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Urban Forest Habitat Heterogeneity and Its Effects on Carabid Beetles

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Tiivistelmä - Referat - Abstract

The ongoing growth and densification of urban areas is threatening biodiversity in cities. Previously continuous habitats are reduced and fragmented into smaller areas, which increases the edge effect and changes the qualities of the original habitat. Urban greenspaces are frequently used by people, and disturbances, such as trampling, and understorey management are increasing the similarity of habitat patches (i.e. homogenisation).

In this study, I investigated the effects of small-scale homogeneity in forests produced by urbanisation on the distribution patterns and trait composition of carabid beetles. Sampling was done with pitfall traps during the summer of 2021 and altogether 21 study sites were selected in the City of Lahti, Finland. The study sites represented three different environments: 1) structurally complex (heterogenous) habitat in remnant spruce forests in the city, 2) structurally simple (homogenous) habitat in remnant spruce forests in the city, 3) structurally simple habitat under spruce trees in managed urban parks. In addition to the beetles, a set of environmental variables was collected to quantify the complexity of the three habitat types.

As expected, habitat homogeneity affected carabid beetle species composition so that the proportion of generalist and open-habitat species was greater in homogenous sites, including homogenous forest remnants and highly homogenous urban parks, whereas the proportion of forest specialists was greater in heterogenous forests. Species richness was higher in the homogenous sites due to species-rich open-habitat genera in the carabid beetle family.

Trait distribution at the community level showed clear differences between the three studied habitat types. As expected, the proportions of large and heavy species were higher in the forest habitats than in the parks, whereas homogenous habitats, especially highly homogenous park sites consisted of a higher proportion of flight capable species than heterogenous forests. At the species level, individual beetles were generally smaller in the parks, whereas the results between the two forest types varied and a clear difference between habitat specialists and generalists could not be detected.

As cities grow, keeping the management of greenspaces moderate, selecting native vegetation, and preserving decaying woody material are ways to increase habitat heterogeneity, which according to this study, can support biodiversity and life of different organisms in urban areas.

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Urban ecology, entomology, soil science, biodiversity, ecosystem services, carabid beetles, insects, remnant forests, parks, heterogeneity, homogeneity

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Tiivistelmä - Referat - Abstract

Kaupunkialueiden jatkuva kasvu ja tiivistyminen uhkaavat luonnon monimuotoisuutta. Aiemmin yhtenäiset elinympäristöt pirstoutuvat pienemmiksi alueiksi, mikä lisää reunavaikutusta ja muuttaa alkuperäisen elinympäristön ominaisuuksia. Kaupunkien viheralueet ovat usein ihmisten käytössä ja häiriöt, kuten tallautuminen ja aluskasvillisuuden hoito, johtavat elinympäristöjen samankaltaistumiseen (homogenisoitumiseen).

Tässä tutkimuksessa selvitin kaupungistumisen tuottaman pienen mittakaavan homogeenisuuden vaikutuksia maakiitäjäiskovakuoriaisten dispersaaliin (levittäytymiseen) ja ominaisuuksiin. Näytteenotto tehtiin kuoppapyydyksillä 21 tutkimusalueella Lahdessa kesällä 2021. Tutkimuskohteet edustivat kolmea erilaista ympäristöä: 1) rakenteellisesti monimutkainen (heterogeeninen) elinympäristö kaupungin jäännöskuusimetsissä, 2) rakenteellisesti yksinkertainen (homogeeninen) elinympäristö kaupungin jäännöskuusimetsissä, 3) rakenteellisesti yksinkertainen elinympäristö hoidettujen kaupunkipuistojen kuusien alla. Kuoriaisten lisäksi kerättiin joukko ympäristömuuttujia kunkin elinympäristön monimuotoisuuden määrittämiseksi.

Elinympäristön homogeenisuus vaikutti maakiitäjäisten lajikoostumukseen odotetusti siten, että generalistien ja avoimen ympäristön lajien osuus oli suurempi homogeenisilla alueilla, mukaan lukien jäännösmetsät ja erittäin homogeeniset kaupunkipuistot, kun taas metsälajien osuus oli suurempi heterogeenisissa metsissä. Lajirikkaus oli korkeampi homogeenisilla alueilla johtuen avoimen ympäristön lajien suuresta määrästä maakiitäjäisten heimossa.

Ominaisuuksien jakautuminen yhteisötasolla osoitti selviä eroja kolmen tutkitun elinympäristötyypin välillä. Suurten ja painavien lajien osuudet olivat odotetusti suuremmat metsissä kuin puistoissa. Homogeenisissa elinympäristöissä, erityisesti erittäin homogeenisilla puistoalueilla, esiintyi enemmän lentokykyisiä lajeja kuin heterogeenisissa metsissä. Yksittäisten lajien tasolla maakiitäjäiset olivat puistoissa pääsääntöisesti pienempiä kuin metsissä, kun taas tulokset kahden metsätyypin välillä vaihtelivat, eikä selvää eroa spesialistien ja generalistien välillä voitu havaita.

Kaupunkien kasvaessa viheralueiden maltillinen hoito, kotoperäisen kasvillisuuden suosiminen ja lahoavan puuaineksen säilyttäminen ovat keinoja lisätä elinympäristön heterogeenisuutta ja tutkimustulosteni perusteella tukea ja suojella kaupunkiluonnon monimuotoisuutta.

Avainsanat – Nyckelord - Keywords
Kaupunkiekologia, entomologia, maaperätiede, biodiversiteetti, ekosysteemipalvelut, maakiitäjäiset, hyönteiset, jäännösmetsät, puistot, heterogeenisuus, homogeenisuus

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1. Introduction

The growth and densification of urban areas has led to habitat loss and fragmentation, which are considered to be two of the main causes of a decrease in biodiversity (Beninde et al., 2015). With habitat fragmentation, a formerly continuous area is reduced and fragmented into smaller patches, which does not only reduce the size and increase isolation of the habitat, but also increases edge effects, where the quality of the original habitat reduces from its core to its interface with the surrounding habitat (Fahrig, 2003).

Vegetation is considered crucial for urban fauna, providing habitat and food (Beninde et al., 2015). Isolation and reduced quality of the "green" habitat often lead to a decrease in species richness and abundance (Jones & Leather, 2012). Urban green areas that still exist are frequently used by people and experience disturbances such as trampling and management of vegetation. Landscaping and maintenance of greenspaces, such as parks and roadside verges, often involve the removal of shrubs and dead wood (Marzluff & Erwing, 2001). This kind of landscaping increases similarity of urban habitat patches (i.e. homogenisation), which can be detrimental to native and specialist species but may simultaneously create new habitats and increase spatial heterogeneity that can sometimes produce greater species richness than surrounding rural areas (Wania et al., 2006). While urban environments may be harsh for many specialist species, they can offer plenty of resources for generalists that are not so specific in terms of their habitat requirements (Noreika & Kotze, 2012).

Urban forests are not an exception when it comes to human induced disturbance. Trampling and understorey management lead to a simplified structure at ground level. Yet, small-scale heterogeneity exists in these remnants, including piles of dead and decaying wood, boggy areas, and lush vegetation (Hamberg et al., 2008; Noreika et al., 2015; Korhonen et al., 2020). This structural heterogeneity increases the availability of different niches for diverse fauna, including ground-dwelling arthropods.

In this study, I investigate the response of an indicator taxon, carabid beetles (Coleoptera, Carabidae), to small-scale within site homogeneity produced by urbanisation, both from a taxonomic and functional trait perspective. Carabid beetles are a taxonomically and ecologically well-known group of arthropods, commonly used in ecological studies, due to their sensitivity to environmental change and habitat alteration (Rainio & Niemelä, 2003; Koivula, 2011; Kotze et al., 2011; Sukhodolskaya, 2013). They are present at different trophic levels (predacious, omnivores, granivorous), can be habitat generalists or specialists and have different potentials in dispersal capacity given their wing morphology differences (Lindroth, 1985, 1986). Furthermore, carabids are easy and cost-efficient to collect by using pitfall traps.

