Bumblebee diversity in urban brownfields as affected by local and landscape characteristics

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Tiivistelmä - Referat - Abstract

Kimalaiset ovat tärkeitä pölyttäjiä globaalisti ja erityisesti Fennoskandiassa. Niiden kuitenkin tiedetään vähenevän. Myös luonnollisen kasvillisuuden määrä kaupungeissa vähenee kaupungistumisen myötä. Sen vuoksi kimalaisille sopivia elinympäristöjä kaupungeissa katoaa. Joutomaat voivat olla tärkeitä elinympäristöjä kaupunkien kimalaisille, koska ne muistuttavat niiden luonnontilaisia elinympäristöjä.

Tässä tutkielmassa tutkin urbaaneita kimalaisyhteisöjä joutomailla. Tavoitteeni oli arvioida paikallisten ja maisemallisten tekijöiden vaikutusta joutomaiden soveltuvuuteen kimalaisten elinympäristöksi. Selvitin myös, korostuvatko tietyt toiminnalliset piirteet joutomailla. Oletin, että paikalliset tekijät ja erityisesti kasvillisuuden peittämän alueen osuus ja alueen koko vaikuttavat kimalaisten runsauteen ja lajirikkauteen. Oletin myös, että kimalaislajit, jotka käyttävät ravintokasveja monipuolisesti, ovat joutomaiden yhteisöille tyypillisiä.

Aineiston keruuseen käytin linjalaskentamenetelmää. Perustin linjat 15 joutomaa-alueelle Lahden seudulle. Suoritin laskennan kaksi kertaa kuukaudessa, yhteensä kuusi kertaa kesällä 2020. Eri maanpeitetyyppien osuus joutomaa-alueista sekä alueiden ympäriltä 300 metrin säteellä arvioitiin. Tietoja käytettiin analysoimaan paikallisten ja maisemallisten tekijöiden vaikutusta kimalaisyhteisöjen koostumukseen, lajirikkauteen, ja runsauteen joutomaa-alueilla. Toiminnallisten piirteiden analyysiä käytettiin arvioimaan kimalaisten piirteiden ja ympäristötekijöiden välistä yhteyttä.

Osoitin, että paikalliset ympäristötekijät vaikuttavat kimalaisten runsauteen ja lajirikkauteen, mutta maisemalliset tekijät eivät. Maisemallisilla tekijöillä kuten metsällä ja teollisella maankäytöllä on kuitenkin vaikutusta kimalaisyhteisöjen koostumukseen. Vastoin odotuksia joutomaa-alueen koko ei vaikuttanut yhteisöjen koostumukseen, lajirikkauteen tai kimalaisten runsauteen. Tietyt toiminnalliset piirteet korostuivat joutomaa-alueilla – erityisesti lyhyt kieli, joka liitetään monipuoliseen ravintokasvien käyttöön.

Joutomaa-alueilla esiintyi runsaasti kimalaisia. Ne ovat sopivia elinympäristöjä kimalaisille huolimatta ympäröivän alueen kaupungistumisen asteesta. Jopa pienet joutomaa-alueet voivat tukea kimalaisten monimuotoisuutta. Luonnontilaisten alueiden määrän vähentyessä joutomaa-alueita on kaupunkisuunnittelussa pidettävä tärkeinä elinympäristöinä kimalaisille ja muille pölyttäjille.

Avainsanat - Nyckelord
Kaupunkiekologia, kimalaiset, joutomaat, paikalliset ja maisemalliset tekijät, kimalaisten suojelu

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Tiivistelmä - Referat - Abstract

Bumblebees are important pollinators globally and especially in Fennoscandia, yet they are declining. The amount of natural vegetation in cities is decreasing with urbanisation. Hence suitable habitats for urban bumblebees are diminishing. Brownfields can be important habitats for bumblebees in cities because they resemble natural habitats.

I studied bumblebee communities in urban brownfields. My main aims were to evaluate how local and landscape scale environmental factors affect the suitability of a brownfield to be a habitat for bumblebees. I also evaluated whether certain bumblebee functional traits are filtered in the brownfields. I expected that especially local characteristics and primarily the amount of flowering plant cover and the size of a site would affect bumblebee richness and abundance. I also expected the bumblebee communities to be characterised by generalist feeders.

I collected bumblebees using line tracking in 15 brownfield sites in the city of Lahti and sampled bumblebees six times during the summer of 2020. The share of ground cover types within each site was estimated, as well as the share of different habitat types within a 300 m buffer zone around the sites. The data were used to analyse which local and landscape characteristics affect bumblebee community composition, species richness, and abundance in a brownfield site. Trait analyses were used to test the relationship between bumblebee traits and environmental factors.

I showed that bumblebee abundance and richness were affected by local site characteristics but not landscape-scale factors. However, community composition was associated with landscape characteristics, including forest and commercial or industrial areas. Unexpectedly, the size of a brownfield site did not affect community composition, richness, or abundance. Functional traits were filtered in brownfield sites, especially the prevalence of a short proboscis, which is linked to a generalist diet in these bees.

Brownfield sites are rich in bumblebees. Brownfields are suitable habitats for bumblebees regardless of the scale of urbanisation, and even small sites can host a diversity of bumblebees. As the amount of natural habitat in urban areas is decreasing, brownfields should be considered important habitats for bumblebees and other pollinators in urban planning.

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Contents

1   Introduction

1.1   Background

Driven by global population growth and the shift from rural to urban life, the world's urban population is projected to reach almost 68 % of the total population by 2050 (UN 2019). Alarmingly, urban areas have been expanding at an even greater rate than their population (Angel et al. 2011, Seto et al. 2011). Urban expansion and related land-use change negatively affect urban green infrastructure by fragmenting urban greenspaces into smaller and isolated patches and causing habitat loss and decreased connectivity between patches. Habitat loss and fragmentation threaten biodiversity in many ways (McKinney 2008, Gagné & Fahrig 2011, Gomes et al. 2011, Reis et al. 2012, Wenzel et al. 2020) and is a significant driver of biodiversity loss since smaller and more isolated patches do not maintain similar levels of diversity (Cane et al. 2006).

Cities' green infrastructure consists of different types of habitats including maintained green areas and low-maintenance ephemeral habitats. Informal greenspaces of low maintenance are often urban biodiversity hotspots as management practices can affect biodiversity negatively (Rupprecht et al. 2015). Informal greenspaces at an early successional stage in particular can be important habitats (Öckinger et al. 2009). Such spontaneously vegetated greenspaces include brownfields but are also referred to as 'urban spontaneous vegetation' (Robinson & Lundholm 2012), 'ruderal vegetation' (McKinney 2002), 'urban wasteland' (Gardiner et al. 2013, Bonthoux et al. 2014), 'urban vacant land' (Gardiner et al. 2013) and 'derelict land' (Small et al. 2002). Brownfields are of significant conservation value because they often harbour more species than other urban greenspaces (Bonthoux et al. 2014) and host a diversity of pollinating fauna (Macgregor et al. 2022).

Pollination by insects plays a crucial role in maintaining natural ecosystems as around 80 % of wild plant species depend on insect pollination (Thomann et al. 2013). A decrease in ecosystem services due to a lack of pollinator insects can have serious consequences for the global economy (Gallai et al. 2009), the health of native ecosystems (Goulson et al. 2008), and food production and security (Garibaldi et al. 2009, Vasiliev 2021) with 35

% of the world's food supply estimated to depend directly on bee pollination (Klein et al. 2007, Potts et al. 2010).

Due to their importance as pollinators and because they are declining, it is important to support bumblebee diversity in urban areas (Potts et al. 2010). Pollinator insects' response to urbanisation is varied (Baldock et al. 2019, Wenzel et al. 2020). For instance, urbanisation is shown to simplify pollinator insect communities by shifting community composition toward generalist species (Deguines et al. 2016) and increase the incidence of introduced species in some taxonomic groups (McKinney 2008, Gagné & Fahrlig 2011). On the other hand, urban greenspaces can play an important role in supporting pollinator insect assemblages (Dylewski et al. 2019). In this thesis, I will investigate bumblebee community composition and diversity in urban brownfields in the city of Lahti, southern Finland.

