.3	17.3	72.0	98.0	28.3	11.3	12.0	42.7	17.7
Diversity (Shannon-Wiener *H*)	1.6	1.8	0.9	1.8	1.8	1.6	1.2	1.5	1.4	1.4
Evenness (Simpson's *J*)	0.7	0.8	0.5	0.8	0.8	0.8	0.7	0.7	0.7	0.7
Vascular plants (mean/sampling station)										
Number of species	13.3	15.7	10.3	13.3	14.7	15.0	16.0	11.7	13.0	18.7
Diversity (Shannon-Wiener *H*)	1.8	2.1	1.8	1.8	2.0	2.1	2.2	1.6	1.7	2.1
Evenness (Simpson's *J*)	0.7	0.8	0.8	0.7	0.7	0.8	0.8	0.7	0.7	0.7

Stand identities are indicated with two-part abbreviations based on site name and treatment. AI, Ainola; AR, Ainolanranta; KU, Kuokkala; LO, Lohikoski; RA, Rasinrinne (compare Fig. 1); UN, untreated; TR, treated (undergrowth removed). The structural variables are based on data from the city of Jyväskylä (indicated with *) and on our own inventories; the richness measures for carabid beetles and plants are based on data used in this study.

below. The treatment was done by city timberjacks using clearing saws and was accompanied by removals of logging residue, which is a normal procedure in urban forest management in Finland.

We sampled carabids and vascular plants during May–September 2009, i.e. 0.5–2.5 years after the treatment. Within each of the 10 stands, we established three sampling stations: at 0 m, i.e. the stand edge, and at distances 10 and 20 m into the forest interior. We acknowledge that edge effects may reach at least 25–30 m into the forest interior (e.g. Chen, Franklin, and Spies 1993) but we consistently applied the 20 m distance because this was the farthest from the nearest edge in some stands. The compass directions of edge facing varied independently in treated and untreated stands (Table 1).

To collect carabids, we used pitfall traps (mouth diameter 70 mm, volume 0.25 l, half filled with 30% propylene glycol and a drop of detergent, covered with a 10 × 10 cm plastic roof set 2–3 cm above the trap rim; e.g. Koivula et al. 2003). We placed four traps into each corner of a 4 × 4 m square of each sampling station (Fig. 1). The traps were operating from late May to early September and were serviced every 2–4 weeks. We sorted the samples and identified the collected beetles in a laboratory. For the purposes of analysis, we pooled the samples of a given station over the whole summer, thus resulting in (10 stands × 3 stations) 30 samples.

We carried out vegetation inventories in June by establishing three 1 x 1 m plots at each sampling station in each stand

(Fig. 1). For each plot, we recorded each plant species along with its percent cover. For analysis purposes we pooled vegetation data by averaging percent covers of each plant species per sampling station, thus resulting in a total of 30 samples. Table 1 shows structural variation in our study stands. These variables were not used in analyses, however, as they represent different spatial scale from our sampling, and our focus was on undergrowth removal and edge proximity.

We analyzed the carabid and plant abundance and richness data using generalized linear mixed-effects models (GLMMs; Zuur et al. 2009). Our response variables were the total number of species, Shannon-Wiener and Simpson diversity indices, pooled samples of three ecological groups (forest, generalist and open-habitat species), and number of captured individuals (for carabids) or percent cover (for plants) of abundant species. Regarding the three ecological groups of species, we based the grouping on Niemelä, Koivula, and Kotze (2007) for carabids and Reinikainen et al. (2000) and Mossberg and Stenberg (2003) for plants (Appendix). We analyzed both the pooled abundance (for carabids) or percent cover (for plants) and the number of species for groups or species found in >50% of samples, and excluded sites with no observations (one site for the beetle *Pterostichus melanarius*, and for the plants *Calamagrostis arundinaceus* and *Rubus saxatilis*). It must be noted that passive collecting methods (such as pitfall trapping) do not collect different species with their true relative proportions but are biased toward larger and more actively moving species (Koivula 2011), which limits the interpretation of indices or community analyses for carabids.

In GLMM, we set site (each with two stands) as a random factor to account for spatial inter-dependence of adjacent stands and their sampling stations, and treatment (undergrowth not removed, undergrowth removed in the winter of 2006/2007, or undergrowth removed in the winter of 2008/2009) and edge proximity (0, 10 or 20 m into the patch interior) as fixed factors. Due to the often low sample sizes, we did not include an interaction between treatment and edge proximity in our models. Regarding carabid data, sample losses were rare and apparently random; preliminary runs with sampling effort as a covariate suggested no effect so we excluded effort from our models. We initially used untransformed data with Gaussian error distribution and checked the normality of residuals using Q–Q plots. If these plots indicated a lack of normality, we square-root transformed the data and reran the models, and if the issue still persisted, we applied quasi-Poisson error distribution (e.g. Ver Hoef and Boveng 2007). The Q–Q plots of final models are shown in Supplementary Figures S1 and S2.

We also explored the possibility for edge responses to differ between treated and untreated stands by calculating separate Spearman rank correlation coefficients between the edge proximity and the number of species, the two indices, the abundance and richness of the three ecological groups of species, and the abundance or percent cover of different species. Due to the high number of comparisons we interpret these results with caution.

To assess community responses to treatment and edge proximity, we used Non-metric Multi-Dimensional Scaling (NMDS; Borg and Groenen 2005) by applying the Bray-Curtis distance matrix. We analyzed beetle and plant data separately. We tested the distinctiveness of samples of untreated stands, and stands treated in the winters of 2006/2007 or 2008/2009, and samples collected at different edge distances (0, 10 or 20 m), using permutational multivariate analysis of variance (ANOVA) (adonis function with strata = site in the R package vegan; Oksanen et al. 2018).

We ran the analyses using R 3.4.4 (R Core Team 2018) with car (Fox and Weisberg 2011), MASS (Venables and Ripley 2002), vegan (Oksanen et al. 2018) and lme4 packages (Bates et al. 2015).

Results

We collected 1167 carabid individuals of 26 species and found 61 vascular plant species (canopy trees excluded; Appendix). Six carabid species (*Calathus micropterus*, *Carabus nemoralis*, *Leistus terminatus*, *P.melanarius*, *Pterostichus oblongopunctatus* and *Trechus secalis*) and nine plant species (*C.arundinaceus*, *Deschampsia flexuosa*, *Geranium sylvaticum*, *Maianthemum bifolium*, *Oxalis acetocella*, *R.saxatilis*, *S.aucuparia*, *Trientalis europaea* and *Vaccinium myrtillus*) occupied more than half of the sampling stations and were thus subjected to GLMM, in addition to the total and species-group abundances and richness measures.

Responses to the undergrowth removal

In carabids, the treatment did not affect the number of species, but the two indices peaked in stands treated in the winter of 2008/2009 (Table 2). In terms of carabid abundance, forest carabids had lowest, and open-habitat carabids had highest, catches in stands treated in the winter of 2006/2007 (Fig. 2); generalists did not respond significantly to the treatment. In terms of species richness, forest or generalist carabids did not respond significantly to the treatment, whereas open-habitat carabids were significantly more speciose in stands treated in the winter of 2006/2007 than in untreated stands (Table 2).

Regarding the plant community, the number of species or the two indices did not show a treatment response (Table 2). Furthermore, forest plants had lower cover in treated than in untreated stands, irrespective of time since treatment (Fig. 2), whereas generalist plants had marginally higher cover in stands treated in the winter of 2006/2007 than in untreated stands. Plant species richness measures for the three ecological groups did not show a treatment response (Table 2).

Three carabid species showed a detectable treatment response (Table 3). *Carabus nemoralis* was marginally more abundant in stands treated in the winter of 2008/2009 than in untreated stands. *Leistus terminatus* was marginally less numerous in stands treated in the winter of 2006/2007, and *P.oblongopunctatus* was marginally less numerous in stands treated in the winter of 2008/2009, than in untreated stands (Table 3).

Six plant species responded significantly or marginally significantly to the treatment (Table 3). *Oxalis acetocella* and *V.myrtillus* had lower cover in treated than in untreated stands, irrespective of time since undergrowth removal (Fig. 3), whereas *G.sylvaticum* had lower cover in the 2008/2009, but not in the 2006/2007, than in untreated stands. *Maianthemum bifolium* had higher cover in stands treated in both winters (2006/2007 and 2008/2009; Fig. 3), *R.saxatilis* had higher cover in 2006/2007, and *S.aucuparia* had higher cover in 2008/2009, than in untreated stands (Table 3).

Responses to the edge proximity

Regarding both carabids and plants, edge proximity did not significantly affect the total diversity measures or the ecological groups of species (Table 2). However, the abundance and richness of open-habitat carabids were marginally lower at 10 m from than at the edge.