The aim of this study is to investigate the effects of ground-level habitat homogeneity in urban forests and parks on carabid beetle species richness, composition, and functional traits, such as length, mass and type of wings. Finnish cities provide a great opportunity to investigate this, since they consist of remnant forests that are differently used, thus creating homogenous and heterogenous under-growth and varying complexity of woody debris. The dominant tree species, Norway spruce, is common to all urban habitats irrespective of their disturbance level, and thus it can also be found in urban parks with a highly homogenous under-growth.

I hypothesise that habitat homogeneity will have a significant effect on carabid beetle species composition, with homogenous (managed) sites consisting of more generalist and open-habitat species, while heterogenous (more natural) sites will be characterised by a larger proportion of forest species (McKinney, 2006; Gaublomme et al., 2008). Additionally, since open-habitat genera in the carabid beetle family are species rich (see Lindroth 1985, 1986), I hypothesise that these homogenous sites will be species richer than the heterogenous sites (Jones & Leather, 2012). If structural homogenisation at ground level place these beetles under higher stress in terms of reduced resources and increased predation pressure, I hypothesise that beetles in homogenous sites will be smaller in body size, and lighter in mass (McGeoch, 1998). Additionally, these communities are also expected to consist of a higher proportion of flight capable species compared to those in heterogenous sites (Sadler et al., 2006).

2. Materials and methods

2.1. Study area and sites

The study was conducted in the City of Lahti, southern Finland. Altogether, 21 sampling sites were selected within the city that is located in the southern boreal vegetation zone (Karlsen et al., 2002). The sites were divided into three different habitat types (7 replicates per type): heterogenous and homogenous spruce dominated urban remnant forests, and highly homogenous urban parks (Fig. 1). In the park sites, pitfall traps were placed directly under a conifer canopy to avoid possible disturbance caused by passers-by.

Selecting the forest sites was implemented by visually estimating the habitat (Fig. 2). The main indicator for heterogeneity in this study was the amount of dead and decaying wood, while homogenous sites had very little dead wood or none at all. Unlike park traps, forest traps were not placed directly underneath a canopy of one tree, but somewhere in the middle of a forest patch that filled the criteria for heterogenous or homogenous remnant forest.

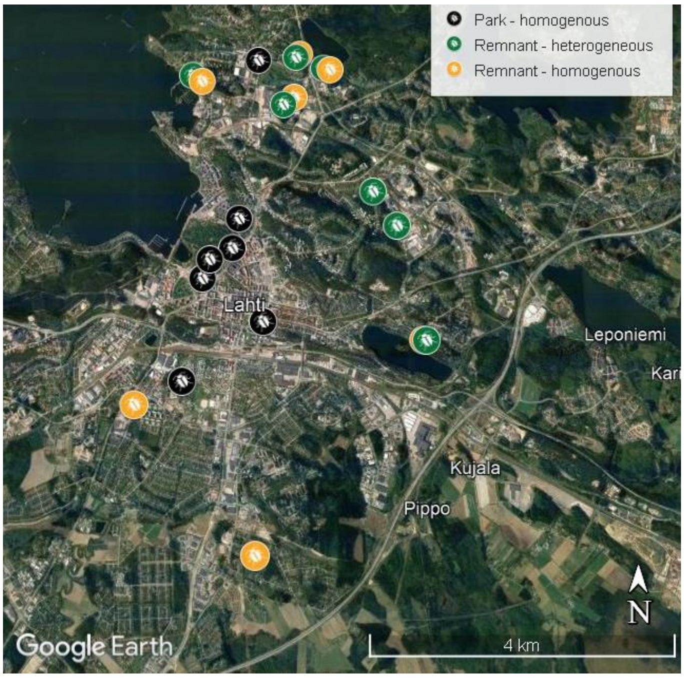

Figure 1. The locations of study sites in Lahti. (Google Earth Pro, 18.1.2022). Site coordinates are listed in Appendix 1.

Figure 2. A visual representation of the habitat types included in my study. From left to right, heterogenous remnant forest, homogenous remnant forest and highly homogenous urban park.

2.2. Carabid beetle sampling

Carabid beetles were sampled by pitfall trapping in 2021 from late May to late August. Placing pitfall traps in the environment is a passive way to collect specimen and is affected by the activity of the beetles in their habitat as well as the size of the population (Lövei & Sunderland, 1996). Samples were collected every third week, resulting in four visits. Five traps were installed at each site (105 traps altogether) and placed within a square meter, with four traps placed at the square's corners and the fifth trap in the middle of the square. The catch of the five traps per site was pooled per visit.

The traps were plastic cups (depth and mouth diameter ~ 7 cm) that were dug into the ground, their rim at the level of the ground surface. Each cup was half-filled with 50 % propylene glycol – aqueous solution to preserve the beetles and prevent them from escaping. Above each trap, a 10 x 10 cm plastic roof was placed at about 2 cm above ground to protect the traps from rain, excessive debris and possible disturbance caused by small mammals ending up in the traps or eating the catch. All trap losses along with other noteworthy remarks of the condition of each site were recorded and considered in data analysis. The collected catches were preserved in denatured alcohol before sorting and identification.

From each sample, the number of carabid beetles were recorded. Every individual was identified to species level with the identification keys in Lindroth (1985, 1986) and supporting online materials, such as laji.fi and kerbtier.de.

Identification was conducted using a Leica S4E stereo zoom microscope. Body length, elytra length and dry body mass (air dried in the laboratory for 2 days before weighing on an analytical balance) were measured for each carabid beetle collected. Elytra length was chosen to represent body length, since it is easier to measure accurately than full body length of a beetle. Wing type (brachypterous = reduced wings, dimorphic = either has wings or doesn't have, macropterous = full wings) was also recorded from the collected individuals.

2.3. Environmental variables and habitat quantification

In mid-August 2021, several environmental variables were recorded at each of the 21 sampling sites. This was done to determine whether the sites I selected were indeed different in terms of my visual homogeneity/heterogeneity classification in the field. From a 10 x 10-meter square around the traps, the number and type (conifer/deciduous) of canopy and sub-canopy trees were recorded, along with the quantity of dead and decaying wood, such as logs and stumps. From these squares, the area (%) of trampling and the presence of anthropogenic items were visually estimated.

In addition to the 10 x 10-meter areas, five smaller squares (1 m^2 each) were selected inside the bigger square – one around the set of traps and four randomly. From these five squares, percentage ground covers (field layer, ground layer, bare ground), canopy and quantity of dead wood were visually estimated. Soil litter layer depth (cm) was measured with a nail from three different spots within each of the small squares. In order to measure soil pH, soil moisture (%) and soil organic matter (%), soil samples were collected from each of the five squares of each sampling site from the top 5 - 10 cm of soil, excluding the litter layer.

Soil samples were stored in a cold room (~ 5 °C) and analysed during the autumn of 2021. Before analysis, the samples were homogenised with a sieve and a bucket. To avoid contamination, the sieve and the bucket were rinsed and dried between each sample using warm tap water and clean paper towels.

Soil pH was measured with an inoLab pH 720 meter from a well-mixed and stabilised soil and distilled water suspension (1:4 (v/v) ratio). Soil moisture content was determined by weighing the soil before and after ~ 24 h in an oven at 105 °C. These dry samples were placed into a muffle oven (5 h at 550 °C), the loss of ignition indicated the amount of organic matter. The percentage of moisture and organic matter were calculated by using before and after oven masses.

For data analysis, the average of each environmental variable measured from the five squares were calculated in order to get one value per variable per sampling site.

2.4. Data Analysis

A Principal Component Analysis was performed in R (R Core Team, 2021) to determine whether the three habitat types (heterogenous forest, homogenous forest, homogenous park) were different in structure based on my visual selection of the sites. Variables used in this analysis are shown in Table 1 and the PCA analysis in Fig. 3. Indeed, heterogenous and homogenous forest sites were different from one another (PC2), while the homogenous park sites were, as expected, clearly different from the forest sites (PC1) (Fig. 3). Variables separating forest sites from park sites (PC1) include litter layer depth, ground layer cover (%), soil moisture (%), organic matter (%) and soil pH, while variables distinguishing heterogenous from homogenous forest sites (PC2) include conifer canopy, deciduous canopy, canopy in general, area of trampling and dead wood (%) (Table 1).

