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Bees and pollination in grassland habitats in Helsinki (Finland) are diverse but dominated by polylectic species

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Abstract

Bees constitute a key taxon of grassland ecosystems and are the main providers of the essential Ecosystem Service of pollination. We studied bee assemblages of 17 grassland sites in Helsinki, Finland. Bees were sampled using coloured pan traps. The total catch comprised 353 individuals of 35 species. The most abundant species were *Lasioglossum leucopus, Lasioglossum lucidulum* and *Bombus lucorum* complex. We used NMDS ordination to depict habitat associations, and GLMM to model the responses of species and trophic groups to habitat type and level of urbanization. Polylectic ground-nesting species were the most abundant trait group. There were only few records of oligolectic species, which showed a significant preference for areas with the lowest level of urbanization. We recommend the provision and maintenance of a diverse range of grassland habitats, with particular attention to the conservation of late successional meadow habitats.

Keywords: Anthophila; Brownfield; Cavity-nesting; Ground-nesting; Hymenoptera; Oligolectic; Polylectic; Urbanization

Introduction

In the current situation of declining global biodiversity (IPBES, 2018; WWF, 2020), loss of insect diversity (e.g. Hallmann et al., 2017) and ongoing land-use change (IPBES, 2018), which is a major driver of biodiversity loss, the role of urban green infrastructure (UGI) as a potential resource for supporting biodiversity, is growing (Aronson et al., 2017; Lepczyk et al., 2017). We use the term urban green infrastructure to refer to the complete system of vegetated habitats in an urban region (Tzoulas et al., 2007). This term is commonly used in urban planning to consider the benefits and services such a system provides (Horwood, 2011; Tzoulas et al., 2007; Tzoulas et al., 2020). UGI is important for the provision of ecosystem services, including pollination, in urban areas (Niemelä et al., 2010). However, from the perspective of the conservation of biodiversity, the potential of UGI is unclear, as there is considerable variation in the capacity of different taxa to persist in urbanized regions (McDonnell & Hahs, 2015; Venn, Novitsky, Vershinin, & Kreuzberg, 2018). Urban and peri-urban areas (Snep et al.,

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2006) contain many habitats with resources for pollinating insects. Many taxa of insect pollinators, such as bees, include both generalist eurytopic species that tolerate high levels of urbanization, and less tolerant stenotopic species, which have specific requirements regarding their habitat preferences and diet (Hernandez, Frankie, & Thorp, 2009; Prendergast & Ollerton, 2021), and which are generally less tolerant of urbanization (Frankie et al., 2005; Hernandez et al., 2009; Klausnitzer, 1993). Regarding bees, there are several studies which report diverse urban bee fauna (e.g. Baldock et al., 2015; McFrederick & LeBuhn, 2006; Saure, 1996), though others report negative effects of urbanization (McIntyre & Hostetler, 2001; Winfree, Griswold, & Kremen, 2007) on bee assemblages and a scarcity of oligolectic and kleptoparasitic species in urban regions (Frankie et al., 2005). The increasing popularity of urban food production initiatives has led to concern about the provision of the ecosystem service of pollination in urban areas, and a number of studies suggest that provision of pollination is limited in urban areas with more extensive cover of impervious surfaces and less provision of UGI (Hausmann, Petermann, & Rolff, 2016). This has been demonstrated through increased seed-set and fruit crops in urban areas with higher rates of pollinator visits (Harrison & Winfree, 2015; Lowenstein, Matteson, & Minor, 2015).