In terms of individual species, none of the carabids responded to the edge gradient (Table 3). Regarding plant

Table 2: GLMM summary for carabid beetles and vascular plants sampled in 10 forest stands in Jyväskylä, Finland

Variable	Effect	SE	*t*	*P*	Variable	Effect	SE	*t*	*P*
Carabids, number of species					Plants, number of species				
(Intercept)	6.77	1.01	6.70	0.000	(Intercept)	14.43	1.46	9.87	0.000
Treat 06/07	−0.37	1.27	−0.29	0.771	Treat 06/07	1.83	1.93	0.95	0.352
Treat 08/09	1.03	1.08	0.95	0.350	Treat 08/09	1.33	1.69	0.79	0.437
Prox 10 m	−0.20	1.09	−0.18	0.857	Prox 10 m	−1.40	1.79	−0.78	0.442
Prox 20 m	0.70	1.09	0.64	0.530	Prox 20 m	−1.90	1.79	−1.06	0.299
Carabids, Shannon-Wiener diversity (H)					Plants, Shannon-Wiener diversity (H)				
(Intercept)	1.41	0.13	10.77	0.000	(Intercept)	1.87	0.12	15.00	0.000
Treat 06/07	0.08	0.17	0.46	0.653	Treat 06/07	−0.06	0.17	−0.34	0.735
Treat 08/09	0.36	0.15	2.45	0.022	Treat 08/09	0.13	0.14	0.88	0.388
Prox 10 m	0.00	0.15	0.00	1.000	Prox 10 m	−0.04	0.15	−0.26	0.796
Prox 20 m	−0.04	0.15	−0.26	0.796	Prox 20 m	0.04	0.15	0.26	0.796
Carabids, Simpson evenness (J)					Plants, Simpson evenness (J)				
(Intercept)	0.69	0.04	16.90	0.000	(Intercept)	0.76	0.03	26.08	0.000
Treat 06/07	0.02	0.05	0.43	0.674	Treat 06/07	−0.01	0.04	−0.17	0.865
Treat 08/09	0.13	0.05	2.78	0.010	Treat 08/09	0.03	0.03	0.79	0.438
Prox 10 m	−0.01	0.05	−0.21	0.840	Prox 10 m	0.02	0.04	0.56	0.582
Prox 20 m	−0.07	0.05	−1.43	0.166	Prox 20 m	0.01	0.04	0.28	0.783
Forest carabids, abundance (SQRT)					Forest plants, % cover				
(Intercept)	3.52	0.84	4.18	0.001	(Intercept)	0.27	0.08	3.19	0.009
Treat 06/07	−1.88	1.08	−1.74	0.094	Treat 06/07	−0.22	0.09	−2.30	0.030
Treat 08/09	−0.89	0.92	−0.97	0.340	Treat 08/09	−0.19	0.08	−2.40	0.025
Prox 10 m	0.96	0.94	1.02	0.320	Prox 10 m	0.13	0.08	1.60	0.123
Prox 20 m	1.62	0.94	1.72	0.100	Prox 20 m	0.04	0.08	0.56	0.583
Generalist carabids, abundance (SQRT)					Generalist plants, % cover				
(Intercept)	4.01	0.84	4.79	0.003	(Intercept)	0.32	0.08	4.06	0.000
Treat 06/07	−0.19	0.84	−0.23	0.822	Treat 06/07	0.20	0.11	1.88	0.071
Treat 08/09	0.12	0.69	0.18	0.862	Treat 08/09	−0.07	0.09	−0.71	0.484
Prox 10 m	−0.30	0.68	−0.45	0.658	Prox 10 m	−0.04	0.10	−0.45	0.657
Prox 20 m	0.15	0.68	0.22	0.832	Prox 20 m	−0.13	0.10	−1.37	0.184
Open-habitat carabids, abundance (SQRT)					Open-habitat plants, % cover				
(Intercept)	0.37	0.21	1.78	0.092	(Intercept)	0.35	0.12	2.85	0.026
Treat 06/07	0.81	0.27	3.04	0.006	Treat 06/07	0.10	0.11	0.86	0.399
Treat 08/09	0.28	0.23	1.21	0.238	Treat 08/09	0.02	0.09	0.21	0.836
Prox 10 m	−0.41	0.24	−1.75	0.094	Prox 10 m	−0.02	0.09	−0.26	0.799
Prox 20 m	−0.29	0.24	−1.23	0.232	Prox 20 m	−0.04	0.09	−0.45	0.655
Forest carabids, number of species (QP)					Forest plants, number of species				
(Intercept)	0.85	0.20	4.17	0.000	(Intercept)	2.77	0.59	4.71	0.001
Treat 06/07	−0.31	0.25	−1.22	0.238	Treat 06/07	−0.09	0.61	−0.14	0.890
Treat 08/09	−0.06	0.21	−0.29	0.773	Treat 08/09	−0.50	0.51	−0.98	0.337
Prox 10 m	0.17	0.21	0.78	0.443	Prox 10 m	0.20	0.50	0.40	0.692
Prox 20 m	0.24	0.21	1.15	0.264	Prox 20 m	−0.10	0.50	−0.20	0.843
Generalist carabids, number of species					Generalist plants, number of speies				
(Intercept)	4.00	0.86	4.64	0.002	(Intercept)	7.50	1.01	7.44	0.000
Treat 06/07	0.12	0.90	0.14	0.892	Treat 06/07	0.66	1.18	0.56	0.579
Treat 08/09	0.58	0.75	0.79	0.441	Treat 08/09	0.89	0.99	0.91	0.374
Prox 10 m	−0.20	0.73	−0.27	0.787	Prox 10 m	−0.90	0.98	−0.92	0.369
Prox 20 m	0.40	0.73	0.55	0.590	Prox 20 m	−0.40	0.98	−0.41	0.688
Open-habitat carabids, number of species					Open-habitat plants, number of species				
(Intercept)	0.37	0.20	1.84	0.084	(Intercept)	3.83	0.65	5.87	0.000
Treat 06/07	0.81	0.25	3.17	0.004	Treat 06/07	−0.10	0.86	−0.12	0.909
Treat 08/09	0.24	0.22	1.11	0.277	Treat 08/09	0.29	0.75	0.38	0.705
Prox 10 m	−0.40	0.22	−1.81	0.085	Prox 10 m	−0.60	0.80	−0.75	0.460
Prox 20 m	−0.30	0.22	−1.36	0.190	Prox 20 m	−1.10	0.80	−1.38	0.181

Independent or explanatory variables are model intercept, treatment (Treat; undergrowth not removed, or removed in the winter of 2006/2007 or 2008/2009) and edge proximity (Prox; 0, 10 or 20 m from stand edge toward the patch interior). Effect, estimated effect; SE, standard error for Effect; t shows test statistics for untransformed data unless specified otherwise (SQRT, square-root transformation or QP, quasi-Poisson error distribution, were applied to improve normality); *P* = probability for no effect. In all analyses site was a random variable to account for spatial autocorrelation. Sample size = 30. For details, see text.

species, *O.acetocella* had significantly higher cover at 20 m from than at the edge, whereas *R.saxatilis* peaked marginally at 10 m and *T.europaea* also marginally at 20 m.

In our exploration of possible interactions between treatment and edge proximity, most correlations in untreated or in treated stands were weak and non-significant (Table 4).

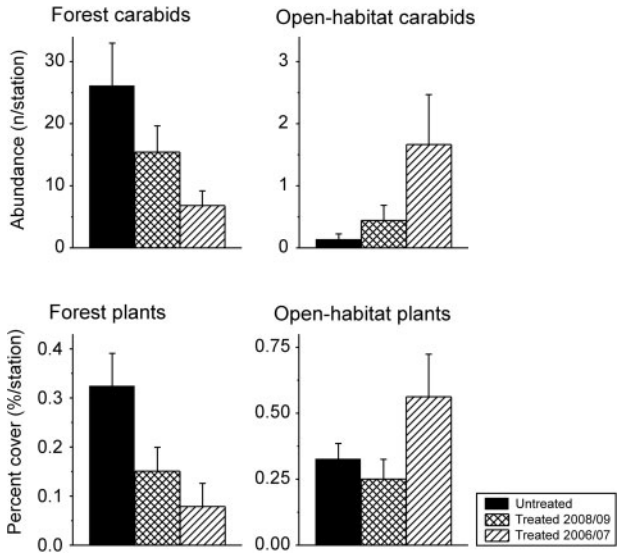

Figure 2: Column plots (mean + SE) For the number of individuals of forest and open-habitat associated carabids (top) and the percent cover of forest and open-habitat plants (bottom). See Table 2 for statistics.