Table 1. Environmental variables included in a Principal Component Analysis and loadings of principal components. The top five variables on the two PC axes are marked in bold.

PCA	Environmental variable	Unit	PC1	PC2
	conifer canopy	number of trees	-0.0894	**0.4880**
	deciduous canopy	number of trees	-0.2150	**-0.3276**
	conifer sub-canopy	number of trees	-0.1798	0.0884
	deciduous sub-canopy	number of trees	-0.2453	-0.2079
	coarse woody debris	cm^3	-0.1232	-0.2162
	litter layer depth	cm	**-0.3217**	0.0939
	anthropogenic items	%	0.1933	-0.0780
	canopy	%	-0.0583	**0.5061**
	field layer cover	%	0.3186	-0.2134
	ground layer cover	%	**-0.3539**	-0.0921
	bare ground	%	0.0870	0.0272
	trampling	%	0.1156	**0.2982**
	deadwood	%	-0.2235	**-0.3055**
	soil moisture	%	**-0.3496**	0.0267
	soil organic matter	%	**-0.3391**	0.2188
	soil pH		**0.3987**	0.0002

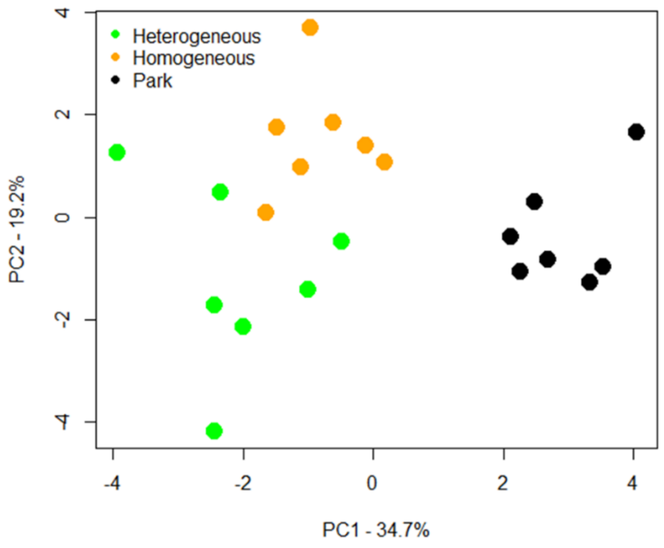

Figure 3. Principal Component Analysis plot of the measured environmental variables across the sampling sites. Heterogeneous = heterogeneous forest sites, Homogeneous = homogeneous forest sites, Park = homogeneous park sites. Percentage variance explained by the two axes are also presented.

Species diversity of each of the three habitat types was visualised with a rarefaction curve, using the iNEXT interpolation and extrapolation richness code (Chao et al., 2014; Hsieh et al., 2020), together with ggplot2 (Wickham, 2016) in R.

Non-metric multidimensional scaling (NMDS) was used to study how the beetle communities differ from each other between the heterogenous forest, homogenous forest, and homogenous park sites. Due to lost traps, the number of individual beetles was standardised to 100 trapping days before performing the analysis in R using the *vegan* package (Oksanen et al., 2020).

All species collected were classified into small (< 4.1 mm), medium (4.1 – 8.0 mm) and large (> 8.0 mm) by elytra length, light (< 0.0075 g), medium (0.0075 – 0.045 g) and heavy (> 0.045 g) by standardised body mass (see below) and brachypterous, dimorphic and macropterous by wings. Differences in the proportions of size, mass, and wing type across the three habitat types were tested using general linear models (GLM). The predictor variable was habitat type, a factor with three levels (heterogenous forest, homogenous forest, homogenous park).

In addition, species-specific analyses were conducted regarding elytra length (mm), and standardised body mass (mass divided by elytra length, g/mm) for the eight most abundantly collected species that were present (minimum of five individuals per site) in at least two of the habitat types. These included, *Pterostichus melanarius*, *Carabus nemoralis*, *Calathus micropterus*, *Pterostichus oblongopunctatus*, *Patrobus atrorufus*, *Amara brunnea*, *Pterostichus niger* and *Trechus secalis*. Differences in beetle size and mass across the three habitat types were tested using GLM, while normality of the response variables was tested using the Shapiro-Wilk normality test and were transformed to approximate normality where appropriate.

3. Results

3.1. Species diversity in urban forests and parks

I collected a total of 1284 individuals from 34 carabid beetle species (Appendix 2). Park sites had the highest number (23) of species collected, but the lowest number (176) of individuals. The most abundant species in the parks were *C. nemoralis* (66 individuals), *Nebria brevicollis* (43) and *P. melanarius* (16), while all other species had less than ten individuals captured. From the homogenous forest sites, 21 species were collected (892 individuals). The most abundant species were *P. melanarius* (282), *P. oblongopunctatus* (109), *C. micropterus* (144), *P. atrorufus* (106), *C. nemoralis* (89), *A. brunnea* (57), *P. niger* (46), *Harpalus laevipes* (16) and *Pterostichus strenuus* (11). The heterogenous forest sites had the lowest species richness, altogether 15 species (216 individuals), with the most abundant species being *C. nemoralis* (52), *C. micropterus* (49), *T. secalis* (24), *P. oblongopunctatus* (22), *P. atrorufus* (16), *A. brunnea* (11) and *P. melanarius* (11). Species diversity of the three habitat types sampled reflects the raw values, with parks showing a clearly higher rarefied richness compared to the two forest types, which were similar in richness (Fig. 4).

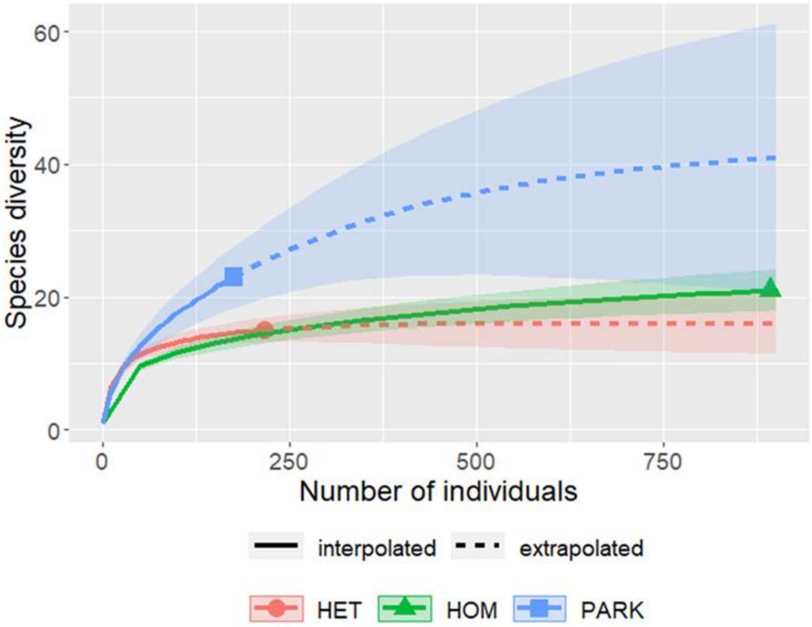

Figure 4. Carabid beetle species diversity across the three habitat types. Since the homogenous forest sites had the highest number of specimens collected (892), the curves of the heterogenous forest sites (216) and the homogenous park sites (176) are partly extrapolated.

3.2. Community composition and trait distribution

The non-metric multidimensional scaling shows clear differences in carabid beetle community structure between the homogenous park sites and the two forest site types (Fig. 5). The forest communities were more similar, but variation in the homogenous sites was less than in the heterogenous sites.

The homogenous sites (forests and parks) consisted of more generalist and open-habitat species, while the heterogenous forest sites were mainly characterised by forest species (47 %) and generalist species (53 %). The homogenous forest sites had 33 % of forest species, 52 % of generalist species and 10 % open-habitat species. The highly homogenous park sites had the most open-habitat species (39 %), 47 % generalists and 9 % forest species.