The Finnish bee fauna (Anthophila) comprises 240 species (FinBIF, 2020). The fauna is most speciose in the south and the number of species declines towards the north. In Finland, many bee species have declined in recent decades and 17% of the Finnish bee fauna are currently classified as threatened (Paukkunen et al., 2019). The decline of traditional agriculture and the associated decline in a diverse range of semi-natural grassland habitats (Luoto, Rekolainen, Aakkula, & Pykälä, 2003) are the main causes of the decline of bee species in Finland (Heliölä, Söderman, Kuussaari, & Paukkunen, 2004; Paukkunen et al., 2019) and much of Europe. Currently the cover of semi-natural grassland habitats in Finland has declined due to abandonment and overgrowth to just 0.3% of the total area that was present at the beginning of the 20th century (Vainio, Kekäläinen, Alanen, & Pykälä, 2001). The Helsinki Metropolitan Region includes many areas of semi-natural grassland habitat that are currently managed by the municipality by mowing once or twice *per annum*, though the expanding urban infrastructure and loss of supplementary grassland habitats also affects their capacity to support biodiversity (Manninen, Forss, & Venn, 2010). The UGI of Helsinki also supports a diverse population of bee species, due to the presence of such supplementary habitats as parks, gardens and ruderal habitats (Venn, Kotze, Lassila, & Niemelä, 2013). Regarding grassland habitats, there is a diverse range of meadow habitats that are highly endangered in Finland (Kontula & Raunio, 2019) and a similar national decline in many associated bee, plant and butterfly species in particular (Hyvärinen et al., 2019).

Research questions

The purpose of the Helsinki Meadows project was to study the diversity of plants and selected insect taxa of a network of grassland habitats in the Helsinki Metropolitan Region, Finland. The principle objective of the project has been to determine the potential of a network of grassland habitats in an urban region to support grassland biodiversity and the provision of such ecosystem services as pollination. We focus in particular on grassland habitats that have developed through traditional agricultural practices and fortifications, and we also consider the potential of alternative habitats, such as ruderal or brownfield sites (Alker, Joy, Roberts, & Smith, 2000), to provide supplementary habitat for grassland taxa.

In this study, we sampled the bee assemblages of a set of semi-natural and ruderal grassland habitats in the Helsinki region. We use the term ‘semi-natural grasslands’ (Carboni, Dengler, Mantilla-Contreras, Venn, & Török, 2015; Luoto et al., 2003) to refer to habitats that have been modified through anthropogenic activity but still resemble natural grassland habitats, and ruderal to refer to grasslands that have been highly disturbed. Early-stage ruderal habitats predominantly comprise bare soil and are sparsely vegetated with pioneer species. Over time, ruderal habitats evolve into semi-natural grassland habitats. In this study, we address the following questions:

1 Do ruderal habitats support similar assemblages of vascular plants and bees to semi-natural grassland habitats in urban regions?
2 How similar are the bee assemblages of different kinds of urban grassland habitats?
3 Are stenotopic and oligolectic bee species able to benefit from ruderal habitats as well as the other studied habitats?
4 How do bee species respond to intensity of urbanization?
5 What recommendations can we make for the management of grassland habitats in Helsinki for the benefit of bee diversity and the provision of pollination?

Materials and methods

This study was conducted in a set of 17 grassland sites in the municipalities of Helsinki and Espoo, in the Helsinki Metropolitan Region, Finland (Fig. 1, Appendix A) during summer 2010. The grasslands were divided into four habitat types: 1) early ruderal, 2) late ruderal, 3) sheep fescue dry meadow type and 4) dry meadow on bedrock. Early ruderal habitats comprised sites in which the soil had undergone major disturbance within the past two years, resulting in vegetation dominated by early successional plants. Late ruderal comprised habitats that had undergone major disturbance within the previous 2−30 years, with a field layer dominated by grasses and with bushes and young trees. The two meadow habitat types (3 and 4) are categorized according to the classification of Påhlsson (1998), with dry