However, *P.oblongopunctatus* increased marginally toward forest interior in treated but not in untreated stands, and *C.micropterus* and *L.terminatus* showed similar trends in untreated but not in treated stands.

Community responses to the undergrowth removal and edge proximity

Two-dimensional NMDS solutions had very high stress for both carabids and plants (>0.24; not shown), so we report 3D solutions; final stress for both carabids and plants was 0.15. Carabid samples from untreated stands, and stands treated in the winters of 2006/2007 or 2008/2009, did not differ systematically from each other (permutational multivariate ANOVA; $F = 1.14$, $R^2 = 0.08$, $P = 0.875$) and the samples were also similar with respect to edge proximity ($F = 0.57$, $R^2 = 0.04$, $P = 0.869$). Plant community, however, showed a significant treatment response ($F = 1.82$, $R^2 = 0.12$, $P = 0.029$; Fig. 4) but did not respond to the edge proximity ($F = 0.60$, $R^2 = 0.04$, $P = 0.923$).

Discussion

Strong effects of undergrowth removal on carabids and plants

We found that the carabid diversity—as measured by Shannon-Wiener and Simpson indices—was affected by the understory removal, implying rapid alteration in the community structure. This finding is in line with many species-richness responses to logging (e.g. Kuuluvainen, Tahvonen, and Aakala 2012; Nascimbene, Thor, and Nimis 2013; Fedrowitz et al. 2014) but apparently ephemeral, as the difference was significant for stands treated in the winter of 2008/2009 (treated half a year earlier) but not for 2006/2007 (2.5 years earlier; see discussion below). The lack of a treatment response in plant diversity, on the other hand, may have resulted from the relatively short post-treatment period (Bergstedt and Milberg 2001) and/or urbanization-related, historical landscape-scale change in the plant community (Niemelä et al. 2011). Thus, urban species communities may not consistently host fewer species than rural communities do (Niemelä and Kotze 2009), but they may host fewer habitat specialists (Magura, Lövei, and Tóthmérész 2010, Vallet et al. 2010). Indeed, our data consisted mostly of succession generalists or open-habitat associated species, and specialists of mature or old-growth forests were missing (Appendix). These patterns suggest community homogenization, specialist loss and generalist/opportunist increase in urban ecosystems (Venn, Kotze, and Niemelä 2003; McKinney 2006, 2008).

We also found that the groups of forest plants and forest carabids were less abundant, and open-habitat carabids (but not open-habitat plants) were more abundant and more speciose, in treated than in untreated stands. These findings are in line with our predictions based on responses of these groups to logging (see Introduction section). Moreover, these responses were strongest in stands treated in the winter of 2006/2007, which suggests a 1–3 years response delay, as earlier reported for several forest plants by, e.g. Bergstedt and Milberg (2001) for logging and Ilisson et al. (2006) for windstorm disturbance. Both positive and negative responses to urban stressors are common (e.g. Jones and Leather 2012), and the opposite responses of forest and open-habitat species groups may have resulted in the lack of a detectable response in the total numbers of species. Contrasting responses between ecological groups of species nevertheless reflect the importance of examining different elements of communities rather than just the overall number of species in management and conservation assessments (e.g. Koivula 2011).

At the species level, the plants *M.bifolium* responded positively, and *O.acetocella* and *V.myrtillus* responded negatively, to the undergrowth removal in both the 2006/2007 and 2008/2009 stands. For *M.bifolium*, the positive response may be considered surprising, as the species is associated with shady conditions (Kujala 1926) but may be explained through competition. Thus, the species may have taken the advantage of undergrowth removal per se and negative responses of some common plants to it, such as *V.myrtillus*. The negative responses of *O.acetocella* and *V.myrtillus* are in line with previous studies on the effects of stand-replacing disturbances, such as clear-cutting and windstorm (Atlegrim and Sjöberg 1996; Jalonen and Vanha-Majamaa 2001; Ilisson et al. 2006; Johnson, Strengbom, and Kouki 2014; Tonteri et al. 2016; but see Nybakken, Selås, and Ohlson 2013; Eldegard et al. 2019). All three species may have responded to treatment-caused alterations in shade and/or micro-climate, including variation in wind, temperature and moisture (e.g. Chen et al. 1999; Harper et al. 2015). We did not measure these factors or soil qualities, but further research on these and on interspecific interactions (competition, pollination, predation and herbivory) would shed light on mechanisms behind the detected responses.

Several other carabid and plant species responded to the undergrowth removal only in stands treated in 2006/2007, suggesting a response delay, or only in stands treated in 2008/2009, suggesting an ephemeral response. We found evidence for a time lag in the treatment response of the carabid *L.terminatus*. Time lags in biological responses to habitat change are common and range from days to tens of years (e.g. Vellend et al. 2006) and, regarding logging, can be at least a few years in carabids and other arthropods (e.g. Spence et al. 1996; Vance and Nol 2003; Matveinen-Huju et al. 2006; Koivula et al. 2019). Moreover, some carabid responses were apparently ephemeral: *C.nemoralis* responded positively, and *P.oblongopunctatus* responded negatively, to the treatment in the 2008/2009 but not in the 2006/2007 stands. The former is considered a generalist of open

Table 3: GLMM summary for the abundance of carabid beetle species and percent cover of vascular plant species sampled in 10 forest stands in Jyväskylä, Finland

Variable	Effect	SE	*t*	*P*	Variable	Effect	SE	*t*	*P*
C.micropterus (SQRT-QP)					*G.sylvaticum* (SQRT)				
(Intercept)	−0.49	0.47	−1.04	0.312	(Intercept)	0.11	0.04	2.53	0.027
Treat 06/07	−0.24	0.53	−0.45	0.658	Treat 06/07	0.00	0.05	0.02	0.982
Treat 08/09	0.06	0.41	0.16	0.877	Treat 08/09	−0.11	0.05	−2.49	0.020
Prox 10 m	0.80	0.52	1.53	0.141	Prox 10 m	0.01	0.05	0.27	0.789
Prox 20 m	0.86	0.52	1.65	0.114	Prox 20 m	0.00	0.05	0.01	0.992
C.nemoralis					*M.bifolium* (SQRT)				
(Intercept)	5.30	1.92	2.76	0.017	(Intercept)	0.10	0.04	2.83	0.011
Treat 06/07	−0.13	2.36	−0.05	0.958	Treat 06/07	0.13	0.05	2.80	0.010
Treat 08/09	3.75	1.99	1.88	0.072	Treat 08/09	0.07	0.04	1.89	0.071
Prox 10 m	−2.20	2.01	−1.09	0.287	Prox 10 m	−0.03	0.04	−0.74	0.468
Prox 20 m	1.10	2.01	0.55	0.591	Prox 20 m	0.03	0.04	0.71	0.488
L.terminatus (SQRT)					*O.acetocella* (SQRT-QP)				
(Intercept)	1.25	0.36	3.43	0.002	(Intercept)	0.20	0.06	3.42	0.011
Treat 06/07	−0.87	0.48	−1.80	0.084	Treat 06/07	−0.21	0.06	−3.74	0.001
Treat 08/09	−0.26	0.42	−0.61	0.548	Treat 08/09	−0.10	0.05	−2.11	0.046
Prox 10 m	0.44	0.45	0.98	0.335	Prox 10 m	0.03	0.04	0.63	0.537
Prox 20 m	0.62	0.45	1.39	0.176	Prox 20 m	0.10	0.04	2.32	0.031
P.melanarius					*R.saxatilis* (SQRT)				
(Intercept)	5.71	3.01	1.90	0.073	(Intercept)	0.12	0.06	2.04	0.055
Treat 06/07	−4.83	4.76	−1.02	0.323	Treat 06/07	0.20	0.07	2.74	0.013
Treat 08/09	2.39	3.25	0.73	0.472	Treat 08/09	−0.06	0.07	−0.84	0.409
Prox 10 m	−1.25	3.69	−0.34	0.738	Prox 10 m	0.14	0.07	1.95	0.066
Prox 20 m	−0.38	3.69	−0.10	0.920	Prox 20 m	−0.08	0.07	−1.17	0.256
P.oblongopunctatus					*S.aucuparia* (SQRT)				
(Intercept)	9.93	5.58	1.78	0.110	(Intercept)	0.08	0.06	1.30	0.232
Treat 06/07	−3.41	6.32	−0.54	0.595	Treat 06/07	−0.02	0.06	−0.33	0.748
Treat 08/09	−10.17	5.28	−1.93	0.067	Treat 08/09	0.11	0.05	2.20	0.038
Prox 10 m	3.60	5.23	0.69	0.500	Prox 10 m	0.04	0.05	0.90	0.377
Prox 20 m	9.00	5.23	1.72	0.101	Prox 20 m	−0.01	0.05	−0.27	0.791
T.secalis (SQRT)					*T.europaea* (SQRT)				
(Intercept)	0.95	0.47	2.01	0.055	(Intercept)	0.06	0.02	2.79	0.022
Treat 06/07	−0.75	0.63	−1.19	0.244	Treat 06/07	0.01	0.02	0.28	0.780
Treat 08/09	0.56	0.55	1.03	0.313	Treat 08/09	−0.02	0.02	−1.21	0.240
Prox 10 m	0.31	0.58	0.53	0.599	Prox 10 m	0.03	0.02	1.61	0.123
Prox 20 m	0.29	0.58	0.49	0.626	Prox 20 m	0.03	0.02	1.73	0.099
C.arundinaceus					*V.myrtillus* (SQRT)				
(Intercept)	0.10	0.05	1.88	0.104	(Intercept)	0.23	0.08	2.95	0.017
Treat 06/07	0.05	0.05	1.02	0.321	Treat 06/07	−0.14	0.08	−1.74	0.094
Treat 08/09	−0.02	0.05	−0.40	0.692	Treat 08/09	−0.15	0.07	−2.18	0.040
Prox 10 m	0.01	0.05	0.32	0.755	Prox 10 m	0.06	0.07	0.93	0.365
Prox 20 m	0.00	0.05	0.01	0.991	Prox 20 m	0.02	0.07	0.23	0.818
D.flexuosa (SQRT)									
(Intercept)	0.13	0.05	2.62	0.015					
Treat 06/07	−0.03	0.06	−0.42	0.677					
Treat 08/09	0.00	0.06	−0.03	0.978					
Prox 10 m	−0.03	0.06	−0.52	0.606					
Prox 20 m	−0.04	0.06	−0.72	0.477					