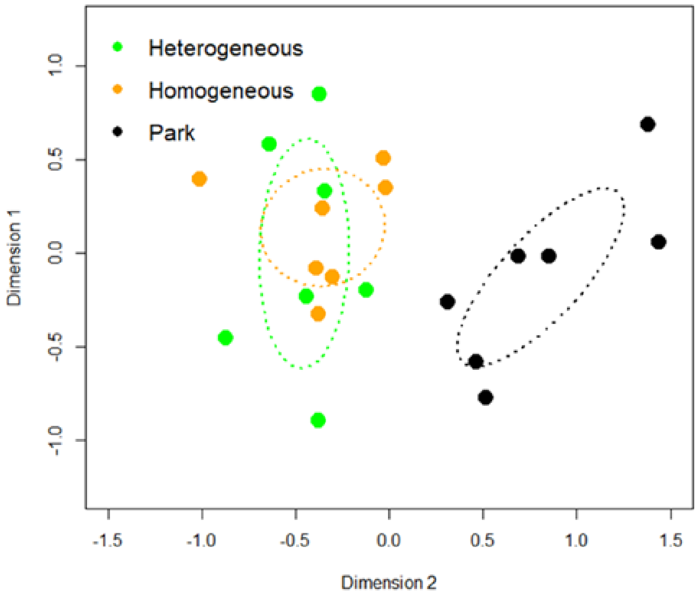

Figure 5. Non-metric multidimensional scaling of carabid beetle assemblages in heterogenous and homogenous forest remnants and urban parks. The ovals represent 1 standard deviation.

The proportion of size classes, i.e. elytra length and body mass, as well as wing categories showed clear differences between the three habitat types. Both the heterogenous and homogenous forest sites were primarily characterised by medium and large-sized species, while park sites were represented by a high proportion of medium-sized species and very few large species (Fig. 6, Table 2). Large species were the most common in heterogenous sites and the rarest in parks. Small species were more common in parks.

The proportion of different body masses did not change much in the homogenous forest sites, but in the parks, the proportion of medium-mass beetles was high, while the proportion of heavy beetles was low. For the heterogenous forest sites, the trend was the opposite, with the proportion of medium-mass species the lowest, while the proportions of light and heavy species were highest compared to the other two habitat types (Fig. 6, Table 2).

Wing classes showed a clear trend – in the homogenous parks, there were mainly dimorphic or macropterous species and very few short-winged (brachypterous) species, while in the heterogenous forest sites the proportion of brachypterous species was highest compared to dimorphic and macropterous species (Table 2, Fig. 6).

Regarding the three studied traits, the homogenous forest sites often seemed to align in between the heterogenous forest and the park sites. There was little variation between the proportions of different size or wing classes in the homogenous sites (Table 2). None of the GLM results from the homogenous forest sites were statistically significant when compared to the intercept. In the heterogenous forest and the park sites, there were more statistically significant variation between the different classes (Table 2, Fig. 6).

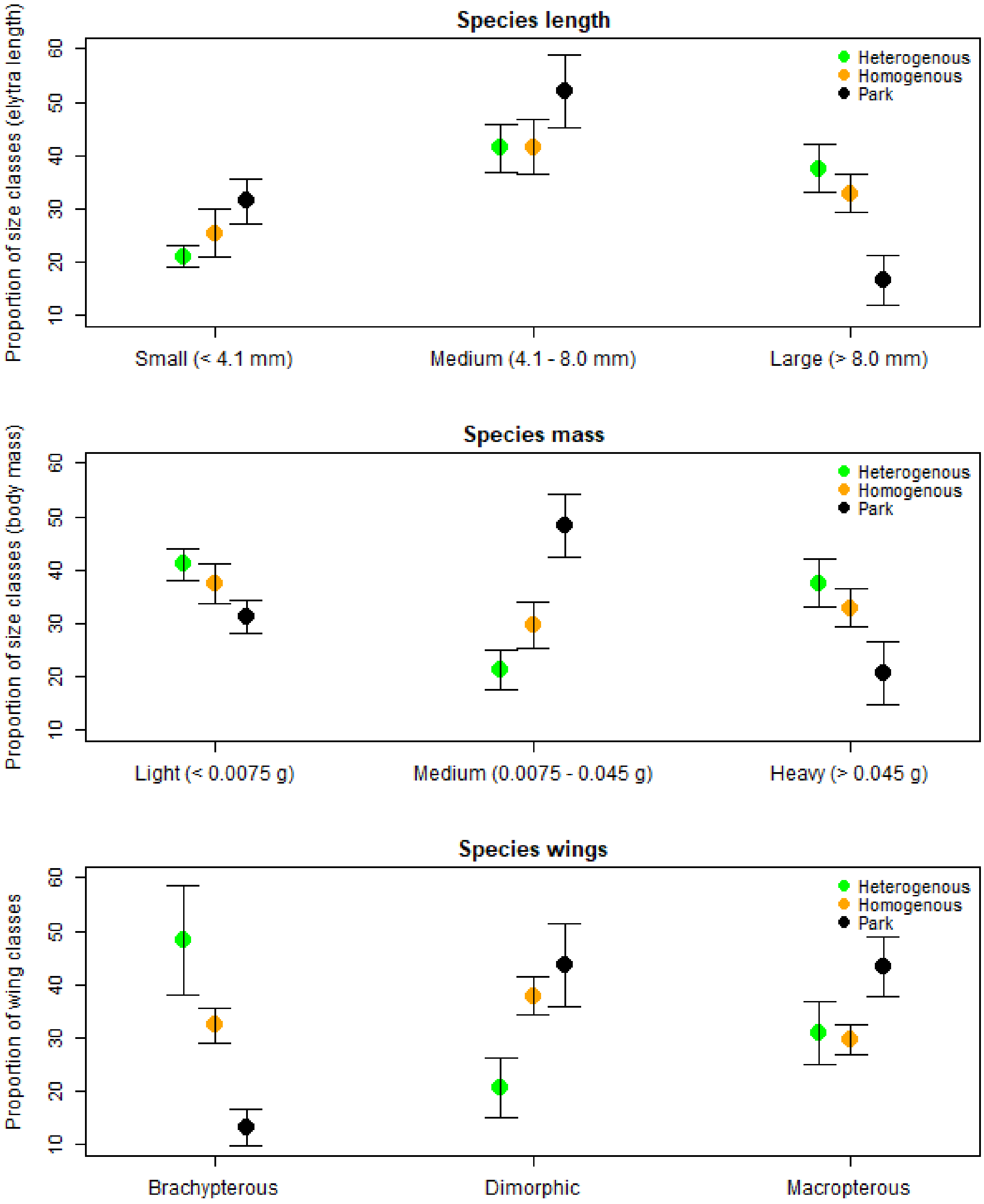

Figure 6. The proportions of traits (elytra length, body mass, wing morphology) at the community level and their distribution across the three habitat types.

Table 2. GLM results (Gaussian models) testing the difference in proportion of wings (B = brachypterous), body mass (H = heavy) and elytra length (L = large) within each of the three habitat types investigated (heterogenous and homogenous remnant forests and urban parks).

Elytra length	**Coefficient (SE)**	**p**	**Body mass**	**Coefficient (SE)**	**p**	**Wings**	**Coefficient (SE)**	**p**
Heterogenous			**Heterogenous**			**Heterogenous**		
Intercept (L)	37.583 (3.889)	< 0.001	Intercept (H)	37.583 (3.794)	< 0.001	Intercept (B)	48.298 (7.568)	< 0.001
medium	3.771 (5.500)	0.502	light	3.544 (5.366)	0.517	dimorphic	-27.495 (10.703)	0.019
small	-16.521 (5.500)	0.008	medium	-16.294 (5.366)	0.007	macropterous	-17.398 (10.703)	0.121
Homogenous			**Homogenous**			**Homogenous**		
Intercept (L)	32.926 (4.405)	< 0.001	Intercept (H)	32.926 (3.951)	< 0.001	Intercept (B)	32.382 (3.205)	< 0.001
medium	8.676 (6.230)	0.181	light	4.453 (5.587)	0.436	dimorphic	5.483 (4.532)	0.242
small	-7.455 (6.230)	0.247	medium	-3.231 (5.587)	0.570	macropterous	-2.631 (4.532)	0.569
Park			**Park**			**Park**		
Intercept (L)	16.630 (5.359)	0.006	Intercept (H)	20.586 (5.169)	< 0.001	Intercept (B)	13.150 (5.933)	0.040
medium	35.348 (7.579)	< 0.001	light	10.623 (7.310)	0.163	dimorphic	30.440 (8.390)	0.002
small	14.762 (7.579)	0.067	medium	27.619 (7.310)	0.001	macropterous	30.110 (8.390)	0.002

3.3. Body length and mass differences of individual species

Species specific analysis regarding the distribution of elytra length and standardised body mass across the three different habitat types shows a number of trends (Fig. 7, Tables 3 & 4). Despite these trends, only the elytra length of *P. atrorufus* and standardised mass of *P. niger* showed statistical significance between heterogenous and the two homogenous habitats. However, some results, such as *P. oblongopunctatus* mass between the heterogenous and homogenous sites, were close to statistical significance. Some species, such as *C. micropterus*, *P. oblongopunctatus*, *P. atrorufus*, *P. niger* and *T. secalis*, were found only from the forest habitats.