1.2 Urban bumblebees

The *Bombus* genus in the Apidae bee family consists of 260 species, including 30 species of cuckoo bumblebees in the *Psithyrus* subgenus. In Finland, there are 37 recorded bumblebee species (Parkkinen et al. 2018). Bumblebees are largely confined to the Northern Hemisphere and adapted to the northern climate with the ability to forage at relatively low temperatures. Bumblebees are effective pollinators due to their characteristic high-frequency buzzing, which results in effective pollen transfer (Grixti et al. 2009, Cameron et al. 2011). The typical foraging distance for a bumblebee is around 200 - 300 m from its nest (McFrederick & LeBuhn 2006), but foraging ranges vary greatly between species (Darvill et al. 2004).

While the honeybee *Apis mellifera* might be the most important pollinator on a global scale, and it is also farmed and used as a pollinator of crops in Finland (SML 2022), the importance of bumblebees as pollinators is emphasized in Finland where the native range of honeybees does not extend (Söderman & Leinonen 2003). Pollination services offered by bumblebees play a crucial role in maintaining natural ecosystems as many wild plants are pollinated predominantly or exclusively by bumblebees (Corbet et al. 1991, Osborne et al. 1991).

Increasing urbanisation, as measured through the increased proportion of impervious surface area, is shown to affect bumblebee abundance and diversity negatively as it leads to the loss and fragmentation of habitats and declining vegetation (Ahrné et al. 2009, Glaum et al. 2017). Urbanisation may reduce the suitability of a habitat for ground-nesting species via soil compaction and loss, and changes in vegetation type and structure (Cane et al. 2006). There is some evidence for a paucity of suitable nesting and breeding sites in urban areas (Goulson et al. 2008), which can lead to competition between bumblebee species (McFrederick & LeBuhn 2006). On the other hand, the abundance of pollinator insects differs among urban land uses (Baldock et al. 2019) and some urban greenspaces can support an even higher density of bumblebee nests (Osborne et al. 2008) and have higher colony reproductive success (Samuelson et al. 2018) than typical farmlands. On the downside, this increased density might potentially contribute to the higher prevalence of parasites among urban bumblebees compared to rural ones (Goulson et al. 2012). The composition of bumblebee communities might be different in urban green areas of different sizes, the most abundant bumblebee species dominating smaller sites while urban green areas larger than 30 ha could provide suitable habitats for more diversified bumblebee communities (Micholap et al. 2017).

Urbanisation affects individual bumblebee species differently (Spaethe & Weidenmüller 2002). The response might be linked to species traits such as body size and wingspan that affect foraging distances (Spaethe & Weidenmüller 2002, Greenleaf et al. 2007) and tongue length, which determines the diet of a species (Goulson & Darvill 2004, Goulson et al. 2005). Differences in foraging ranges may result in certain species occurring only in certain habitats (Goulson et al. 2006, Goulson et al. 2008). Proboscis or tongue length varies greatly between species: the 12.7 mm proboscis of *B. veteranus* is long compared to the relatively short 6.1 mm proboscis of *B. lapidarius* (Arbetman et al. 2017). Long-tongued species are generally more specialized in their diet compared to species with shorter tongues (Goulson & Darvill 2004). A very narrow diet can result in a limited living space, like what has happened to *B. consobrinus* which is specialized to one food plant (Parkkinen et al. 2018). Bumblebee species with narrow pollen specialization are more vulnerable to habitat declines compared to those with a broader diet (Kleijn & Raemakers 2008).

Urbanisation also filters bumblebee species' functional traits (Eggenberger et al. 2019, Theodorou et al. 2021). However, a comprehensive review suggests that we still lack generalisable information about wild bee traits and urbanisation relationships (Buchholz & Egerer 2020). Body size is often negatively associated with increasing urbanisation (Eggenberger et al. 2019, Buchholz & Egerer 2020) but there are also opposite findings (Theodorou et al. 2021). Urban bumblebee populations are also phenotypically more diverse (Eggenberger et al. 2019). Finally, in urban areas, above-ground nesters are more abundant than below- or on-ground nesters (Buchholz & Egerer 2020), possibly due to the scarcity of nesting sites on the ground in cities.

1.3 Brownfields and pollinator communities

Brownfields are sites that have previously been used for industrial or commercial activities but are now abandoned and hence mostly unmanaged (e.g., Rupprecht et al. 2015, Kovacs & Szemmelveisz 2017). Due to their previous use, brownfields can have elevated concentrations of pollutants such as heavy metals and harmful chemicals in the soil, making their redevelopment difficult (Hunter 2014, Kovacs & Szemmelveisz 2017). However, due to their ephemeral nature, brownfields can disappear if the site is developed for other purposes under socio-economic pressure.

The many types of brownfields can be divided into two broad main categories: wetlands and dry ground (Hunter 2014). Such sites can include derelict land, abandoned railway tracks, landfills, and previously developed sites (Kattwinkel et al. 2011). Brownfields are heterogeneous areas due to different successional stages and a lack of management that allows spontaneous vegetation to occur, hence providing habitats similar to more natural ones. They are shown to have rich flora and fauna and can offer habitats for rare species including beetles (Eyre et al. 2003) and vascular plants (Maurer et al. 2000). Diverse nectar-producing vegetation provides food for insects like bumblebees (Harrison & Davies 2002). In urban areas, brownfields have become an important habitat for bumblebees and other pollinators since the amount of natural habitat has decreased in cities.

Brownfields contribute to ecosystem service provisioning in urban areas (Robinson & Lundholm 2012, Sikorski et al. 2021). Compared to managed lawns and remnant forests,

urban spontaneous vegetation is better in habitat provisioning in terms of plant species diversity, invertebrate abundance, and taxonomic diversity (Robinson & Lundholm 2012). However, due to their previous use, brownfields can also impact bumblebee communities negatively. Heavy metals in soil can have cascading negative effects on pollination via plant-pollinator interactions (Meindl & Ashman 2013). Nickel (Ni) is shown to affect bumblebees' foraging patterns, and possibly expose them to the ingestion of toxic resources (Meindl & Ashman 2013). Lead (Pb) and cadmium (Cd) can accumulate in the bodies of bumblebees (Szentgyörgyi et al. 2011). Lead contamination is shown to correlate negatively with the number of workers and larvae present in common Eastern bumblebee *B. impatiens* colonies and hence limit colony growth (Sivakoff et al. 2020). The combined effect of heavy metals may be greater than exposure to individual heavy metals, and limit colony growth even at low concentrations (Scott et al. 2022). High heavy metal concentrations can diminish both the abundance and diversity of wild bees, according to a study on solitary bees in the UK (Morón et al. 2011).

1.4   Objective and hypotheses

The overall aim of my study was to examine whether brownfields in the city of Lahti, southern Finland, can support bumblebee diversity and abundance and whether the bumblebee community in these brownfields can be predicted based on local site characteristics i.e., surface cover (including vegetation) and soil properties as well as various landscape features i.e., the size of a site and the habitat within the foraging range surrounding the brownfields. My hypotheses are the following:

1. Both local site characteristics and landscape features are expected to affect the bumblebee community in brownfields. However, I expect local site features to affect these communities more than landscape features (Ahrné et al. 2009, Williams & Winfree 2012, Bonthoux et al 2014).
    a. I expect a positive relationship between local flowering plant cover and bumblebee abundance and richness (Ahrné et al. 2009).
    b. Increased levels of heavy metal pollutants in the soil are expected to affect bumblebee abundance negatively (Sivakoff et al. 2020).

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c. Abundance and species richness are expected to correlate positively with the size of a brownfield site (Wojcik & McBride 2012).