Independent or explanatory variables are model intercept, treatment (Treat; undergrowth not removed, or removed in the winter of 2006/2007 or 2008/2009) and edge proximity (Prox; 0, 10 or 20 m from stand edge toward the patch interior). Effect, estimated effect; SE, standard error for Effect; *t* shows test statistics for untransformed data unless specified otherwise (SQRT, square-root transformation and/or QP, quasi-Poisson error distribution, were applied to improve normality); *P*, probability for no effect. In all analyses site was a random variable to account for spatial autocorrelation. Sample size = 30 except was 24 for *P.melanarius*, *C.arundinaceus* and *R.saxatilis*. See text for details.

habitats and light forests, whereas the latter occupies different kinds of forest (Lindroth 1985, 1986; Niemelä, Koivula, and Kotze 2007). These responses may result from rapid changes in vegetation (see discussion above), which in turn affects the forest-floor micro-climate, shade and, indirectly, food items of these mostly predatory beetles (Thiele 1977; Kotze et al. 2011). In our study, some changes in vegetation indeed seemed short lived: the covers of *S.aucuparia* and *G.sylvaticum* were lower only in stands treated in the winter of 2008/2009 than in untreated stands. *Sorbus aucuparia* was targeted by the undergrowth removals but may have quickly recovered due to sprouting (Zywiec and Ledwon 2008), explaining the cover similarity in untreated stands and in stands treated in 2006/2007. *Geranium sylvaticum*, on the other hand, might have temporarily suffered

Table 4: Correlations between ground beetles or vascular plants and edge distance in five untreated and five treated (undergrowth removed) stands in Jyväskylä, Finland, using Spearman rank correlation (rho coefficients shown; for details, see text)

Group	Untreated	Treated	Group/species	Untreated	Treated
Carabids, number of species	−0.10	0.42	*C.micropterus*	0.47	0.11
Carabids, diversity (H)	−0.15	0.20	*C.nemoralis*	−0.21	0.25
Carabids, evenness (J)	−0.36	0.02	*L.terminatus*	0.46	0.14
Forest carabids, abundance	0.23	0.40	*P.melanarius*	−0.24	0.00
Generalist carabids, abundance	−0.18	0.26	*P.oblongopunctatus*	0.17	0.45
Open-habitat carabids, abundance	−0.24	−0.27	*T.secalis*	0.07	0.18
Forest carabids, number of species	0.14	0.28	*C.arundinaceus*	0.18	0.12
Generalist carabids, number of species	−0.20	0.31	*D.flexuosa*	−0.23	−0.15
Open-habitat carabids, number of species	−0.24	−0.27	*G.sylvaticum*	0.04	−0.02
Vascular plants, number of species	−0.08	−0.17	*M.bifolium*	0.34	0.11
Vascular plants, diversity (H)	0.09	−0.05	*O.acetocella*	0.37	0.29
Vascular plants, evenness (J)	0.00	0.04	*R.saxatilis*	−0.30	−0.18
Forest plants, % cover	0.34	−0.02	*S.aucuparia*	−0.07	−0.14
Generalist plants, % cover	−0.21	−0.13	*T.europaea*	0.11	0.39
Open-habitat plants, % cover	0.00	−0.08	*V.myrtillus*	−0.09	0.19
Forest plants, number of species	0.06	−0.05			
Generalist plants, number of species	−0.22	−0.18			
Open-habitat plants, number of species	−0.22	−0.26			

None were significant, but coefficients >0.44 are marginally significant.

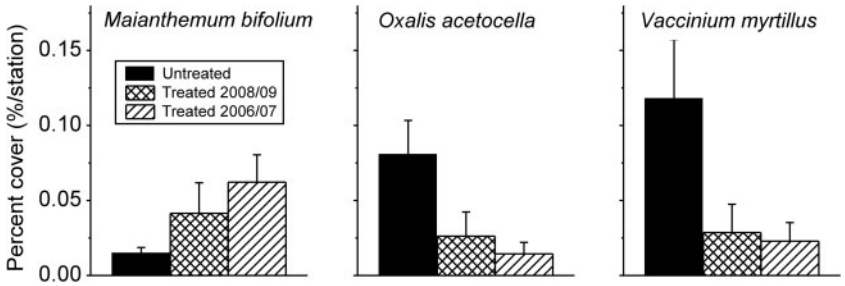

Figure 3: The percent cover (mean + SE) of three plant species showing significant treatment responses. See Table 3 for statistics.

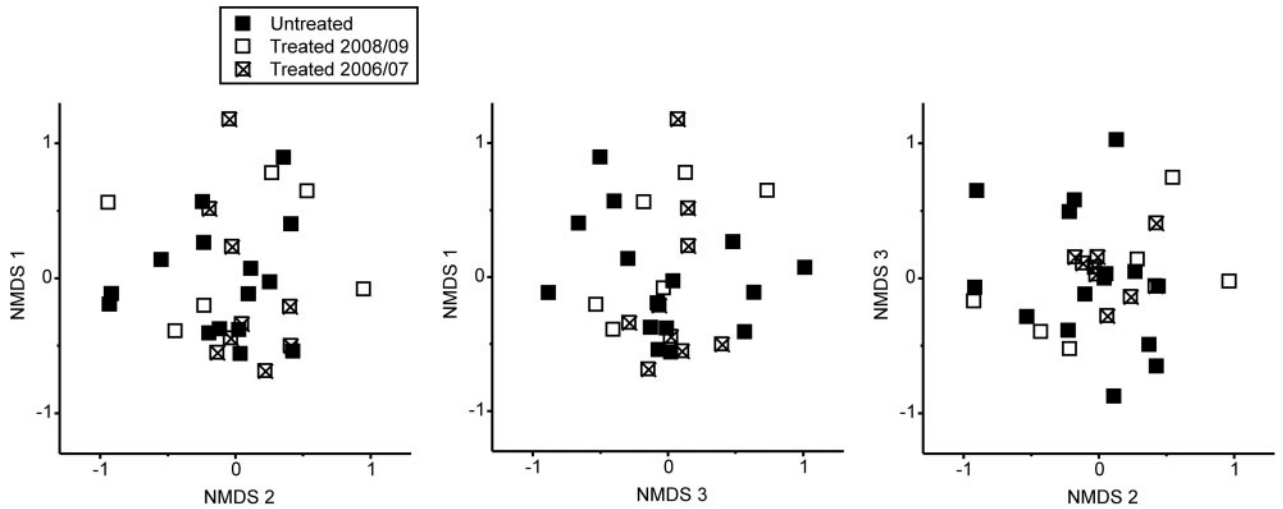

Figure 4: Three-dimensional NMDS plot for vascular plants. Different combinations of the three dimensions of sample scores are shown (NMDS 1–2, 1–3 and 2–3). Solid black symbols indicate sampling stations of untreated stands; cross-center symbols indicate stations of stands treated in the winter of 2008/2009; and hollow symbols indicate stations of stands treated in the winter of 2006/2007. Stations at different edge distances were similar but the three treatment categories differed significantly (see text).

from trampling by personnel doing the undergrowth removals (Hamberg et al. 2008, 2010). Thus, the leaf area but not the number of specimens might have been impacted, allowing a rapid recovery after trampling (Thurston and Reader 2001). Comparisons between counts of specimens and percent covers would confirm this hypothesis; we measured only percent cover.