Species had differing responses in terms of body size to their environment (Fig. 7). Generally, beetles seemed to be smaller in parks (*C. nemoralis*, *P. melanarius*), or smaller in homogenous forests compared to heterogenous forests (*P. melanarius*, *P. niger*, *T. secalis*), except *A. brunnea*, which was slightly, but insignificantly smaller in the forest habitats. Some species were, however, larger in homogenous forests when compared to heterogenous forest, such as *P. atrorufus* (significantly so) and *C. micropterus*. Most responses were not statistically significant. There was no clear difference between habitat specialists and generalists, apart from the fact that some forest species, such as *C. micropterus* and *P. oblongopunctatus* were not found in parks.

The distribution of body mass standardised to elytra length varied between the species. Six species (*C. nemoralis, P. melanarius, T. secalis, P. oblongopunctatus*, *A. brunnea* and *P. atrorufus*) appeared to be lighter in heterogenous than in homogenous forests, yet none statistically significantly so (Table 4). *P. niger* (significantly so) and *C. micropterus* being the only two species that were heavier in the heterogenous sites. Two generalist species abundantly collected from parks, the predacious *C. nemoralis* and the omnivorous *P. melanarius* differed in their mass distribution, with *C. nemoralis* being lighter in parks, and *P. melanarius* being heavier. Most responses were, however, not significantly different.

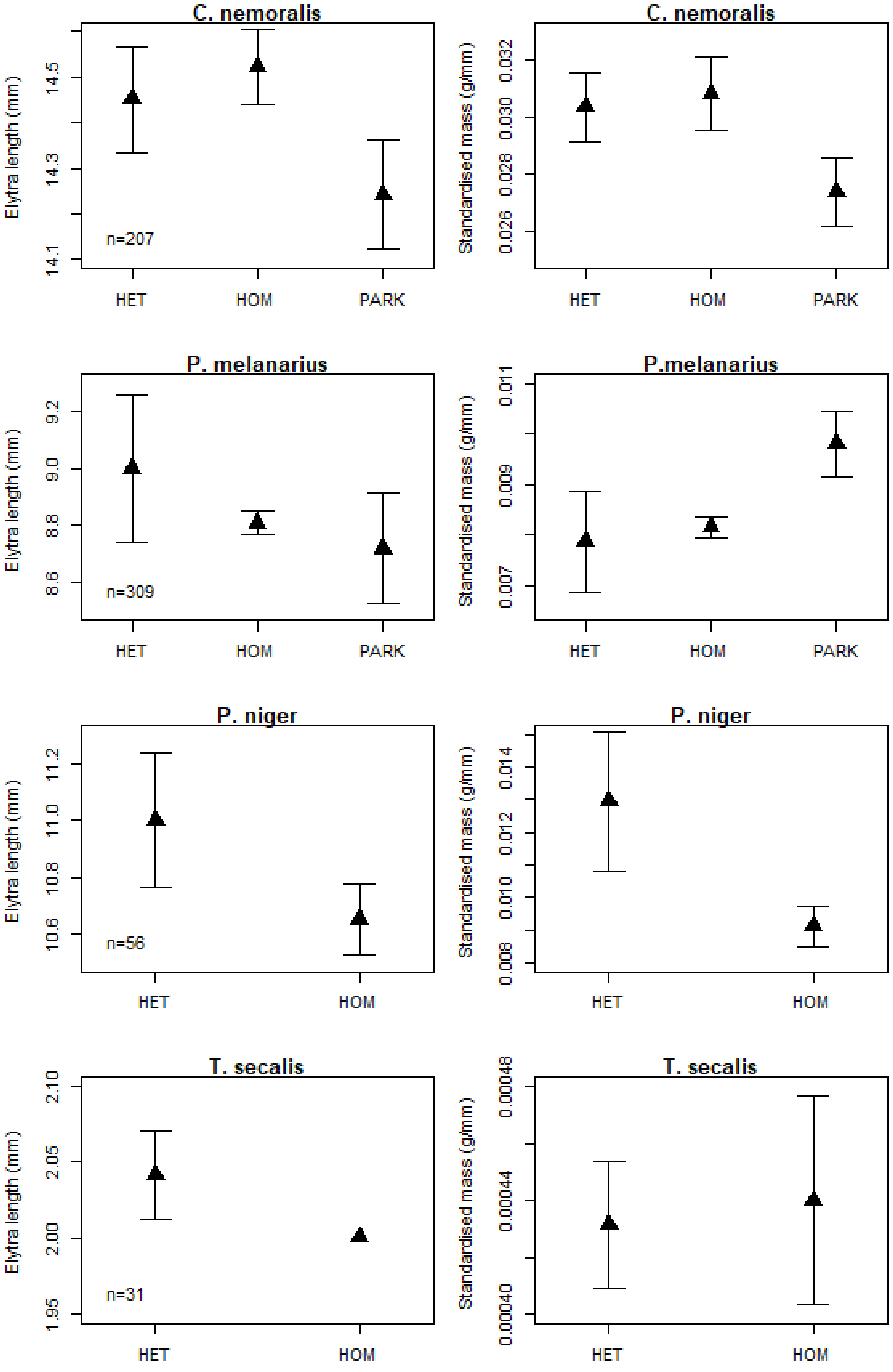

Figure 7. Elytra length (left plots) and standardised mass (right plots) of a number of carabid species across the three habitat types. Means and standard errors are presented, and n = the number of individuals collected. The eight most abundant species that occurred at least in two of the habitat types, are included. The figure continues on the next page.