2. I expect certain bumblebee traits to be filtered in these urban brownfields.
   a. Above-ground nesters are expected to dominate the brownfields (Cane et al. 2006, Buchholz & Egerer 2020).
   b. The communities are expected to be characterised by generalist feeders (Deguines et al. 2016), i.e., species with a short proboscis (Goulson & Darvill 2004).
   c. Body size is expected to be filtered in the communities. The communities might be characterized by larger species because large body size is linked to longer foraging ranges (Greenleaf et al. 2007), which could be an advantage in urban areas where habitats are fragmented. Bumblebees are sometimes found to be larger in cities (Theodorou et al. 2021). However, conflicting results appear in the literature with some urban bumblebees often being smaller than their rural counterparts (Eggenberger et al. 2019).

2 Material and methods

2.1 Study area

The study was conducted in 15 brownfields in the Lahti region (60°59'00''N, 25°39'20''E) in southern Finland (Fig. 1). The brownfields selected for this study are of different sizes and types, including an old railway area, a snow dump, and abandoned industrial and commercial areas. Two sites were excluded from the final analysis due to changes in the structure of the area during the summer as a result of mowing or construction work.

Figure 1. Localities of the 13 brownfield sites in Lahti and Hollola and their corresponding 300 m buffer zones. 1 = Hiekkalinna, 2 = Hämeenlinnantie, 3 = Kahdenkalliontie, 4 = Kasaajankatu, 5 = Keskikankaantie, 6 = Koneharjunkatu, 7 = Launeenkatu, 8 = Niemenkatu, 9 = Puustellintie, 10 = Vaaksakuja, 11 = Valimonkatu, 12 = Varikonkatu, 13 = Yhdyskatu. Google Maps Satellite Image. Exact site coordinates are presented in Appendix 1.

2.2 Bee sampling

Bumblebee sampling was conducted using a line tracking approach and a sweep net. Each line was established so that it went through all relevant vegetated areas within the site. If the site was almost completely vegetated, the line meandered so that parallel lines were at least 4 m apart. The bumblebees were counted within 2 m from the sampling line on both sides. Sampling was conducted twice in June, July, and August 2020 (six times in total), roughly two weeks apart. Samplings were only conducted during the daytime when the weather was mostly sunny, and the temperature was over 17 °C or during cloudy weather when the temperature was at least 20 °C. The first sampling event was performed at a lower temperature due to the general temperature conditions of June.

Bumblebees spotted during the line tracking walks were identified on site. Those that could not be identified immediately were caught in a jar and photographed for later identification. No individuals were killed. The sampling events resulted in a species list of bumblebees collected, together with the number of individuals collected per site. The traits of each species collected and used in the analyses (see below) included proboscis length (in mm), nesting habits (nesting above ground, below or on the ground, and both above and below or on the ground), average body size of a queen (in mm), and average body size of a worker (in mm). Information on proboscis length is from Arbetman et al. (2017). Information on nesting habits and body sizes is from Parkkinen et al. (2018).

2.3   Local site variables

Land cover percentages per site were estimated visually on the spot in July. The land cover types identified were woody plants, herbaceous plants, bare surface, built surface, and woody debris.

Soil samples for calculating pH and heavy metals were collected in late August 2020. Three soil samples were taken from each site. Each of the three samples, taken from different parts of a site, consisted of three subsamples taken from three adjacent spots (ca. 1 m apart) at ca. 2 cm deep, avoiding plant residues, roots, and big rocks. A plastic scoop was used to collect the samples to prevent additional metal residues from entering the sample. The samples (approximately 100 g in total per site) were placed in separate plastic bags. A total of 45 samples were collected from the 15 sites.

2.4   Soil sample analyses

The soil samples collected were stored at 4 °C before analysed. Soil samples were sieved through a 2 mm mesh. Soil pH was measured from all the samples in ultrapure water (1:5 v/v, fresh soil/distilled water) using a glass electrode. Metal analyses were performed on composite samples in which the three samples from each site were combined. To make the composite samples, 5 g of each sample was weighed in the same container and mixed for 60 s in a stirrer. For the pre-treatment, 0.2 g of the composite sample was measured

into a PTFA container with 10 ml HN₃. The same procedure was repeated for each composite sample. The PTFA containers were placed on a turning table with an optical thermometer at the bottom. The turning table was held at 200 °C for 20 min and left to cool overnight. The samples were quantitatively moved to a 50 ml PP-tube. The samples were centrifuged to let the solid matter settle at the bottom of the tubes. The samples were diluted for ICP-MS analysis so that the HNO₃-% was 2 %. The samples were analysed in AlmaLab in Lahti using an Inductively Coupled Plasma Mass Spectrometry (ICP-MS).

An integrated pollution index (PI) was used in the data analyses instead of analysing all heavy metals separately (Bhattacharya et al. 2006). Concentrations of Al, P, V, Cr, Fe, Mn, Ni, Cu, Zn, As, Se, Cd, and Pb were measured but Zn, As, Se, and Cd were excluded from the PI because their concentrations were below the limit of quantification. The least polluted site (site 6) was chosen as the baseline location. The concentrations of all heavy metals were standardized to the baseline location according to the following equation for the single indices (P_i):

$$P_i = \frac{C^i}{C_n^i}$$

where C^i is the concentration of heavy metal i, and C_n^i is the corresponding concentration in the baseline location. The single index is calculated in accordance with the contamination factor suggested by Håkanson (1980). The PI for each site was calculated as the average of the standardized values:

$$PI = \frac{1}{m} \sum_{i=1}^{m} P_i$$

where P_i is the single pollution index of heavy metal i, and m is the count of the heavy metal species.

2.5 Landscape variables

Landscape-scale variables were determined using QGIS Madeira 3.4.15. The vector polygons representing the brownfield sites were buffered with a 300 m radius, which is generally considered the typical foraging distance of bumblebees (McFrederick & LeBuhn 2006). The size of each site in hectares was obtained from the vector polygons. Forest, water, open grassy areas, residential areas, and commercial areas including industrial

sites, commercial and retail sites that are characterized by large buildings and large areas of paved surfaces, were drawn into polygons based on Google Maps Satellite imagery. The share of each habitat type of the buffer zone was calculated and expressed as a percentage of the whole buffer zone.

2.6 Statistical analyses

All statistical analyses were carried out in R 4.0.2 (R Core Team 2020).

Non-metric multidimensional scaling (NMDS) was used to compare the bumblebee communities across sites and to identify significant environmental variables as potential gradients that affect the underlying ecological patterns in community composition. NMDS is a rank-order approach that aims to represent the position of objects in multidimensional space with a reduced number of dimensions. Because of different lengths of transects within sites, the number of bumblebee individuals collected per species was standardized to those observed per 100 m. All variables significantly related to the NMDS space (at the $p = 0.05$ level) were plotted and the results were used to visualize the communities against the significant environmental variables. Significance was assessed based on 999 permutations. The Bray-Curtis dissimilarity index was used, and the analysis was performed using the vegan R library.

Generalised linear models (GLMs) were used to test the effects of a set of local and landscape variables on the overall abundance of bumblebees, bumblebee species richness, and abundantly collected species. Local environmental variables used in the GLM were the percentage of woody plants, herbaceous flowers, bare ground, and built surface, the pollution status of a site (the pollution index), and pH. The share of wood debris was not included in this analysis since it only occurred at one of the sites. Landscape-scale variables included were the size of the selected brownfield site in ha, and the proportions of different land cover types surrounding the sites within a 300 m radius that was based on the average foraging distance of a bumblebee (McFrederick & LeBuhn 2006). The land cover types included in the analyses were forest, commercial area, and residential area. Water and open grassy areas were not included in the analysis due to low coverage.

Due to the large number of variables measured in this study, the GLM analyses per parameter (total abundance, species richness, two of the most abundant species *B. lucorum* and *B. lapidarius*) were divided into three steps. First, I analysed local variables and performed model selection by removing statistically insignificant variables one at a time until only significant variables remained. Then, I analysed landscape variables similarly to the local variables. Finally, I performed a combined analysis with only the significant local and landscape variables and continued the procedure until only significant variables remained in the final model.

The GLM models assumed a Poisson error distribution for all models and were performed using the lme4 R library. An offset term was added for transect length to deal with differences in sampling intensity across sites. Bumblebee species richness was standardized to a certain sample size by using individual-based rarefaction, using the iNEXT R library.