Small effects of edge proximity on carabids and plants

Edge proximity impacted carabids and plants only little, but open-habitat carabids were less abundant and speciose, and the plants *O.acetocella*, *T.europaea* and *R.saxatilis* had higher cover, at 10–20 m from than right at the edge. Changes within the first few tens of meters from the forest edge toward interior have earlier been reported for many taxa, including plants and carabids (e.g. Heliölä, Koivula, and Niemelä 2001; Honnay, Verheyen, and Hermy 2002; Huggard and Vyse 2002; Gallé and Fehér 2006; Hamberg et al. 2008, 2010; Malmivaara-Lämsä et al. 2008). Micro-climatic conditions, including light, apparently differed sufficiently between the edge and the 10−20 m sampling stations to result in detectable responses (Matlack 1993).

The generally low magnitude of edge effects may have occurred because of a general loss of specialists in urban landscapes (see above), and/or the short edge gradients studied here. Edge effects, as reflected by altered species compositions, may reach 50 m into the interior in boreal and temperate forests (e.g. Esseen and Renhorn 1998; Honnay, Verheyen, and Hermy 2002; Hamberg et al. 2008). Thus, the studied 20 m may have only captured small responses of species that do not avoid open habitats but are just less abundant there—generalists to varying degrees. Yet another explanation is that many opportunistic species of surrounding habitats have evidently invaded the studied forest fragments (Burke and Goulet 1998). In total 14 out of the 23 species of plants classified as open-habitat associated occurred at least once in sampling stations that were 20 m from the edge.

Our edge explorations of untreated or treated stands also suggest minor effects (Table 4). All the correlation coefficients were relatively low, and only three were marginally significant, which could occur by chance alone. Three forest-associated carabid species showed edge responses: *P.oblongopunctatus* increased slightly toward forest interior in treated but not in untreated stands, whereas *C.micropterus* and *L.terminatus* showed similar trends in untreated but not in treated stands. Regarding the former species, the more extensive cover by bushes and small trees could mitigate edge effects in untreated stands (Didham and Lawton 1999; Niemelä, Koivula, and Kotze 2007). The intuitively surprising responses by *C.micropterus* and *L.terminatus*, on the other hand, might represent a 'panic reaction' to conditions turned unfavorable. Such reaction could result in higher mobility (Charrier, Petit, and Burel 1997) and consequently elevated catches of these beetles throughout the edge proximity gradient.

Community structure was little affected by undergrowth removal and edge proximity

In terms of the overall community structure, carabids did not respond to the treatment or to the 20-m edge gradient, whereas plants responded to the treatment. Even for plants, the samples of untreated and treated stands may be better described as being different on average rather than being distinctive (Fig. 4). Similarly, the soil microbial community in Finnish urban forests varied only little within 20 m, but was more different 50 m, from edge to interior (Malmivaara-Lämsä et al. 2008; see also Harper et al. 2005). The ambiguity may have been because most species in our data were open-habitat associated, or generalists of habitat openness (Appendix; see discussion above) or, not mutually exclusively, the communities varied remarkably independent of the treatment or edge proximity. Indeed, 40 out of a total of 87 species occurred in only 1–2 stands so that 18 were found solely in treated and 13 solely in untreated stands. Moreover, 27 species occupied 3–5 stands, but only 3 of these were solely found in treated or in untreated stands. Another explanation for such difficult-to-predict occurrences of plants and carabids may be habitat heterogeneity (Honnay, Hermy, and Coppin 1999; Marchand and Houle 2006; Fuller, Oliver, and Leather 2008; see Table 1). Moreover, our stands could have hosted remnant populations of some species; partly for this reason, community heterogeneity may sometimes be higher in fragmented urban than in contiguous rural habitats (e.g. Klausnitzer and Richter 1983; Niemelä et al. 2002; Venn, Kotze, and Niemelä 2003; Magura, Tóthmérész, and Molnár 2008).

Conclusions

Our study is among the first that assesses the impact of undergrowth removal on ecological communities. From ecological, management and conservation perspectives, our most important finding was that species associated with closed-canopy conditions often suffered, and species thriving in open habitats benefited, from undergrowth removal and, to some degree, from edge proximity. Clearly, maintaining variation in urban forest management may generally support biodiversity of urban areas (Rydbeck and Falck 2000). For instance, variable retention potentially benefits species associated with shady conditions (Gustafsson et al. 2012; Fedrowitz et al. 2014), especially if applied to maintain and add structural heterogeneity, such as variation in tree densities and layers, and very large and dead trees (e.g. Craig and Macdonald 2009; Pinzon, Spence, and Langor 2012; Stokland, Siitonen, and Jonsson 2012; Suominen et al. 2015; Heikkala, Martikainen, and Kouki 2016; Joelsson et al. 2017). Based on present results, we also recommend managers of urban forests to assess the local fauna and flora before harvesting operations, such as undergrowth removal, to avoid potentially negative impacts on rare and threatened species requiring shady conditions.

Data availability

Data are available at Dryad repository. DOI: 10.5061/dryad.h15c4sp

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Supplementary data

Supplementary data are available at *JUECOL* online.

Conflict of interest statement. None declared.

References

Aavik, T. et al. (2009) 'Vegetation Change in Boreonemoral Forest during Succession – Trends in Species Composition, Richness and Differentiation Diversity', *Annales Zoologici Fennici*, **46**: 326–35.

Alvey, A. A. (2006) 'Promoting and Preserving Biodiversity in the Urban Forest', *Urban Forestry & Urban Greening*, **5**: 195–201.

Atlegrim, O., and Sjöberg, K. (1996) 'Response of Bilberry (*Vaccinium myrtillus*) to Clear-Cutting and Single-Tree Selection Harvests in Uneven-Aged Boreal *Picea abies* Forests', *Forest Ecology and Management*, **86**: 39–50.

Bates, D. et al. (2015) 'Fitting Linear Mixed Effects Models Using lme4', *Journal of Statistical Software*, **67**: 1–48.

Bergstedt, J., and Milberg, P. (2001) 'The Impact of Logging Intensity on Field-Layer Vegetation in Swedish Boreal Forests', *Forest Ecology and Management*, **154**: 105–15.

Bescond, H., Fenton, N. J., and Bergeron, Y. (2011) 'Partial Harvests in the Boreal Forest: Response of the Understory Vegetation Five Years after Harvest', *Forestry Chronicle*, **87**: 86–98.

Borg, I., and Groenen, P. (2005) *Modern Multidimensional Scaling: Theory and Applications*, 2nd ed., p. 471. Springer.

Burke, D., and Goulet, H. (1998) 'Landscape and Area Effects on Beetle Assemblages in Ontario', *Ecography*, **21**: 472–9.

Cajander, A. K. (1949) 'Forest Types and Their Significance', *Acta Forestalia Fennica*, **56**: 1–71.

Charrier, S., Petit, S., and Burel, F. (1997) 'Movements of Abax Parallelepipedus (Coleoptera, Carabidae) in Woody Habitats of a Hedgerow Network Landscape: A Radio-Tracing Study', *Agriculture, Ecosystems & Environment*, **61**: 133–44.

Chen, J., Franklin, J. F., and Spies, T. A. (1993) 'Contrasting Microclimates among Clearcut, Edge, and Interior of Old-Growth Douglas-Fir Forest', *Agricultural and Forest Meteorology*, **63**: 219–37.

—— et al. (1999) 'Microclimate in Forest Ecosystem and Landscape Ecology: Variations in Local Climate Can Be Used to Monitor and Compare the Effects of Different Management Regimes', *BioScience*, **49**: 288–97.

Chiesura, A. (2004) 'The Role of Urban Parks for the Sustainable City', *Landscape and Urban Planning*, **68**: 129–38.

Craig, A., and Macdonald, S. E. (2009) 'Threshold Effects of Variable Retention Harvesting on Understory Plant Communities in the Boreal Mixedwood Forest', *Forest Ecology and Management*, **258**: 2619–27.

Didham, R. K., and Lawton, J. H. (1999) 'Edge Structure Determines the Magnitude of Changes in Microclimate and Vegetation Structure in Tropical Forest Remnants', *Biotropica*, **31**: 17–30.