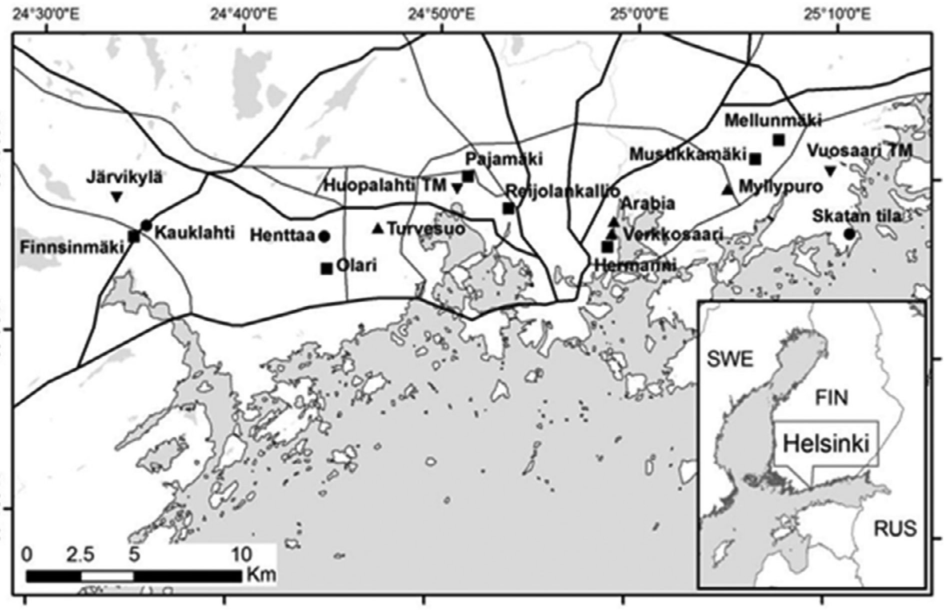

Fig. 1. Map showing the locations of the study sites in the Helsinki Metropolitan Region, Finland. Upright triangles indicate early stage ruderal sites, inverted triangles late stage ruderals sites, squares indicate dry meadows on bedrock and circles indicate sheep fescue meadows. The inset shows the location of the study region within Finland. .

meadow on bedrock comprising shallow soil and extensively exposed bedrock and plant species heartsease (*Viola tricolour*), orpine (*Hylotelephium telephium*) and maiden pink (*Dianthus deltoides*), and sheep fescue dry meadow generally having a sandy shallow soil, little or no exposed bedrock and lady's bedstraw (*Galium verum*).

Vegetation

The vegetation was sampled at each site using three, randomly located 1 m^2 quadrats, from which all of the vascular plant species were identified to species and their cover within the quadrat estimated. The purpose of sampling vegetation was primarily to check the habitat classification of the sites, the similarity of which was compared on the basis of a Non-metric multidimensional scaling (NMDS) ordination. A more comprehensive study of the vegetation of urban meadows in Helsinki has been published by Manninen et al. (2010).

Urbanization

In order to consider the effects of urbanization on the bee assemblages, the urbanization level of each site was estimated on the basis of human population density within 1 km^2 of the site, obtained from official demographic data (*HSY, 2011*). A three-stage categorization was applied as follows: <1000 residents/km^2 = low urbanization (6 sites); 1001−2500 residents/km^2 = medium urbanization (4 sites); >2501 residents/km^2 = high urbanization (7 sites).

Bees

Bees were sampled using pan-traps comprising plastic picnic plates of 17 cm diameter. Five traps of four colours were placed on the ground at each site, left for 24 h and removed the following day. The traps were placed in flat and open area, without tall vegetation and not shaded by trees or shrubs. All sites were sampled during the same 24 h period and in the same sequence, so that the sampling period was as similar as possible. The colours used were white, yellow, pink and blue, which reflect UV light effectively (Chittka, Shmida, Troje, & Menzel, 1994; Moreira et al., 2016; Vrdoljak & Samways, 2012) and represent the colours of the predominant flowers at these sites. The purpose of these colours was to test whether different bee species favoured particular colours. Two white pan traps were used so that we could check whether the differences between the species caught in different coloured traps was greater than that between two traps of the same colour. We did not have any expectation that relative position within the grid of five traps might affect their catches. These data will be analysed in a subsequent paper based on three years of sampling.

The traps were set out in a square of four, with a fifth trap at the centre of the square. The arrangement of the colours was random. The traps were set at a minimum distance of circa 4 m from each other, where the ground was suitably level, and with no shading from tall vegetation or trees. The plates were filled with water containing a small amount (circa 150 μl per 1 l water) of detergent as a surfactant. Sampling was only conducted on warm sunny days with a weather forecast of no rain and minimum daytime maximum temperature of $>$ 15 °C, and was repeated throughout the summer at 2- to 3-week intervals, according to the weather conditions. Sampling in 2010 was initiated on 26th May and completed on 31st August; a total of six occasions. The sampling protocol was developed collaboratively by students participating in the project. When the traps were emptied, the contents were poured into a nylon cloth, labelled and closed with a wire fastener. The catches of the pan-traps were not pooled but kept separate per trap and per emptying date. These bags were transferred to a bucket of 50% alcohol (aq.) for transport and storage. The material was later sorted, with hoverflies (Syrphidae) and bees transferred to separate specimen containers with 70% alcohol. The bees were subsequently identified using the following keys: Amiet (1996); Amiet, Herrmann, Müller, and Neumeyer (2001); Amiet, Herrmann, Müller, and Neumeyer (2004); Amiet, Herrmann, Müller, and Neumeyer (2007) and Amiet, Herrmann, Müller, and Neumeyer (2010); Amiet, Müller, and Neumeyer (1999).