Finally, RLQ and fourth corner analyses were used to test the relationships between bumblebee traits and environmental variables. RLQ analysis was used to examine a covariance matrix between traits and environmental variables weighted by species abundances (Dray et al. 2014). Fourth corner analysis was used to test the associations between individual traits and environmental variables (Dray et al. 2014). Together, these analyses search for species traits that explain abundances by fitting a predictive model for species abundance as a function of environmental variables, species traits, and their interaction (Brown et al. 2014, Dray et al. 2014). These multivariate analyses link data from three tables: the species table (L) which includes the species relative abundances per site, the traits table (Q) which includes the biological traits per species, and the environmental table (R) which includes the local and landscape environmental variables per site.

The L table was analysed by correspondence analysis, the traits table was analysed by Hill-Smith principal components analysis, and the environmental variables table was analysed by principal components analysis for continuous variables. The correspondence analysis site scores of the species ordination were used as row weights for the R table and the site ordination for the Q table in the principal components analyses. The standardized number of bumblebees observed per 100 m was used in the analyses. Significance was assessed based on 999 permutations. The analyses were done using the ade4 library in R (Dray & Dufour 2007).

Fourth corner analyses were applied to the results of the RLQ analysis to quantify and statistically test the relationships between bumblebee traits and environmental variables. The p-values were adjusted by the false discovery rate method (FDR). Significance was assessed based on 999 permutations.

3   Results

I recorded a total of 3145 bumblebee individuals of which 116 were cuckoo bumblebees and 3029 true bumblebees (Table 1). Two of the sites were excluded from the analyses due to major changes in the sites during the late summer, which left 2832 individuals including 108 cuckoo bumblebees. Nineteen bumblebee species were collected, of which four were cuckoo species. The cuckoo species are excluded from the analyses. One bumblebee, *Bombus semenoviellus*, is excluded from the combined RLQ and Fourth corner analysis due to a lack of information about its traits. Various local and landscape variables were measured (Table 2), and the most representative ones were used in the analyses.

Table 1. Bumblebee (*Bombus*) species and their catch at the 15 sites sampled in and around the city of Lahti form June to August 2020. Species similar to *Bombus lucorum* (grp) are presented as a group because they cannot be distinguished with certainty without DNA testing. Sites 14 and 15 were removed from the analyses. For site names and localities, see Fig. 1.

Species / Site	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Total
B. distinguendus	1	1					1		1	4				1		9
B. hortorum			2			1	1	5	2	7	2		1	2	1	24
B. hypnorum	29	2	19	1	4	21	1	36		28	5	4	11		22	183
B. lapidarius	15	82	179	44	17	40	128	331	189	110	152	37	45	27	101	1497
B. lucorum (grp)	5	19	26	5	10	26	9	69	42	36	28	48	3	14	22	362
B. pascuorum	2	11	3			35	1	4	13	83	1	1	6		1	161
B. pratorum	2		8			23			2	41		1		1	4	82
B. ruderarius	7	21	31	12	3	8	32	58	15	9	33	11	7	16	36	299
B. schrencki				1						3						4
B. semenoviellus		1	2						6		3				1	13
B. soroeensis	1					1	1	3		2			2			10
B. subterraneus	9	43	1	1		7	8	11	3	5	12	2	1		8	111
B. sylvarum									2							2
B. terrestris	2		8	2	7	23	16	44	2	22	19	16	9	14	14	198
B. veteranus	1												1	2		4
Bombus sp.	1	4	4	3	1	2	3	17	5	4	7		1	6	12	70
B. bohemicus	1									5						6
B. campestris	2					1		1		1	1					6
B. rupestris	3	3	8		3			15	24	6	3				5	70
B. sylvestris		2		1		1					24		1			29
B. psithyrus sp.						1		1						3		5
Total ind.	81	189	291	70	45	190	201	595	306	390	266	121	87	86	227	
Total spp.	14	10	11	8	6	12	10	11	12	16	11	9	10	8	11	

Table 2. The proportions of different ground covers within sites and of different landscape variables within a 300 m radius of the sites. Soil pH and the PI (pollution index) are also presented. Individual heavy metal data are presented in Appendix 2. For site names and localities, see Fig. 1.

| | Local variables (%) | | | | | | | | Landscape variables (%) | | | | | |
Site	Woody plants	Herbaceous plants	Bare ground	Built sur-face	Wood debris	pH	PI		Forest	Water	Grass	Residential	Commercial	Area (ha)
1	11	83	6	0	0	6.66	2		29.85	0	1.03	21.46	15.88	0.149
2	15	54	25	6	0	6.60	1.88		55.28	0	0	4.25	0	0.651
3	8	27	65	0	0	7.30	1.39		41.56	0.40	0	0	41.95	0.881
4	24	59	17	0	0	6.80	1.75		12.57	0	0.94	2.51	58.05	0.215
5	21	36	31	12	0	6.60	1		3.61	0	0	0	86	0.224
6	18	29	34	13	6	6.7	1.24		55.45	5.38	0	3.86	4.97	1.365
7	7	4	47	6	0	6.83	2.40		7.95	0	11.04	11.81	28.28	0.253
8	16	35	48	1	0	7.43	1.50		14.92	19.42	3.43	23.34	19.87	1.411
9	11	49	39	1	0	6.92	1.38		62.08	1.36	0	12.79	4.95	0.960
10	3	53	36	8	0	6.30	1.96		46.7	0	0	7.31	31.04	1.155
11	17	41	36	6	0	6.95	1.10		20.02	0	1.34	13.35	32.58	1.316
12	8	57	35	0	0	7.07	2.07		6.32	4.87	1.47	22.47	36.15	0.249
13	3	31	39	1	0	7.08	1.24		11.54	0	0.24	0.11	73.58	0.228

3.1 Bumblebee community structure

Contrary to my hypothesis, neither the size of the site nor its pollution status was important in structuring the bumblebee community (Table 3). However, two landscape variables i.e. the proportion of forest and commercial cover in the surroundings (300 m radius) were significant variables at the community level (Fig. 2).
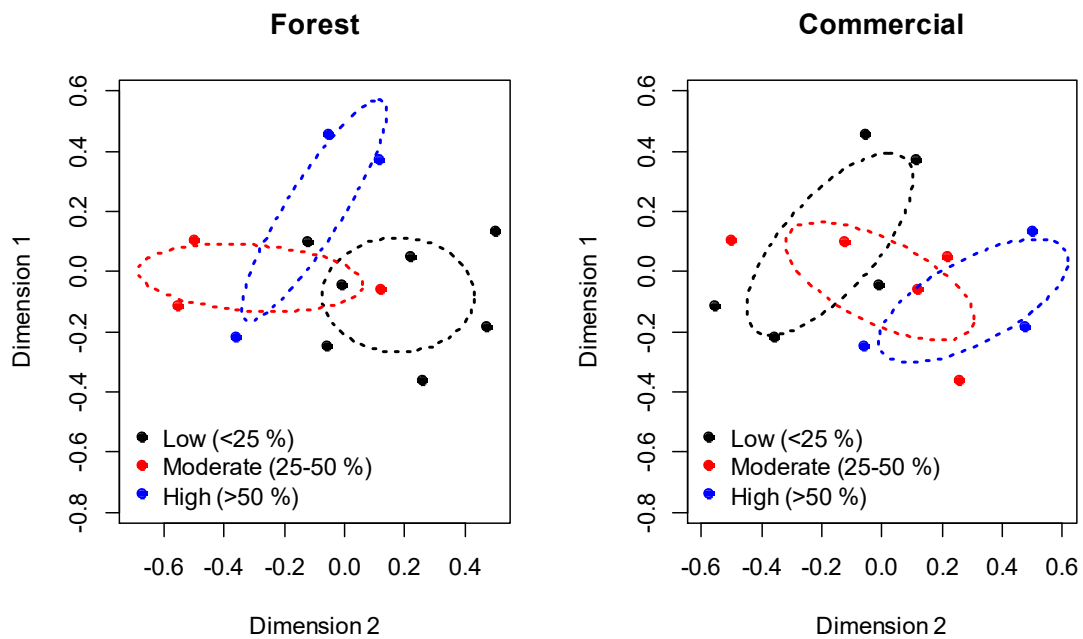

Figure 2. Bumblebee community plots in NMDS space, based on the proportion of forest or commercial area in the surroundings (300 m radius) of the sites. Points represent the sites. The more similar the communities are, the closer the points (sites) are to each other. Ellipses represent the standard deviation of the categories. Percentages in parentheses indicate how much of the 300 m buffer zone surrounding the area is forest or commercial area.