Duguid, M. C., and Ashton, M. S. (2013) 'A Meta-Analysis of the Effect of Forest Management for Timber on Understory Plant Diversity in Temperate Forests', *Forest Ecology and Management*, **303**: 81–90.

Eldegard, K. et al. (2019) 'The Influence of Stand Density on Bilberry (*Vaccinium myrtillus* L.) Cover Depends on Stand Age, Solar Irradiation, and Tree Species Composition', *Forest Ecology and Management*, **432**: 582–90.

Ellermaa, M. (2018) *Helsingin Tärkeät Lintualueet ja Merkittävä Linnusto 2017*. Helsinki: Kaupunkiympäristön Julkaisuja, **2018**: 8. (In Finnish)

Esseen, P.-A., and Renhorn, K.-E. (1998) 'Edge Effects on an Epiphytic Lichen in Fragmented Forests', *Conservation Biology*, **12**: 1307–17.

Fedrowitz, K. et al. (2014) 'Can Retention Forestry Help Conserve Biodiversity? a Meta-Analysis', *Journal of Applied Ecology*, **51**: 1669–79.

Forman, R. T. T. (2008) Urban Regions. *Ecology and Planning Beyond the City*. Cambridge University Press.

Fox, J., and Weisberg, S. (2011) *An R Companion to Applied Regression*. 2nd ed. Thousand Oaks, CA. <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion> accessed 30 Mar 2019.

Fuller, R. J., Oliver, T. H., and Leather, S. R. (2008) 'Forest Management Effects on Carabid Beetle Communities in Coniferous and Broadleaved Forests: Implications for Conservation', *Insect Conservation and Diversity*, **1**: 242–52.

Gallé, R., and Fehér, B. (2006) 'Edge Effect on Spider Assemblages', *Tiscia*, **35**: 37–40.

Grimm, N. B. et al. (2008) 'Global Change and the Ecology of Cities', *Science (New York, N.Y.)*, **319**: 756–60.

Guirado, M., Pino, J., and Roda, F. (2006) 'Understorey Plant Species Richness and Composition in Metropolitan Forest Archipelagos: Effects of Forest Size, Adjacent Land Use and Distance to the Edge', *Global Ecology and Biogeography*, **15**: 50–62.

Gustafsson, L. et al. (2012) 'Retention Forestry to Maintain Multifunctional Forests: A World Perspective', *BioScience*, **62**: 633–45.

Hamberg, L. et al. (2008) 'The Effects of Habitat Edges and Trampling on Understorey Vegetation in Urban Forests in Helsinki, Finland', *Applied Vegetation Science*, **11**: 83–98.

—— et al. (2010) 'Quantifying the Effects of Trampling and Habitat Edges on Forest Understory Vegetation – A Field Experiment', *Journal of Environmental Management*, **91**: 1811–20.

——, Löfström, I.& Häkkinen, I., eds. (2012) *Taajamametsät – Suunnittelu ja Hoito*, p. 156. Finnish Forest Research Institute and Metsäkustannus. (In Finnish)

Harper, K. A. et al. (2005) 'Edge Influence on Forest Structure and Composition in Fragmented Landscapes', *Conservation Biology*, **19**: 768–82.

—— et al. (2015) 'Edge Influence on Vegetation at Natural and Anthropogenic Edges of Boreal Forests in Canada and Fennoscandia', *Journal of Ecology*, **103**: 550–62.

Heikkala, O., Martikainen, P., and Kouki, J. (2016) 'Decadal Effects of Emulating Natural Disturbances in Forest Management on Saproxylic Beetle Assemblages', *Biological Conservation*, **194**: 39–47.

Heliölä, J., Koivula, M., and Niemelä, J. (2001) 'Distribution of Carabid Beetles (Coleoptera, Carabidae) Across a Boreal Forest-Clearcut Ecotone', *Conservation Biology*, **15**: 370–7.

Honnay, O., Hermy, M., and Coppin, P. (1999) 'Effects of Area, Age and Diversity of Forest Patches in Belgium on Plant Species Richness, and Implications for Conservation and Reforestation', *Biological Conservation*, **87**: 73–84.

——, Verheyen, K., and Hermy, M. (2002) 'Permeability of Ancient Forest Edges for Weedy Plant Species Invasion', *Forest Ecology and Management*, **161**: 109–22.

Huggard, D. J., and Vyse, A. (2002) 'Edge Effects in High-Elevation Forests at Sicamous Creek', Extension Note, 62. British Columbia Ministry of Forests Forest Science Program, Victoria, BC, pp. 1–8.

Ilisson, T. et al. (2006) 'Vascular Plant Response to Windthrow Severity in Norway Spruce-Dominated Myrtillus Site Type Forests in Estonia', *Ecoscience*, **13**: 193–202.

Ives, C. D. et al. (2016) 'Cities Are Hotspots for Threatened Species', *Global Ecology and Biogeography*, **25**: 117–26.

Jalonen, J., and Vanha-Majamaa, I. (2001) 'Immediate Effects of Four Different Felling Methods on Mature Spruce Forest Understorey Vegetation in Southern Finland', *Forest Ecology and Management*, **146**: 25–34.

Joelsson, K. et al. (2017) 'Uneven-Aged Silviculture Can Reduce Negative Effects of Forest Management on Beetles', *Forest Ecology and Management*, **391**: 436–45.

Johnson, S., Strengbom, J., and Kouki, J. (2014) 'Low Levels of Retention Do Not Mitigate the Effects of Clearcutting on Ground Vegetation Dynamics', *Forest Ecology and Management*, **330**: 67–74.

Jones, E. L., and Leather, S. R. (2012) 'Invertebrates in Urban Areas: A Review', *European Journal of Entomology*, **109**: 463–78.

Kabisch, N., Qureshi, S., and Haase, D. (2015) 'Human-Environment Interactions in Urban Green Spaces – A Systematic Review of Contemporary Issues and Prospects for Future Research', *Environmental Impact Assessment Review*, **50**: 25–34.

Klausnitzer, B., and Richter, K. (1983) 'Presence of Urban Gradient Demonstrated for Carabid Associations', *Oecologia*, **59**: 79–82.

Koivula, M. (2002) 'Alternative Harvesting Methods and Boreal Carabid Beetles (Coleoptera, Carabidae)', *Forest Ecology and Management*, **167**: 103–21.

——, Hyyryläinen, V., and Soininen, E. (2004) 'Carabid Beetles (Coleoptera: Carabidae) at Forest-Farmland Edges in Southern Finland', *Journal of Insect Conservation*, **8**: 297–309.

—— et al. (2003) 'Pitfall Trap Efficiency: Do Trap Size, Collecting Fluid and Vegetation Structure Matter?', *Entomologica Fennica*, **14**: 1–14.

Koivula, M. J. (2011) 'Useful Model Organisms, Indicators, or Both? Ground Beetles (Coleoptera, Carabidae) Reflecting Environmental Conditions', *ZooKeys*, **100**: 287–317.

—— (2012) 'Under Which Conditions Does Retention Harvesting Support Ground Beetles of Boreal Forests? ', *Baltic Journal of Coleopterology*, **12**: 7–26.

—— et al. (2019) 'Responses of Ground Beetles (Coleoptera, Carabidae) to Different Logging Regimes Ten Years Post Harvest', *Forest Ecology and Management*, **436**: 27–38.

Kotze, D. J. et al. (2011) 'Forty Years of Carabid Beetle Research in Europe – From Taxonomy, Biology, Ecology and Population Studies to Bioindication, Habitat Assessment and Conservation', *ZooKeys*, **100**: 55–148.

—— et al. (2012) 'Effects of Habitat Edges and Trampling on the Distribution of Ground Beetles (Coleoptera, Carabidae) in Urban Forests', *Journal of Insect Conservation*, **16**: 883–97.

Kujala, V. (1926) 'Untersuchungen Über Die Waldvegetation in Süd- Und Mittelfinnland. I. Zur Kenntnis Des Ökologisch-Biologischen Charakters Der Pflanzenarten Unter Speziellen Berücksichtigung Der Bildung Von Pflanzenvereinen. A. Gefässpflanzen', *Communicationes Ex Instituto Quaestionum Forestalium Finlandiae*, **10**: 1–140. (In German)

Kurtto, A. (2002) *Helsingin Uhanalaiset, Silmälläpidettävät ja Muuten Huomionarvoiset Putkilokasvit*. Helsingin Kaupungin Ympäristökeskus, p. 34. (In Finnish)

Kuuluvainen, T., Tahvonen, O., and Aakala, T. (2012) 'Even-Aged and Uneven-Aged Forest Management in Boreal Fennoscandia: A Review', *Ambio*, **41**: 720–37.