Statistical analyses

An NMDS ordination was made of both vegetation (Fig. 2) and bee (Fig. 3) data in R version 4.0.3 (R Core Team, 2020) using the library Vegan 2.5−7, with the Bray-Curtis dissimilarity matrices and Wisconsin double standardization. The environmental data comprised habitat type (four categories) and urbanization (population density within 1 km^2 of each site).

Generalized Linear Mixed Model (Crawley, 2002; Zuur, Ieno, Walker, Saveliev, & Smith, 2009) was applied using R version 4.2.1 (R Core Team, 2022). GLMER was applied using the lme-4 library (Bates et al., 2015)5. For the GLMM analyses, we combined the groups early ruderal (1) and late ruderal (2) to form a single group ruderal (1), as a result of which sheep fescue dry meadow became group 2 and dry meadow on bedrock became group 3. This was because the two ruderal groups showed considerable overlap in the vegetation ordination, and to improve the level of replication. We used a Poisson distribution and three variables: visit (sampling occasion), urbanization level (three levels: low, medium or high) and habitat type (three levels: ruderal, dry and rocky). We also used site as a random factor, to correct for spatial autocorrelation. The structure of the random variables was nested hierarchically such that trap colour (pan) was nested within habitat type, which was nested within urbanization (three levels). The interaction term could not be included because all habitat types did not occur in each urbanization level.

The GLMM analysis was run for number of species and number of individuals. Only four bee species (*Lasioglossum leucopus* (Kirby, 1802), *Lasioglossum lucidulum* (Schenck, 1861), *Bombus lucorum* (Linnaeus, 1761) complex and *Halictus tumulorum* (Linnaeus, 1758) were sufficiently abundant to apply the GLMM at the species level. The three species comprising the group *Bombus lucorum* complex (*Bombus lucorum, B. cryptarum* (Fabricius, 1775) and *B. magnus* Vogt, 1911 were not separated in this study, as they are very difficult to determine reliably without the aid of