Table 3. Maximum correlations (r) of vectors in the NMDS ordination configuration of the bumblebee communities in the sites and their statistical significance (p).

Variable	Woody plants	Herbaceous plants	Bare ground	Built surface	Wood debris	pH	PI	Forest	Water	Grass	Residential area	Commercial area	Area (ha)
r	0.468	0.298	0.110	0.124	0.427	0.394	0.344	0.725	0.211	0.089	0.273	0.708	0.342
p	0.285	0.648	0.934	0.941	0.652	0.432	0.525	0.031	0.841	0.947	0.670	0.031	0.523

3.2 Bumblebee abundance and richness in relation to the environmental variables

None of the landscape variables affected the overall abundance and species richness of bumblebees in these brownfield sites, neither did the landscape affect the two individually analysed species *B. lucorum* and *B. lapidarius*.

Bumblebee abundance was negatively correlated with the shares of woody plants, herbaceous plants, and built surface (Fig. 3, Table 4). The proportion of herbaceous plants of a site affected species richness negatively while the increasing pollution level of the soil, affected species richness positively (Fig. 3, Table 4).

Two species (*B. lucorum* and *B. lapidarius*) were analysed individually since a sufficient number of individuals were collected to perform a GLM analysis on them. The abundance of *B. lucorum* was negatively associated with the proportion of woody plants (Fig. 4, Table 4). The proportion of bare ground had a positive correlation with the abundance of *B. lapidarius* while the proportion of built surface affected this species' abundance negatively (Fig. 4, Table 4).

Table 4. Generalized Linear Model results. Coefficients (standard errors) and p-values are presented. Analyses were performed on total bumblebee abundance, bumblebee species richness, and the two most abundantly collected bumblebee species. Predictor variables that are retained in the final models are presented here.

| | Local variables | | | | | | Landscape variables | | | | |
Parameter	Intercept	Woody plants	Herbaceous plants	Bare ground	Built surface	pH	PI	Forest	Residential area	Commercial area	Area (ha)
Bumblebee abundance	1.372 (0.117) < 0.001	-2.232 (0.340) < 0.001	-0.786 (0.176) 0.002		-2.209 (0.566) 0.004						
Bumblebee richness	6.578 (3.429) 0.084		-12.350 (6.746) 0.097				6.704 (2.456) 0.021				
B. lucorum	2.6040 (0.413) < 0.001	-5.626 (2.538) 0.049									
B. lapidarius	5.412 (8.196) 0.5239			84.453 (20.298) 0.002	-137.519 (62.851) 0.054						
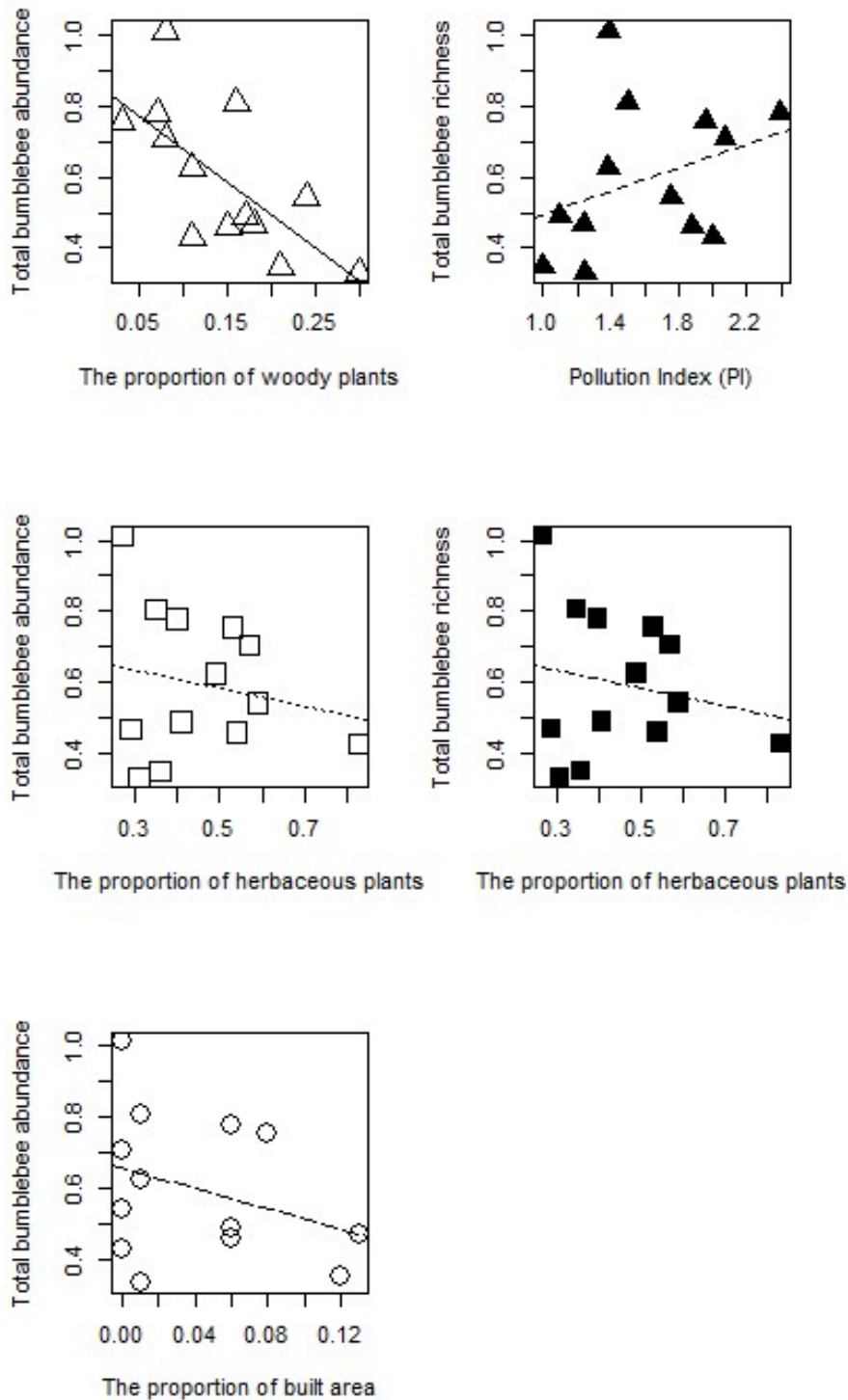
Figure 3. Based on the GLM models, bumblebee abundance responded negatively to the proportion of woody plants, the proportion of herbaceous plants, and the proportion of built surface at the brownfield sites. Species richness responded negatively to the proportion of herbaceous plants at the brownfield sites and positively to the pollution index (PI).
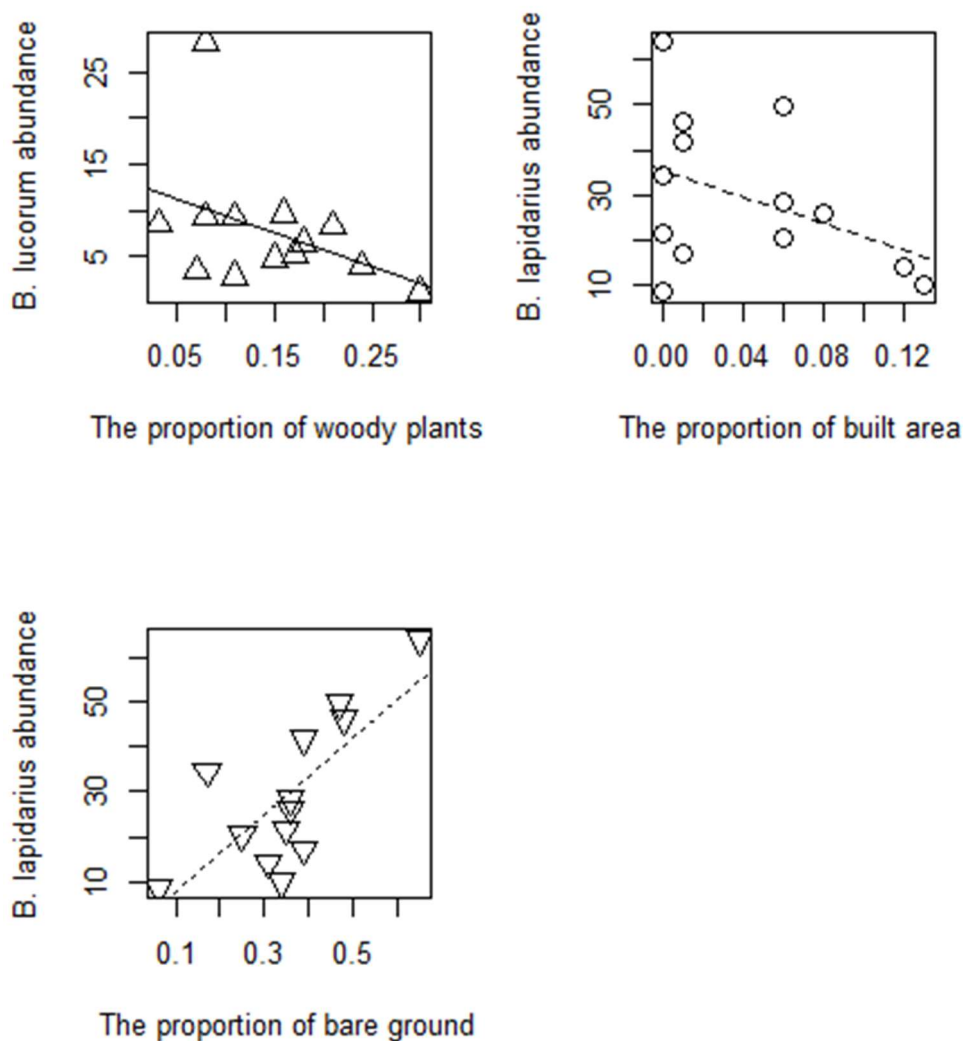
Figure 4. Based on the GLM models, the abundance of *B. lucorum* responded negatively to the proportion of woody plants while the abundance of *B. lapidarius* responded negatively to the proportion of built area and positively to the proportion of bare ground.