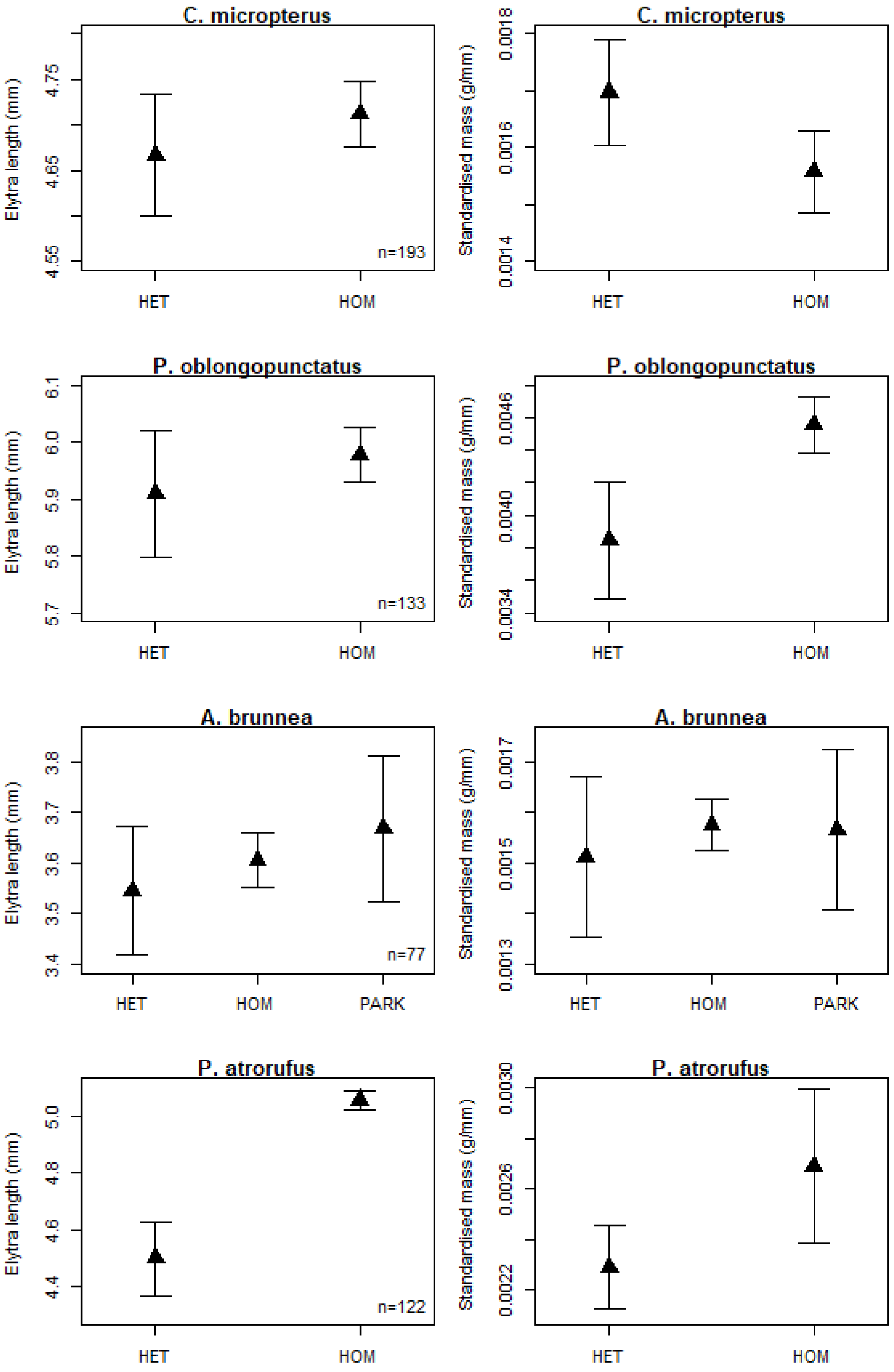

Figure 7. Continued.

Table 3. GLM results (Gaussian models) testing for differences in elytra length of individual species within the three different habitat types investigated (heterogenous and homogenous remnant forests and urban parks). Heterogenous forest is the intercept. See Fig. 7.

	Coefficient (SE)	**p**		**Coefficient (SE)**	**p**
Carabus nemoralis			***Calathus micropterus***		
Intercept	14.451 (0.121)	< 0.001	Intercept	4.667 (0.062)	< 0.001
Homogenous	0.071 (0.152)	0.64	Homogenous	0.045 (0.072)	0.534
Park	-0.209 (0.162)	0.198			
Pterostichus melanarius			***Pterostichus oblongopunctatus***		
Intercept	9.000 (0.225)	< 0.001	Intercept	5.909 (0.108)	< 0.001
Homogenous	-0.192 (0.229)	0.403	Homogenous	0.068 (0.118)	0.566
Park	-0.281 (0.287)	0.327			
Pterostichus niger			***Amara brunnea***		
Intercept	11.000 (0.275)	< 0.001	Intercept	3.545 (0.124)	< 0.00
Homogenous	-0.348 (0.300)	0.252	Homogenous	0.060 (0.136)	0.661
			Park	0.121 (0.185)	0.515
Trechus secalis			***Patrobus atrorufus***		
Intercept	2.042 (0.027)	< 0.001	Intercept	4.500 (0.090)	< 0.001
Homogenous	-0.042 (0.064)	0.521	Homogenous	0.557 (0.097)	< 0.001

Table 4. GLM results (Gaussian models) testing for differences in body mass (standardised to elytra length) of individual species within the three different habitat types investigated (heterogenous and homogenous remnant forests and urban parks). Heterogenous forest is the intercept. See Fig. 7.

	Coefficient (SE)	**p**		**Coefficient (SE)**	**p**
Carabus nemoralis			***Calathus micropterus***		
Intercept	0.030 (0.002)	< 0.001	Intercept	0.002 (0.0001)	< 0.001
Homogenous	0.0005 (0.002)	0.796	Homogenous	-0.0001 (0.0001)	0.302
Park	-0.003 (0.002)	0.142			
Pterostichus melanarius			***Pterostichus oblongopunctatus***		
Intercept	0.008 (0.001)	< 0.001	Intercept	0.004 (0.0004)	< 0.001
Homogenous	0.0003 (0.001)	0.794	Homogenous	0.0007 (0.0004)	0.089
Park	0.002 (0.001)	0.159			
Pterostichus niger			***Amara brunnea*** *		
Intercept	0.013 (0.002)	< 0.001	Intercept	-6.546 (0.077)	< 0.001
Homogenous	-0.004 (0.002)	0.025	Homogenous	0.065 (0.084)	0.444
			Park	0.051 (0.115)	0.656
Trechus secalis *			***Patrobus atrorufus*** *		
Intercept	-7.781 (0.052)	< 0.001	Intercept	-6.125 (0.132)	< 0.001
Homogenous	0.0388 (0.125)	0.760	Homogenous	0.011 (0.142)	0.938

* log transformed

4. Discussion

The carabid beetle communities show differences between the three habitat types (Fig. 5). In accordance with my hypotheses, homogenous forest sites and highly homogenous park sites were species richer than heterogenous forest sites. Homogenous sites (both the forests and parks) consisted of more generalist and open-habitat species, whereas heterogenous sites had more forest species. Trait distribution at the community level showed clear trends between the three habitat types. There was considerable variation in terms of elytra length and mass of the beetles. However, as expected, the proportions of large and heavy species were higher in the forest habitats than in the parks. The distribution of wings showed clear differences, and homogenous habitats, especially the highly homogenous park sites, consisted of a higher proportion of flight capable species than the heterogenous sites.

At the species level, individual beetles seemed to be generally smaller in the highly homogenous park sites compared to the two forest habitats. The results between the two forest types varied and a clear difference between habitat specialists and generalists could not be detected, apart from the fact that some forest species were not found in parks.

4.1. Carabid beetle community

As hypothesised, homogenous forest (21 species) and park sites (23) were species richer than heterogenous forest sites (15). This was also reflected in the projected rarefied species richness across habitat types. Even though species richness was highest in the parks, species abundances were often low, which may be related to higher competition rates in highly disturbed sites and some species', such as *N. brevicollis,* ability to fly and take advantage of sites with less competition (Jones, 2010). The proportion of forest species decreased from the heterogenous forests to more homogenous habitats, parks having the least of forest species. Open-habitat species had an opposing trend and none of these species were found from the heterogenous sites, while generalists were residing all the tree habitat types equally. Marrec et al. (2020) noted similar patterns in their study, where forest species (specialists and generalists) were positively affected by biotic and abiotic habitat heterogeneity, whereas the number of open-habitat species was mostly affected by different land-cover types and decreased with increasing vegetation heterogeneity.

Responses of carabid species and assemblages to habitat type are related to environmental variables. Of the measured variables, litter layer depth (cm), ground layer cover (%), soil moisture (%), organic matter (%), soil pH, type of canopy (deciduous/coniferous), canopy (%), level of trampling and dead wood (%) (Table 1) were instrumental in structuring these habitats. For instance, a deeper litter depth, a greater ground layer cover, higher soil moisture, organic matter and a lower pH distinguished forest habitats from the park habitat and are likely important in structuring the carabid beetle community (compare Figs 3 & 5, Table 1). Forest communities were also structured differently, with homogenous sites having a greater canopy (and conifer canopy) cover, while heterogenous sites had a greater deciduous canopy cover. Homogenous sites experience higher levels of trampling and heterogenous sites have more decaying woody matter (PC2, Table 1).

Vegetation, litter layer and different soil characteristic, such as bare soil cover, pH, soil moisture and soil organic matter have been identified to be important in structuring the carabid beetle communities (Lindroth, 1985, 1986; Magura et al., 2004). Ground cover measures and soil characteristics affect carabid beetle distributions, while vegetation and the litter layer act as a shelter and provide prey for predacious beetles and seeds for granivorous species (Koivula et al., 1999; Honek et al., 2007; Kotze et al., 2011).