Lindroth, C. H. (1985) 'The Carabidae (Coleoptera) of Fennoscandia and Denmark', *Fauna Entomologica Scandinavica*, **15**: 1–225.

—— (1986) 'The Carabidae (Coleoptera) of Fennoscandia and Denmark', *Fauna Entomologica Scandinavica*, **15**: 233–497.

Littlemore, J., and Barker, S. (2001) 'The Ecological Response of Forest Ground Flora and Soils to Experimental Trampling in British Urban Woodlands', *Urban Ecosystems*, **5**: 257–76.

Macdonald, S. E., and Fenniak, T. E. (2007) 'Understory Plant Communities of Boreal Mixedwood Forests in Western Canada: Natural Patterns and Response to Variable-Retention Harvesting', *Forest Ecology and Management*, **242**: 34–48.

Magura, T. (2002) 'Carabids and Forest Edge: Spatial Pattern and Edge Effect', *Forest Ecology and Management*, **157**: 23–37.

——, Tóthmérész, B., and Molnár, T. (2008) 'A Species-Level Comparison of Occurrence Patterns in Carabids along an Urbanisation Gradient', *Landscape and Urban Planning*, **86**: 134–40.

——, Lövei, G. L., and Tóthmérész, B. (2010) 'Does Urbanization Decrease Diversity in Ground Beetle (Carabidae) Assemblages?', *Global Ecology and Biogeography*, **19**: 16–26.

Malmivaara, M., Löfström, I., and Vanha-Majamaa, I. (2002) 'Anthropogenic Effects on Understorey Vegetation in Myrtillus Type Urban Forests in Southern Finland', *Silva Fennica*, **36**: 367–81.

Malmivaara-Lämsä, M. et al. (2008) 'Edge Effects and Trampling in Boreal Urban Forest Fragments – Impacts on the Soil Microbial Community', *Soil Biology and Biochemistry*, **40**: 1612–21.

Marchand, P., and Houle, G. (2006) 'Spatial Patterns of Plant Species Richness along a Forest Edge: What Are Their Determinants?', *Forest Ecology and Management*, **223**: 113–24.

Matlack, G. R. (1993) 'Microenvironment Variation within and among Forest Edge Sites in the Eastern United States', *Biological Conservation*, **66**: 185–94.

Matveinen-Huju, K. et al. (2006) 'Retention-Tree Groups in Clear-Cuts: Do They Constitute 'Life Boats' for Spiders and Carabids?', *Forest Ecology and Management*, **230**: 119–35.

McDonnell, M. J. et al. (1997) 'Ecosystem Processes along an Urban-to-Rural Gradient', *Urban Ecosystems*, **1**: 21–6.

McKinney, M. L. (2006) 'Urbanization as a Major Cause of Biotic Homogenization', *Biological Conservation*, **127**: 247–60.

—— (2008) 'Effects of Urbanization on Species Richness: A Review of Plants and Animals', *Urban Ecosystems*, **11**: 161–76.

Mossberg, B., and Stenberg, L., eds. (2003) *Den Nya Nordiska Floran*. 2nd ed. Stockholm: Wahlström & Widstrand. (In Swedish)

Murcia, C. (1995) 'Edge Effects in Fragmented Forests: Implications for Conservation', *Trends in Ecology & Evolution*, **10**: 58–62.

Nascimbene, J., Thor, G., and Nimis, P. L. (2013) 'Effects of Forest Management on Epiphytic Lichens in Temperate Deciduous Forests of Europe – A Review', *Forest Ecology and Management*, **298**: 27–38.

Nielsen, A. B. et al. (2014) 'Species Richness in Urban Parks and Its Drivers: A Review of Empirical Evidence', *Urban Ecosystems*, **17**: 305–27.

Niemelä, J. (1997) 'Invertebrates and Boreal Forest Management', *Conservation Biology*, **11**: 601–10.

——, and Kotze, J. (2009) 'Carabid Beetle Assemblages along Urban to Rural Gradients: A Review', *Landscape and Urban Planning*, **92**: 65–71.

—— et al. (1988) 'The Distribution of Carabid Beetles in Fragments of Old Coniferous Taiga and Adjacent Managed Forest', *Annales Zoologici Fennici*, **25**: 107–19.

—— et al. (2002) 'Carabid Beetle Assemblages (Coleoptera, Carabidae) across Urban-Rural Gradients: An International Comparison', *Landscape Ecology*, **17**: 387–401.

——, Koivula, M., and Kotze, D. J. (2007) 'The Effects of Forestry on Carabid Beetles (Coleoptera: Carabidae) in Boreal Forests', *Journal of Insect Conservation*, **11**: 5–18.

——, et al., eds. (2011) *Urban Ecology: Patterns, Processes and Applications*, p. 374. Oxford University Press.

Nittérus, K., Åström, M., and Gunnarsson, B. (2007) 'Commercial Harvest of Logging Residue in Clear-Cuts Affects the Diversity and Community Composition of Ground Beetles (Coleoptera: Carabidae)', *Scandinavian Journal of Forest Research*, **22**: 231–40.

Nybakken, L., Selås, V., and Ohlson, M. (2013) 'Increased Growth and Phenolic Compounds in Bilberry (*Vaccinium myrtillus* L.) following Forest Clear-Cutting', *Scandinavian Journal of Forest Research*, **28**: 319–30.

Oksanen, J. et al. (2018) 'Vegan: Community Ecology Package Version 2.5-2, Vienna, Austria', <https://CRAN.R-project.org/package=vegan> accessed 30 Mar 2019.

Palviainen, M. (2005) 'Logging Residues and Ground Vegetation in Nutrient Dynamics of a Clear-Cut Boreal Forest', PhD thesis, Faculty of Forestry, University of Joensuu, Finland.

—— et al. (2005) 'Responses of Ground Vegetation Species to Clear-Cutting in a Boreal Forest: Aboveground Biomass and Nutrient Contents during the First 7 Years', *Ecological Research*, **20**: 652–60.

Pinzon, J., Spence, J. R., and Langor, D. W. (2012) 'Responses of Gorund-Dwelling Spiders (Araneae) to Variable Retention Harvesting Practices in the Boreal Forest', *Forest Ecology and Management*, **266**: 42–53.

Prass, M. et al. (2017) 'The Matrix Affects Carabid Beetle Assemblages in Linear Urban Ruderal Habitats', *Urban Ecosystems*, **20**: 971–81.

Pykälä, J. (2004) 'Immediate Increase in Plant Species Richness after Clear-Cutting of Boreal Herb-Rich Forests', *Applied Vegetation Science*, **7**: 29–34.

R Core Team. (2018) *R: A Language and Environment for Statistical Computing*. Vienna, Austria. <http://www.r-project.org> accessed 30 Mar 2019.

Reinikainen, A., et al., eds. (2000) *Kasvit Muuttuvassa Metsäluonnossa*. Helsinki: Kustannusosakeyhtiö Tammi. (In Finnish)

Rydbeck, D., and Falck, J. (2000) 'Urban Forestry in Sweden from a Silvicultural Perspective: A Review', *Landscape and Urban Planning*, **47**: 1–18.

Sadler, J. P. et al. (2006) 'Investigating Environmental Variation and Landscape Characteristics of an Urban-Rural Gradient Using Woodland Carabid Assemblages', *Journal of Biogeography*, **33**: 1126–38.

Salo, K., ed. (2015) *Metsä: Monikäyttö ja Ekosysteemipalvelut*, p. 328. Natural Resources Institute Finland (Luke). (In Finnish)

Savola, K. (2012) 'Helsingin Metsien Kääpäselvitys 2011', *Helsingin Kaupungin Ympäristökeskuksen Julkaisuja* 5/2012, p. 46. (In Finnish)

Seto, K. C., Guneralp, B., and Hutyra, L. R. (2012) 'Global Forecasts of Urban Expansion to 2030 and Direct Impacts on Biodiversity and Carbon Pools', *Proceedings of the National Academy of Sciences of the United States of America*, **109**: 16083–8.

Spence, J. R. et al. (1996) 'Northern Forestry and Carabids: The Case for Concern about Old-Growth Species', *Annales Zoologici Fennici*, **33**: 173–84.

Stokland, J., Siitonen, J., and Jonsson, B. G. (2012) *Biodiversity in Dead Wood*, p. 509. Cambridge: Cambridge University Press.

Suominen, M. et al. (2015) 'Combined Effects of Retention Forestry and Prescribed Burning on Polypore Fungi', *Journal of Applied Ecology*, **52**: 1001–8.