3.3 The link between bumblebee traits and environmental variables

The combined RLQ and fourth corner analysis were run at the 20 % significance level (p ≤ 0.2) and is considered exploratory. The first axis in the RLQ analysis explained 71.7% of the variance in the fourth corner statistics for the bumblebee community. The first axis in the RLQ ordination diagram was positively associated with pH, the proportion of bare ground, and commercial area in the surroundings, and negatively with the proportion of herbaceous plants and PI (Fig. 5 A). Of the species traits and modalities, the first axis was

negatively correlated with the long and medium proboscis (Fig. 5 B). *Bombus lapidarius* is positively associated with the first axis while *B. schrencki*, *B. pascuorum*, *B. ruderarius*, *and B. hortorum* are negatively associated with it (Fig. 5 C).

The second axis accounted for 22.5 % of the variance. Of the environmental variables, the second axis was positively associated with the proportion of forest, the proportion of built surface, and the size of a site, and negatively with the proportion of residential area, and the proportion of woody plants (Fig. 5 A). Of the species traits, the second axis was negatively associated with nesting above ground and body size of workers while the other traits were not strongly associated with this axis. *Bombus terrestris* is the only species that is primarily and negatively related to the second axis (Fig. 5 C).

In the combined RLQ and fourth corner analysis, the first axis was positively and significantly associated with short proboscis length (p = 0.007), nesting both above and below or on the ground (p = 0.052), and large body size of a queen (p = 0.061) (Table 5, Fig. 6). Significant associations between traits and environmental variables were not found (Fig. 6). None of the traits were associated with the second axis, and none of the associated environmental variables stood out as significant (Table 5, Fig. 6).
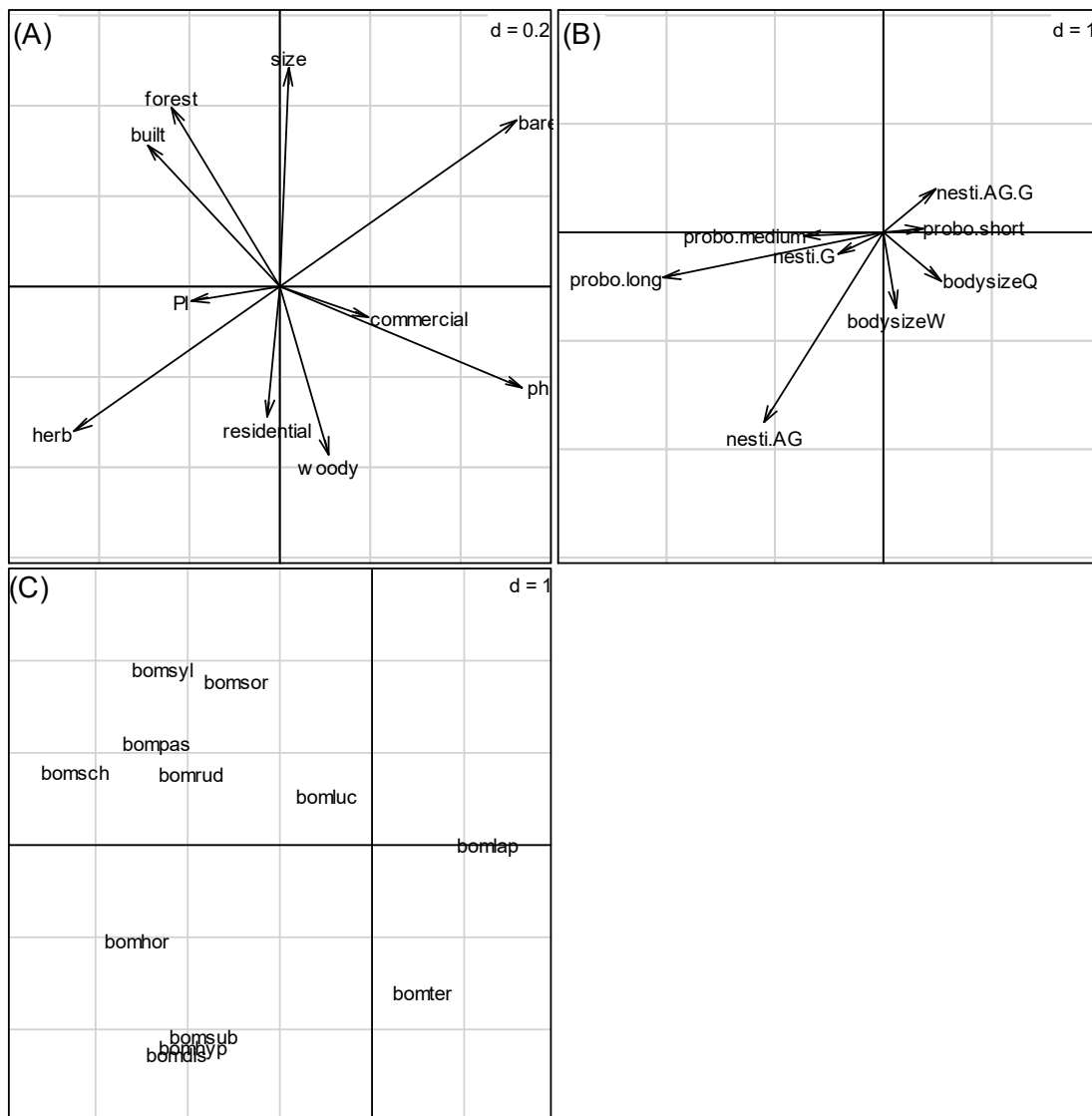
Figure 5. Coefficients for the environmental variables (A) and traits (B) of the first two axes of the RLQ analysis. Traits included in the plot: proboscis short (probo.short), medium (probo.medium), long (probo.long), nesting on or below ground (nesti.G), nesting above ground (nesti.AG), nesting on or below and above ground (nesti.AG/G), the average body size of queens (bodySizeQ), the average body size of workers (bodySize.W). Species scores of the first two axes of the RLQ analysis (C). Full species names are presented in Table 1.