The importance of soil moisture for carabid beetles is widely recognised (Kirichenko-Babko et al., 2020), but the effects of soil pH are less known. Paje and Mossakowski (1984) stated that some species are acidophiles and prefer lower pH, whereas some are not affected by the H-ion concentration. Merivee et al. (2005) and Milius et al. (2006) found pH receptors in carabid beetles, which are yet to be found in other insects. In carabids, the receptors are probably related to habitat choice and the pH preferences of adult beetles could be related to their habitat requirements as eggs, larva, or pupa (Paje & Mossakowski, 1984). For instance, the pH receptors of forest-dwelling *P. oblongopunctatus* show none or only a small response towards typical forest pH (3 – 6), whereas higher pH, that can sometimes be measured for example in urban parks, causes a stronger response (Merivee et al., 2005).

Following my hypothesis, generalist species seemed to do well in all of the three studied habitat types, whereas forest specialists clearly favoured heterogenous forests. Compared to homogenous sites (forests and parks) heterogenous sites had more diverse vegetation, including canopy trees and understorey vegetation (Table 1). Habitat complexity creates a variety of microhabitats for arthropod communities (Raupp et al., 2010) and provides food resources (Stork & Grimbacher, 2006), thereby offering an array of habitats for a diverse carabid community.

Heterogenous and homogenous forest sites were rather similar in soil organic matter content and litter layer depth. However, the type of canopy, ground layer cover and amount of dead wood affected the type of litter layer.

The litter layer in the homogenous sites consisted mainly of spruce needles, while in the heterogenous sites it consisted also of decaying leaves from the deciduous canopy, that homogenous forest sites and highly homogenous park sites did not have. Scattered deciduous trees are likely to be important for forest-floor fauna via the formation of a more moist and diverse litter layer that may provide suitable niches for species with different habitat requirements (Koivula et al., 1999). This was detected also in my study – moist preferring species, such as *Cychrus caraboides* and *Trechus secalis* were mainly found from the heterogenous sites, whereas dry preferring species, such as *Calathus micropterus* was most abundant in the homogenous forest sites.

Homogenous forest sites experienced clearly more trampling than heterogenous sites, which may be harmful for strict forest specialists, but may simultaneously favour generalist and open-habitat species, by creating more open, lighter, and warmer edge habitats (Davies & Margules, 1998). This could also explain why species richness and abundance were higher in the homogenous sites since generalist and open-habitat genera in the carabid beetle family are species rich (Lindroth 1985, 1986).

In addition to the effects of a higher pH and isolation of surrounding habitats, urban parks experience more understorey management than remnant forests. An increased disturbance, such as lawn mowing, has sometimes been noted to benefit opportunistic carabid species (Gray, 1989; Jones, 2010), which may partly explain the high species richness in urban parks.

Community assemblage is markedly affected by habitat type, but habitat type may also affect pitfall trapping (Ward et al., 2001). It may be that in highly homogenous sites, where there is little to no understorey vegetation, beetles have to be more active and move around to find resources, which may increase the probability of them ending up in the traps (Lövei & Sunderland, 1996). This active moving around can be costly, and beetles that move a lot may become lighter in mass if they are not able to find enough resources.

Despite the critique of using pitfall trap data to measure community patterns, it is still widely used and a relatively reliable method in carabid beetle studies (Lövei & Sunderland, 1996).

4.2. Trait distribution at the community and species levels

The distribution of traits at the community level and at the individual species level showed clear differences between the three studied habitat types. The most common traits previously investigated in carabid beetle studies are length of the individual (full body or elytra length) and type of wings (Kotze & O'Hara, 2003).

Increasing disturbance is detrimental especially for large species, that have larger ranges, smaller population size, lower reproductive output and longer life cycle, thus also slow response to changes in their habitat (Blake et al., 1994; Kotze & O'Hara, 2003). A larger size and longer lifespan require stable resources (Blake et al., 1994) that may be sparse in highly homogenised and fragmented urban locations. In my study, human induced disturbances were expected to increase from heterogenous forest remnants to homogenous forest remnants, urban parks being the most prone to disturbing factors, such as trampling, isolation, the presence of anthropogenic items and the overall homogenisation of the habitat due to various reasons.

The proportion of small species (< 4.1 mm, by elytra length) was higher in the homogenous sites (both the forest and park) than in the heterogenous forests, which follows the "decreasing body size hypothesis" suggested by Szyszko (1983), Gray (1989) and Blake et al. (1994), according to which smaller carabid beetles tolerate higher disturbance better than larger ones. On the contrary, the proportion of large species (> 8 mm) was highest in the heterogenous forest sites. Medium-length species (4.1 – 8.0 mm) were common in all three habitat types, but especially in parks, which could be partly explained by the large generalist and open-habitat species genera that include many medium-length species, such as *N. brevicollis* (~ 7 mm), *Amara apricaria* (~ 5 mm) and *Harpalus affinis* (~ 6 mm).

While body length of carabid beetles has been widely investigated (e.g. Gray, 1989; Blake et al., 1994; Lövei & Sunderland, 1996), there are less studies regarding body mass of these beetles. In this study, proportions of different body mass classes did not vary a lot in the homogenous forest sites. The other two habitat types showed more variation. Parks were dominated by medium-mass beetles, while the proportion of heavy species was low. In the heterogenous forests, the proportions of light and heavy species were higher than the proportion of medium-mass beetles. A change in body size, either in body length or body mass, indicates that the beetle is experiencing environmental stress (McGeoch, 1998). Large and heavy species may experience more stress due to higher disturbance levels in the homogenous forest sites and highly homogenous park sites. Heterogenous forest sites may offer more diverse niches for specialised forest species, such as the large *C. caraboides*, simultaneously providing suitable habitat for more generalised species, such as the small *T. secalis* that prefers moist environment. The proportion of medium-mass beetles was lowest in the heterogenous forests, which may again be partially explained by the large number of medium-mass beetles belonging to generalist or open-habitat genera.

The presence of wings, their type and ability to fly is related to the size of the beetle. Small species are generally more likely to be able to fly (Niemelä et al., 2002; Magura et al., 2004). Increased isolation and fragmentation of urban environment is challenging for ground dwelling arthropods (Gilbert, 1989) that may not be able to cross built roads and wide areas of impervious surfaces without fully functional wings. Flying is also the primary way of dispersal for many carabid species (den Boer, 1970; Lövei & Sunderland, 1996).

Following my hypothesis, homogenous communities consisted of higher proportions of macropterous and dimorphic species, with the exception of the heterogenous sites having a slightly higher proportion of macropterous species than the homogenous forest sites. The highly homogenous park sites were clearly dominated by flight capable species, whereas the heterogenous forest sites consisted mostly of brachypterous species that are unable to fly. Previous studies have shown similar patterns in urban areas. Sadler et al. (2006) found that the number of brachypterous species was higher in rural areas and decreased towards more urban areas, where macropterous species were more common (see also Niemelä & Kotze, 2009). My study did not include rural areas, but the heterogenous remnant forests experienced less human induced disturbance than the two homogenous habitat types included in the study, and thus support the findings by Sadler et al. (2006) and Niemelä & Kotze (2009).

The proportions of different traits at the community level changed across the three studied habitat types, but there were, interestingly, changes at the individual species level as well. Even though the elytra length and mass difference results between the two forest types varied and clear differences between habitat specialists and generalists were not detected, the ecological features of the species may have affected the results. Such features could, for example, be the habitat requirements of a species at earlier stages of its life or the way of feeding as an adult.

Weller and Ganzhorn (2004) found that the body length of *C. nemoralis* decreased from the rural surroundings of Hamburg, Germany, towards the urban city centre. Even though most of my individual species analyses were not statistically significantly different in body length between habitat types, similar patterns were noticeable, when comparing *C. nemoralis* from the heterogenous forest sites to the highly homogenous park sites. Differences between the two forest types were not prominent.