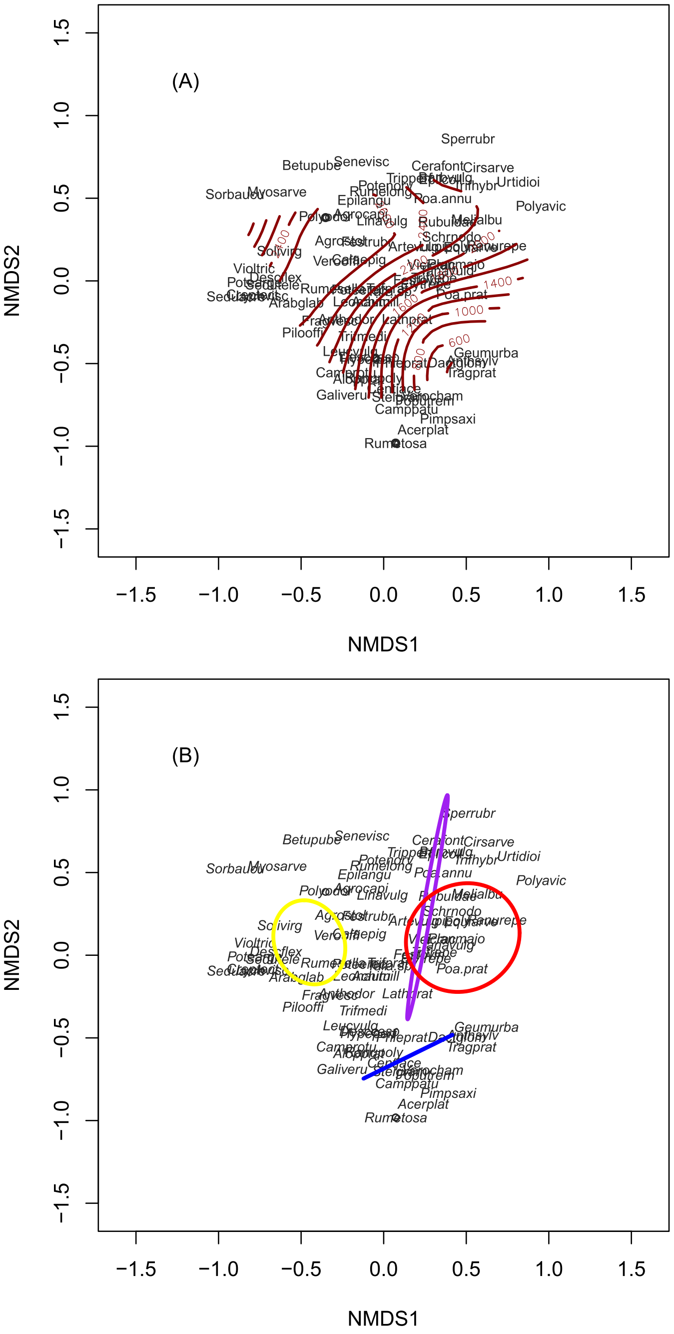

Fig. 2. NMDS ordination of the vegetation of the study sites. Plant species are indicated by their abbreviations and sites are indicated by black open circles. In (A) the contours depict level of urbanization based on the human population density within 1 km^2 of each site. Plants with the least tolerance of urbanization are grouped towards the lower and upper right corners of the plot. In (B), the habitat types are marked with ellipses representing a 95% CI for each habitat type. The yellow ellipse represents dry meadow on bedrock; blue represents sheep fescue dry meadow; the red ellipse is late ruderal and the purple ellipse is early ruderal.