Table 5. Results of the RLQ analysis using environmental variables and species traits. Eigenvalues, (% projected inertia), and % cumulative projected inertia for the first two axes are shown. Ordinations of tables L (correspondence analysis - CA), R (principal components analysis - PCA), and Q (Hill-Smith - HS) are presented. Summary of RLQ analysis: eigenvalues, (projected inertia, %), and cumulative projected inertia (%) accounted for by the first two RLQ axes, covariance, correlation (and % co-inertia) with the correspondence analysis of the L matrix and inertia and co-inertia with the R and Q matrices.

|	Axis 1 (%)	Axis 2 (%)
L table CA (species)	0.234 (38.875) 38.88	0.138 (22.899) 61.77
R table PCA (environment)	3.009 (30.903) 30.09	2.308 (23.084) 53.18
Q table HS (trait)	2.348 (39.125) 39.12	1.590 (26.503) 65.63
RLQ axis eigenvalues (total inertia = 0.4404)	0.334 (71.748) 71.75	0.105 (22.507) 94.26
Covariance	0.578	0.326
Correlation L (species)	0.247	0.184
Inertia and co-inertia R (environment)	2.718	4.856
Inertia and co-inertia Q (trait)	2.018	3.457
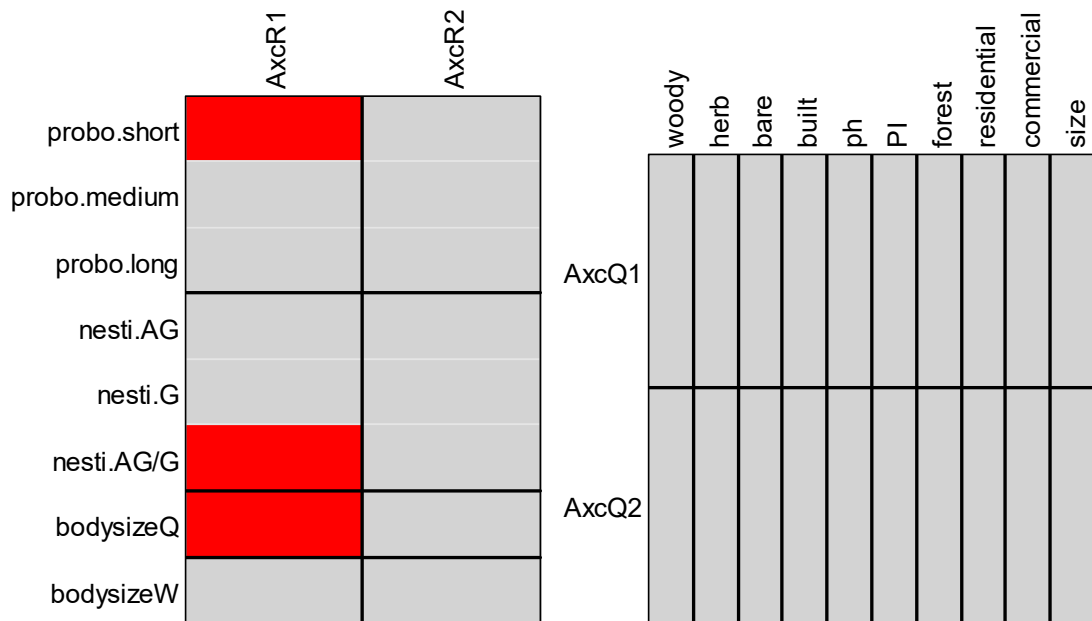
Figure 6. Results from the combined RLQ and fourth corner analysis for traits and environmental variables at p ≤ 0.2. The correlation table between the first RLQ axes for environmental variables and the traits shows that short proboscis, the ability to nest under/on ground and above ground, and queen body size correlated positively with the first environmental axis. The correlation table between the first RLQ axes for traits and the environmental variables shows no significant associations. Red means a positive significant association and grey means no significant association.

4   Discussion

In this study, I explored the link between urban bumblebee communities and environmental variables in brownfields. Nearly all species that could be expected to occur in the area based on its geographical location were recorded. *Bombus lucorum* and *B. lapidarius* were the most abundant among the recorded species, and they are also among the most common species in Finland (Parkkinen et al. 2018).

I expected that urban bumblebee communities are affected by local and landscape factors and that local factors are more important. The NMDS analysis showed that landscape-scale variables are more impactful at the community level, while the GLM analyses re-

vealed that only local variables are significant in terms of bumblebee abundance and species richness. These findings thus partly support my first hypothesis, at least for bumblebee abundance and richness, which is in line with other studies (Ahrné et al. 2009, Williams & Winfree 2012, Bonthoux et al. 2014), but not at the community level. Surprisingly an elevated level of pollution was associated with higher species richness, and brownfield size did not affect bumblebee abundance or richness.

The combined RLQ and fourth corner analysis showed that the functional traits of bumblebees are indeed filtered in the brownfield sites. A short tongue, the ability to nest above ground, and the body size of a queen were common traits in the brownfield sites. Based on these results, some filtering of traits exists, and the second main hypothesis and the hypotheses of generalist feeders dominating the brownfields were supported.

4.1 Local versus regional effects on bumblebees

According to the NMDS analysis, regional features affected bumblebee community composition. The analysis showed that the amount of forest and commercial/industrial area in the surroundings of a brownfield site affected bumblebee community composition, the communities being different in low and high forest/commercial areas (Fig. 2). These differences may be due to differences in floral resources between forested/non-forested and commercial/non-commercial areas. Bumblebee species have different dietary requirements, which may affect their distribution (Moerman et al. 2016). At least one study has found similar results on the impact of the built environment on bumblebee communities; the proportion of built area largely explained the variation in community composition when comparing three urban habitats in Western Poland (Dylewski et al. 2020).

Forests play an important role in bumblebee colonies' life cycle as they provide bumblebees with food and nesting sites (Mola et al. 2021). However, not all species use forests similarly. Some species are characteristic of dense forests, while others prefer open habitats (Richardson et al. 2019). It should be noted that sampling started in June while some queens are at the solitary stage of their life already before that and that the amount of food

available in forests varies during the summer. Therefore, it can be assumed that the number of bees utilizing forest resources differs during the summer, and some of that variation was not captured during the sampling period.

Contrary to my hypothesis, the size of a brownfield was not a significant predictor of community composition. Neither the number of sites nor the size variation between sites was large, which is likely to have had an impact on the results. On the other hand, although size can correlate with the presence of these bees (Wojcik & McBride 2011), there are also studies that have not found such a correlation. Zajdel et al. (2019) studied bumblebee communities in urban parks and found that neither the size of the sites nor any of the studied characteristics of the areas surrounding the sites were significant factors in bumblebee diversity or abundance. Neither was the size of a site found to affect the abundance or richness of bumblebees in a study comparing urban gardens and flowerbeds, possibly due to the heterogeneous character of vegetation in the sites (Gunnarson & Federsel 2014). The variation in vegetation may have affected the fact that the size of the areas has not been found to be significant, in my study as well.

I expected to find a positive relationship between local herbaceous plant cover and bumblebee abundance and richness, but this hypothesis was not supported. In fact, an increasing proportion of flowering plants was found to affect bumblebee abundance and species richness negatively. The occurrence of bumblebees is found to depend more on the composition and species richness of flowering plants rather than urbanisation surrounding smaller sites (Hülsmann et al. 2015). One of the main factors affecting the diversity of functional groups of bumblebees in urban areas is the state of floral resources (Honchar 2020). In this study, only the share of flowering plants of the sites' landcover was studied but not plant species composition, diversity, or flowering frequency, which is known to positively affect bumblebee abundance (Gunnarson & Federsel 2014). I recommend studying the composition of the vegetation in more detail in future studies, which may provide better predictors of the bumblebees visiting brownfields.