Thiele, H.-U. (1977) *Carabid Beetles in Their Environments. Zoophysiology and Ecology 10*, p. 361. Berlin: Springer.

Thurston, E., and Reader, R. J. (2001) 'Impacts of Experimentally Applied Mountain Biking and Hiking on Vegetation and Soil of a Deciduous Forest', *Environmental Management*, **27**: 397–409.

Tonteri, T. (1994) 'Species Richness of Boreal Understorey Forest Vegetation in Relation to Site Type and Successional Factors', *Annales Zoologici Fennici*, **31**: 53–60.

—— et al. (2016) 'Forest Management Regulates Temporal Change in the Cover of Boreal Plant Species', *Forest Ecology and Management*, **381**: 115–24.

Tyrväinen, L., Silvennoinen, H., and Kolehmainen, O. (2003) 'Ecological and Aesthetic Values in Urban Forest Management', *Urban Forestry & Urban Greening*, **1**: 135–49.

United Nations. (2018) 'World Urbanization Prospects 2018',. DESA/Population Division. <https://esa.un.org/unpd/wup/DataQuery/> accessed 26 Jun 2018.

Vallet, J. et al. (2010) 'The Effects of Urban or Rural Landscape Context and Distance from the Edge on Native Woodland Plant Communities', *Biodiversity and Conservation*, **19**: 3375–92.

Vance, C. C., and Nol, E. (2003) 'Temporal Effects of Selection Logging on Ground Beetle Communities in Northern Hardwood Forests of Eastern Canada', *Ecoscience*, **10**: 49–56.

Vellend, M. et al. (2006) 'Extinction Debt of Forest Plants Persists for More than a Century following Habitat Fragmentation', *Ecology*, **87**: 542–8.

Venables, W. N., and Ripley, B. D. (2002) *Modern Applied Statistics with S*, 4th ed. New York: Springer.

Venn, S. J., Kotze, D., and Niemelä, J. (2003) 'Urbanization Effects on Carabid Diversity in Boreal Forests', *European Journal of Entomology*, **100**: 73–80.

Ver Hoef, J. M., and Boveng, P. L. (2007) 'Quasi-Poisson vs. Negative Binomial Regression: How Should We Model Overdispersed Count Data?', *Ecology*, **88**: 2766–72.

Whitford, V., Handley, J., and Ennos, R. (2001) 'City Form and Natural Process – Indicators for the Ecological Performance of Urban Areas', *Landscape and Urban Planning*, **57**: 91–103.

Work, T. T. et al. (2010) 'High Levels of Green-Tree Retention Are Required to Preserve Ground Beetle Biodiversity in Boreal Mixedwood Forests', *Ecological Applications*, **20**: 741–51.

Zuur, A. F. et al. (2009) *Mixed Effects Models and Extensions in Ecology With R*, p. 574. Springer Science + Business Media.

Zywiec, M., and Ledwon, M. (2008) 'Spatial and Temporal Patterns of Rowan (*Sorbus aucuparia* L) Regeneration in West Carpathian Subalpine Spruce Forest', *Plant Ecology*, **194**: 283–91.

Appendix

Table A1: Species of carabid beetles and plants, collected from 10 forest stands in Jyväskylä, Finlanpd, in alphabetical order

Species	HAB	UN TOT	UN OCC	TR TOT	TR OCC	Species	HAB	UN TOT	UN OCC	TR TOT	TR OCC
Carabid beetles (1)						Carabid beetles (2)					
Amara communis	o	1	1	4	3	*Loricera pilicornis*	g	0	0	3	1
Amara lunicollis	o	0	0	1	1	*Notiophilus biguttatus*	g	1	1	1	1
Anisodactylus binotatus	o	0	0	1	1	*Patrobus assimilis*	g	12	3	35	3
Badister lacertosus	g	2	2	2	2	*Patrobus atrorufus*	g	11	6	17	5
Calathus melanocephalus	o	1	1	5	2	*Pterostichus diligens*	g	1	1	2	2
C.micropterus	f	42	10	33	10	*P.melanarius*	g	69	7	62	8
Carabus hortensis	f	82	6	13	2	*Pterostichus niger*	g	10	6	7	4
C.nemoralis	g	74	11	107	14	*Pterostichus nigrita*	g	1	1	0	0
Cychrus caraboides	f	3	1	0	0	*P.oblongopunctatus*	f	100	12	212	11
Harpalus laevipes	g	2	1	2	1	*Pterostichus strenuus*	g	6	5	6	3
Harpalus tardus	o	0	0	3	2	*Synuchus vivalis*	g	10	6	15	7
Leistus ferrugineus	g	23	5	9	5	*Trechus rivularis*	f	1	1	0	0
L.terminatus	f	52	13	33	10	*T.secalis*	g	43	9	47	8
Vascular plants (1)						Vascular plants (2)					
Acer platanoides	f	0.00	0	0.33	4	*Lonicera xylosteum*	f	3.00	2	0.00	0
Actaea spicata	f	0.00	0	1.33	1	*Luzula luzuloides*	g	4.67	1	0.00	0
Aegopodium podagraria	f	2.32	4	3.59	4	*Luzula pilosa*	g	0.02	1	0.13	3
Agrostis capillaris	o	0.47	4	0.00	0	*M.bifolium*	g	1.49	12	4.98	14
Alchemilla sp	o	0.10	3	0.00	0	*Melampyrum pratense*	g	0.49	3	0.63	3
Anthriscus sylvestris	o	0.13	2	0.70	4	*Melampyrum sylvaticum*	g	0.86	5	0.34	2
Artemisia vulgaris	o	0.08	2	0.11	1	*Melica nutans*	g	0.14	2	0.71	6
Athyrium filix-femina	g	1.17	5	0.07	1	*Milium effusum*	f	0.00	0	1.11	1
C.arundinaceus	o	9.56	11	8.31	9	*Nardus stricta*	o	0.00	0	0.22	1
Campanula rotundifolia	o	0.00	0	0.01	1	*O.acetocella*	f	8.07	13	2.16	9
Carex acuta	r	0.02	1	0.00	0	*Paris quadrifolia*	f	0.57	3	0.75	7
Carex canescens	r	0.22	1	0.00	0	*Phleum pratense*	o	0.02	1	0.00	0
Cirsium arvense	o	0.16	2	0.00	0	*Poa chaixii*	o	0.14	2	0.00	0
Convallaria majalis	g	2.96	4	1.19	2	*Ranunculus acris*	o	0.04	1	0.00	0
Deschampsia cespitosa	o	0.37	3	0.00	0	*Ranunculus repens*	o	1.00	2	0.80	3
D.flexuosa	o	2.60	7	2.36	8	*Ribes rubrum*	g	0.16	2	0.56	3
Dryopteris carthusiana	g	0.00	0	0.44	1	*Rubus idaeus*	g	3.24	7	2.74	5
Dryopteris filix-mas	g	0.90	2	1.24	3	*R.saxatilis*	g	2.42	9	7.97	9
Epilobium angustifolium	o	0.00	0	0.51	4	*Scrophularia nodosa*	g	0.13	1	0.00	0
Epilobium montanum	g	0.09	4	0.03	1	*Solidago virgaurea*	g	0.01	1	0.00	0
Equisetum pratense	f	2.36	4	2.09	3	*S.aucuparia*	g	2.98	6	3.21	14
Equisetum sylvaticum	g	0.31	3	0.33	1	*Taraxacum* sp	o	0.00	0	0.04	4
Festuca ovina	o	0.93	1	0.00	0	*T.europaea*	g	1.07	11	0.73	12
Fragaria vesca	o	2.17	3	0.23	5	*Urtica dioica*	g	0.04	1	0.12	2
Galium album	o	0.00	0	1.31	3	*Urtica urens*	g	1.12	2	0.00	0
G.sylvaticum	g	1.13	6	2.69	9	*V.myrtillus*	f	11.78	12	2.64	11
Geum urbanum	g	0.00	0	0.38	2	*Vaccinium vitis-idaea*	g	0.32	5	0.41	5
Gymnocarpium dryopteris	g	0.62	3	1.49	7	*Veronica chamaedrys*	o	0.53	3	0.29	3
Hieracium sylvatica	g	1.74	7	0.19	4	*Veronica officinalis*	o	0.06	2	0.08	1
Hypericum maculatum	o	0.05	1	0.30	3	*Viola riviniana*	g	0.24	6	0.18	6
Linnaea borealis	f	0.00	0	0.27	1						

Columns show, from left to right, habitat association (HAB; f, closed forest; g, forest-open habitat generalist; and o, open habitat), total catch or average percent cover (TOT) and total number of occupied sampling stations (OCC; max 15) for untreated (UN) and treated (TR) stands.