The body length of a beetle is determined by its larval stage. The larva is limited in mobility and, as weakly chitinised, may be more sensitive to disturbances in the soil or changes in the habitat than the adult beetle (Lövei & Sunderland, 1996). Of the studied species, *C. nemoralis* and *P. melanarius* seemed to experience larval stress in the park sites, whereas *A. brunnea* was doing generally better in parks. The two forest habitats had a different effect on larvae. Judged by the adult elytra length, the larvae of *P. melanarius*, *P. niger* and *T. secalis* were doing insignificantly better in the heterogenous sites, whereas *C. nemoralis*, *C. micropterus*, *P. oblongopunctatus*, *A. brunnea* and *P. atrorufus* were doing insignificantly (except *P. atrorufus* significantly) better in the homogenous sites.

Body mass instead, is also affected by the activity and nutriment of an adult beetle. Thus, some species, such as the omnivorous generalist *P. melanarius*, which is abundant in all of the studied habitat types, may show contradictory results when it comes to length and mass of the individuals. According to Fig. 7, this species' larval stage seems to be doing better in the heterogenous forest sites than in the highly homogenous parks, but for the adult beetles the trend is different, with heavier individuals in parks. It may be that omnivorous *P. melanarius* adults have more food resources in parks than in the forests, which is the opposite of what the other generalist species *C. nemoralis* seems to experience. Despite being a generalist, *C. nemoralis* is a large, flightless, and predacious species that may struggle finding resources in highly homogenous and isolated habitats, such as urban parks. Some trends were noticeable also regarding other species. *P. niger* (significantly) and *C. micropterus* (insignificantly) adults did better in the heterogenous forest sites than in the homogenous forest sites, whereas for *T. secalis*, *P. oblongopunctatus*, *A. brunnea* and *P. atrorufus* the trend was (insignificantly) the opposite. Prey and food availability are important factors in determining the body mass of an adult beetle, but more studies are needed to better understand the interlinkages between environmental stress and body mass.

5. Conclusions

The importance of urban nature conservation is increasing while cities continue to grow. Urban greenspaces are share unique characteristics that cannot be found elsewhere (Niemelä, 1999). Even though these habitats are often small and isolated, they support life of many organisms. According to my study, homogenisation of the habitat may simplify community assemblages of different organisms, including carabid beetles. Strict forest specialists have been found to decline with increasing homogeneity, but simultaneously many generalist and open-habitat species are doing well, even in the highly homogenous park sites of my research. However, biodiversity conservation is important for functioning ecosystems and preserving urban forest habitat heterogeneity is one way to affect it. Keeping the management of urban greenspaces moderate, selecting native vegetation, and preserving decaying woody material are easy ways to increase small-scale heterogeneity in urban habitats (Magura et al., 2004; Samways et al., 2020) and thereby protect the different forms of life residing in urban nature.

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Appendices

Appendix 1. Locations of the sampling sites in the City of Lahti, southern Finland. HET = heterogenous remnant forests, HOM = homogenous remnant forests, PARK = urban parks. Coordinates obtained from Google maps (2022).

Site code	Location	Coordinates
HET1	Möysä	60.97803, 25.70786
HET2	Metsäpelto	60.99255, 25.70191
HET3	Metsäpelto	60.997, 25.69604
HET4	Merrasjärvi	61.01369, 25.68422
HET5	Holma	61.00864, 25.67297
HET6	Mukkula	61.01518, 25.67678
HET7	Niemi	61.01257, 25.64845
HOM1	Nikkilä	60.95236, 25.66251
HOM2	Hennala	60.96992, 25.63266
HOM3	Möysä	60.97806, 25.70717
HOM4	Merrasjärvi	61.01349, 25.68599
HOM5	Holma	61.00962, 25.67595
HOM6	Mukkula	61.01562, 25.67787
HOM7	Niemi	61.01177, 25.65099
PARK1	Kisapuisto	60.98804, 25.6524
PARK2	Historical museum	60.9856, 25.65043
PARK3	Oikokatu	60.9802, 25.66595
PARK4	Kaarikatu	60.9728, 25.64486
PARK5	Kariniemenkatu	60.98951, 25.65838
PARK6	Mukkula school	61.01473, 25.6665
PARK7	Ankkuri	60.99333, 25.66029

Appendix 2. A list of the collected species. Standard errors of elytra length and body mass included, if more than one individual of the species were found. Habitat preferation: OD = open dry habitat, OG = open habitat generalist, OM = open moist habitat, GD = dry habitat generalist, G = habitat generalist, GM = moist habitat generalist, FD = dryforest, FM = moist forest. Wings: M = macropterous, D = dimorphic, B = brachypterous. Feeding: P = predacious, O = omnivorous, G = granivorous. Species traits and habitat associations follow Lindroth (1985, 1986) and Luff (2007).

Species	Habitat preferation	Feeding	Wings	Elytra length (mm) mean	Elytra length SE	Mass (g) mean	Mass SE	HET	HOM	PARK	Total
Agonum muelleri	OG	P	M	5.000		0.013		0	0	1	1
Amara apricaria	OG	G	M	4.667	0.167	0.009	0.00053	0	0	6	6
Amara aulica	OM	G	M	7.000	0.000	0.036	0.00815	0	1	1	2
Amara bifrons	OD	G	M	4.000		0.005		0	0	1	1
Amara brunnea	G	G	M	3.604	0.047	0.006	0.00017	11	57	9	77
Amara plebeja	GM	G	M	4.000		0.011		0	0	1	1
Badister lacertosus	FM	P	M	4.000	0.000	0.004	0.00050	2	0	0	2
Bembidion properans	OM		D	2.500		0.003		0	0	1	1
Calathus micropterus	FD	P	B	4.701	0.031	0.007	0.00027	49	144	0	193
Carabus hortensis	FD	P	B	16.667	0.667	0.642	0.05928	1	2	0	3
Carabus nemoralis	G	P	B	14.413	0.060	0.430	0.01160	52	89	66	207
Cychrus caraboides	FM	P	B	10.600	0.400	0.157	0.02711	4	1	0	5
Dromius fenestratus			M	3.000		0.003		0	0	1	1
Harpalus affinis	OD	G	M	6.000	0.000	0.022	0.00384	0	0	3	3
Harpalus laevipes	GM	G	M	5.727	0.097	0.029	0.00171	5	16	1	22
Harpalus latus	G	G	M	5.667	0.333	0.023	0.00371	0	3	0	3
Harpalus rufipes	OG	O	M	8.000	0.548	0.064	0.01554	0	0	5	5
Leistus ferrugineus	OD	P	D	4.000	0.000	0.005	0.00061	0	3	7	10
Leistus terminatus	FM	P	M	4.143	0.143	0.005	0.00050	7	0	0	7
Limodromus assimilis			M	6.000		0.025		0	1	0	1
Loricera pilicornis	GM	P	M	4.875	0.125	0.005	0.00084	0	0	4	4
Nebria brevicollis	GM	P	D	7.273	0.088	0.028	0.00197	0	1	43	44
Notiohphilus biguttatus	FD	P	D	3.000	0.000	0.003	0.00022	0	4	0	4
Patrobus atrorufus	GM	P	B	4.984	0.037	0.013	0.00147	16	106	0	122
Poecilus versicolor	OG		M	7.000	0.000	0.045	0.00230	0	0	2	2
Pterostichus aethiops	FM		B	7.000	0.000	0.039	0.00444	0	8	0	8
Pterostichus melanarius	G	O	D	8.807	0.040	0.073	0.00180	11	282	16	309
Pterostichus niger	GM	P	M	10.679	0.114	0.104	0.00683	9	46	1	56
Pterostichus oblongopunctatus	FD		D	5.966	0.043	0.027	0.00096	22	109	2	133
Pterostichus strenuus	GM	P	D	3.462	0.144	0.004	0.00047	1	11	1	13
Pterostichus vernalis	GM		D	4.000		0.005		0	0	1	1
Stomis pumicatus	G		D	4.375	0.239	0.005	0.00057	2	1	1	4
Synuchus vivalis	GD	G	D	4.000	0.000	0.006	0.00215	0	2	0	2
Trechus secalis	GM	P	B	2.048	0.027	0.001	0.00003	24	5	2	31