The proportion of woody plants affected overall bumblebee abundance and the abundance of *B. lucorum* negatively. The proportion of woody plants is linked to the successional stage of a site since it increases over time which, based on these results, could negatively affect the abundance of bumblebees. On the other hand, the pollen of woody plants is an

important food source for bumblebees early in the season: around 80 % of spring pollen loads in *B. terrestris* are from tree pollen (Mola et al. 2021). Woody plants were included in the analyses as a group, and they were not distinguished based on their importance as food sources. Sampling also started after the appearance of early queens for which, for example, willow would provide food at the beginning of the season. These factors could have affected the results.

Contrary to my hypothesis, increasing levels of heavy metal pollutants in the soil did not affect bumblebee abundance negatively. Instead, PI correlated positively with bumblebee richness. However, the recorded pollution levels were not high and corresponded to the concentrations of unpolluted sites in pollution gradient studies (Szentgyörgyi et al. 2011, Morón et al. 2011). Bumblebees are not negatively affected by heavy metals at low concentrations (Szentgyörgyi et al. 2011). These low pollution concentrations are also unlikely to affect ground-nesting bumblebees directly, while low levels of pollution in the soil may not be reflected in the pollen and nectar sources in flowering plants.

Not surprisingly, the overall abundance of bumblebees and the abundance of *B. lapidarius* were negatively affected by the proportion of built surface that reduces the amount of vegetated surface. The abundance of under-and-above-ground-nesting *B. lapidarius* was positively affected by the amount of bare ground, which might reflect their preference for open habitats (Svensson et al. 2000).

4.2   Trait contraction

As expected, some bumblebee traits were filtered, according to the combined RLQ and fourth-corner analysis. Of the individual traits and modalities, short proboscis, the ability to nest under, on and above ground, and queen body size correlated positively with the first environmental axis. However, the first axis is not associated with any of the tested environmental variables and thus they do not explain the filtering of the traits. Functional traits were studied only from an interspecific point of view but there can be intraspecific variations that this analysis could not reveal (Theodorou et al. 2021; Eggenberger et al. 2019).

Species with a short proboscis dominate the brownfield sites, as expected. A short proboscis is linked to a varied diet, i.e., the ability to use a greater variety of flowers as a food source (Goulson & Darvill, 2004). The hypothesis of above-ground nesters being characteristic to the brownfield sites (Buchholz & Egerer 2020) was not supported as species that can nest both under/on the ground and above ground were found to dominate these sites. In other words, species that are most generalist in their nesting habits did best in the urban brownfield sites. The preference of the large body size of queens might be linked to foraging ranges as foraging distances increase with body size (Greenleaf et al. 2007), which could be beneficial in fragmented habitats and in the beginning of the season when resources are scarce. The body size of workers that arrive in the summer when resources are more plentiful, did not appear to be important. The most frequently met species, *B. lucorum* and *B. lapidarius*, both have short tongues and relatively large queens. *Bombus lapidarius* is also a generalist in its nesting habits.

4.3 Conclusions

The brownfield sites were rich in bumblebee species. Nearly all the species that could be expected to be collected based on the geographical location of the sites were recorded. The number of species in a site varied from six to sixteen, which is a typical number of species within a location in southern Finland.

Bumblebee richness and abundance were affected by local characteristics of a site rather than landscape features, while community composition was primarily affected by landscape characteristics. Local characteristics affect species differently. Traits were filtered to some extent, yet it remains unclear what the determinant environmental factors could be. A short tongue, which is linked to a generalist diet, was the most common trait observed in these urban brownfields. The most common bumblebee species in southern Finland fall into this category.

Bumblebees are declining globally, which may have extensive negative consequences for human well-being (Garibaldi et al. 2009, Vasiliev 2021) and ecosystem health (Goulson et al. 2008, Thomann et al. 2013). With urbanisation, the amount and integrity of urban greenspaces are decreasing, which reduces the number of suitable habitats for bumblebees

and other pollinator insects. Hence the importance of brownfields and other informal greenspaces as a habitat for bumblebees is emphasized.

This study along with previous research (Williams & Winfree 2012) shows that local habitat quality can be of great importance compared to landscape urbanisation as the size of a site and the level of landscape urbanisation were not found to significantly affect bumblebee richness and abundance in a site. Hence even relatively small and isolated sites could help to maintain biodiversity. In urban planning, brownfields should be considered important habitats for bumblebees.

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6 Appendices

Appendix 1. Coordinates of the brownfield sites.

Site	Coordinates
#1	60.98846, 25.52722
#2	60.98186, 25.61772
#3	61.00632, 25.67503
#4	60.9707, 25.70383
#5	60.99048, 25.5374
#6	60.99151, 25.55716
#7	60.96957, 25.65368
#8	61.00335, 25.64811
#9	60.97559, 25.71912
#10	60.99692, 25.53206
#11	60.97481, 25.68637
#12	60.97734, 25.6332
#13	60.99348, 25.70731

Appendix 2. Results from the heavy metal analyses. Site numbers correspond to those in Fig. 1.

Site	m (dry weight)	Al	P	V	Cr	Fe	Mn	Co	Ni	Cu	Zn	As	Se	Cd	Pb
#1	202.5	9200	450	27	23	12000	230	6.2	11	15	51	4.2	<LOQ (0.35)	<LOQ (0.081)	6.3
#1 replicate	200.8	8400	450	23	20	11000	180	5.3	10	15	<LOQ (47)	4.0	<LOQ (0.3)	<LOQ (0.072)	5.4
#2	200.5	7800	540	22	19	10000	140	4.7	9.8	15	<LOQ (45)	<LOQ (2.2)	<LOQ (0.29)	<LOQ (0.057)	7.5
#3	203.8	4600	310	17	16	7400	89	5.3	8.7	23	61	<LOQ (0.86)	<LOQ (0.25)	<LOQ (0.04)	3.7
#4	203.0	6400	690	19	18	10000	130	4.2	9.2	18	<LOQ (49)	<LOQ (1.6)	<LOQ (0.27)	<LOQ (0.055)	5.0
#5	203.4	3800	210	10	9,4	6600	78	3.5	5.9	21	51	<LOQ (0.69)	<LOQ (0.21)	<LOQ (0.043)	2.6
#6	203.8	4700	330	13	11	7700	110	3.6	7.3	13	<LOQ (35)	<LOQ (2.3)	<LOQ (0.15)	<LOQ (0.053)	4.3
#7	203.8	8600	620	28	25	13000	190	6.4	14	24	62	<LOQ (2.3)	<LOQ (0.28)	<LOQ (0.08)	9.2
#8	201.6	5500	340	15	14	8100	110	3.8	7.8	15	78	<LOQ (2)	<LOQ (0.22)	<LOQ (0.06)	8.9
#8 replicate	203.8	6100	400	15	12	8400	120	4.1	8.4	17	<LOQ (42)	4.5	<LOQ (0.24)	<LOQ (0.045)	5.7
#9	202.3	6700	250	17	17	8300	95	4.2	8.1	19	55	<LOQ (0.67)	<LOQ (0.15)	<LOQ (0.038)	3.6
#10	201.4	8100	510	21	24	10000	150	5.3	12	23	<LOQ (43)	<LOQ (2)	<LOQ (0.46)	<LOQ (0.059)	5.9
#11	202.1	4600	300	12	10	6700	76	3.0	7.2	14	<LOQ (32)	<LOQ (1.8)	<LOQ (0.18)	<LOQ (0.042)	3.5
#12	201.7	5500	300	16	17	11000	130	4.8	10	23	62	3.9	<LOQ (0.25)	<LOQ (0.093)	18
#13	203.6	4300	310	12	12	6600	89	3.6	9.2	17	<LOQ (38)	<LOQ (2.3)	<LOQ (0.25)	<LOQ (0.056)	4.7

LOQ = limit of quantification