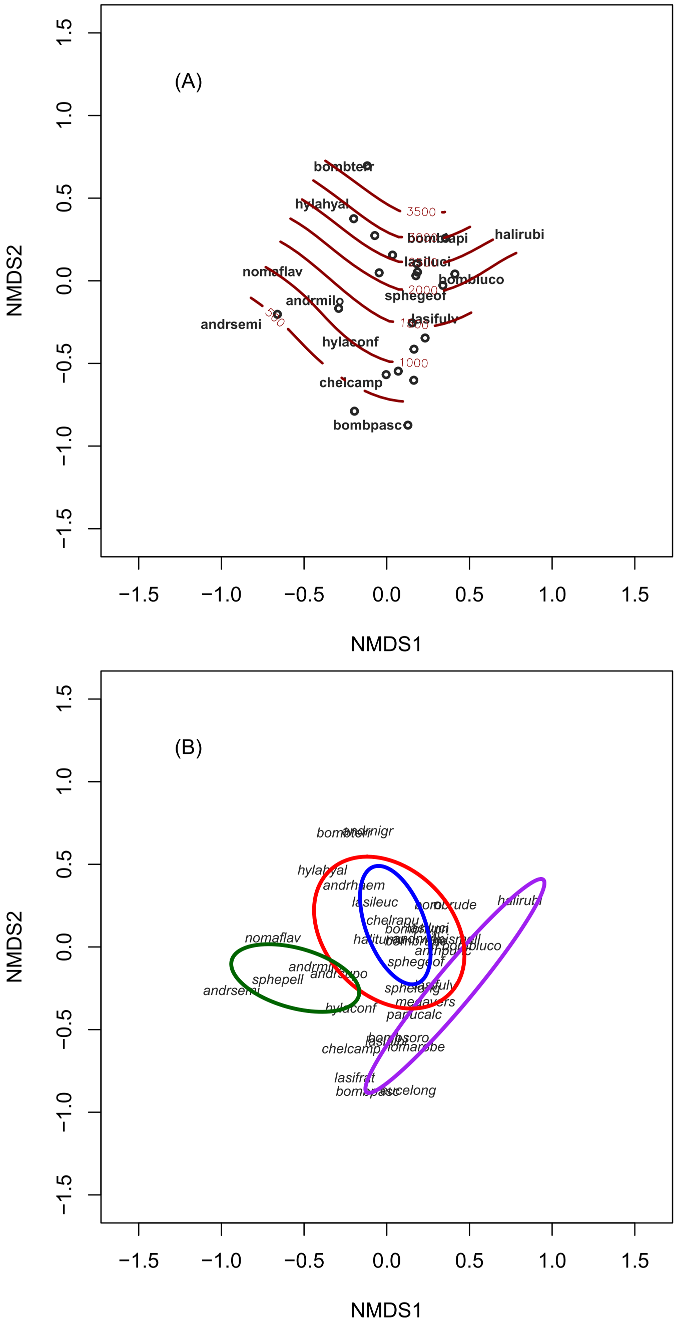

Fig. 3. NMDS ordination of the bee species recorded at each site. In (A) the contours depict level of urbanization based on the human population density within 1 km^2 of each site and urbanization increases from the bottom and lower edge towards the top centre of the plot. *Andrena semilaevis, Lasioglossum fratellum, Bombus pascuorum*, and *Eucera longicornis* are least tolerant of urbanization and *Andrena nigroaenea* and *Bombus terrestris* are the most tolerant. In (B), the habitat types are marked with ellipses representing a 95% CI for each habitat type. The green ellipse represents sheep fescue dry meadow, which was favoured by *Andrena semilaevis* and *Sphecodes pellucidus*; the purple ellipse represents early ruderal, and *Eucera longicornis* dry meadow on bedrock. Dry meadow on bedrock (blue) and late ruderal (red) are more-or-less concentric, indicating a high level of similarity in their species composition.

molecular techniques (Alferink, Marshall, De Jonghe, & Biesmeijer, 2020; Persson, Rundlöf, Clough, & Smith, 2015), so they were treated as a single species. The remaining bee species were grouped according to ecological traits, and the GLMM was also run for these trait groups. The traits used were host plant specificity (polylectic/oligolectic), nesting type (ground/cavity nesters) (Pekkarinen, 1997), and three groups were made according to the four possible combinations of these traits: polylectic ground-nesting PG, polylectic cavity-nesting PC and oligolectic species OL, as there were insufficient observations of oligolectic species to permit further subdividing them according to traits. A fourth group PK comprised kleptoparasites making a total of four trait groups.

The equation used for the GLMM analysis was:

Model = glmer(Species1 $\sim$ visit + urban + habitat + (1| urban/habitat/pan), family = poisson (link = ”log”), na. action = na.exclude)

Results

We recorded a total of 353 bees of 35 species (Appendix B), which comprises almost a quarter of the Finnish bee fauna. The most abundant species was the solitary bee *Lasioglossum leucopus*, (109 individuals), which represented circa 25% of the material. The next most abundant species were *L. lucidulum* (Schenck, 1861) (32), *Bombus lucorum* complex (31), *Halictus tumulorum* (Linnaeus, 1758) (25), *Nomada flavoguttata* (Kirby, 1802) (11), *B. lapidarius* (Linnaeus, 1758) (10) and *Andrena haemorrhoa* (Fabricius, 1781) (10). There were no threatened species in the material, though *A. minutula* (Kirby, 1802) was a relatively scarce and newly colonizing species to the region, which has subsequently become established in Helsinki (corrected formatting). Unlike other species of ground-nesting bees in this region, it regularly produces two generations per year, which has helped it to become established rapidly. Most of the species recorded were polylectic ground-nesting (PG, n = 20) species. The other trait groups were relatively scarce, with just six kleptoparasites (PK), five polylectic cavity-nesters (PC), three oligolectic ground-nesters and two oligolectic cavity-nesters.

The vegetation ordination (Fig. 2) reached an optimal solution after 20 iterations with a goodness of fit value for urbanization of $r^2 = 0.2209$ ($P = 0.163$) and for habitat of $r^2 = 0.6935$ ($P < 0.001$). The plant species showed a response to urbanization (Fig. 2A), with the species *Pimpinella saxifraga, Tragopogon pratensis, Dactylis glomerata, Anthriscus sylvestris* and *Geum urbanum* having a low tolerance of urbanization and *Agrostis stolonifera, Festuca rubra, Veronica officinalis* and *Calamagrostis epigejos*, being highly tolerant. The responses to habitat types (Fig. 2B) showed clear separation of the assemblages of meadows on bedrock and sheep fescue dry meadows, though there was considerable overlap of the two ruderal habitat types. Meadows on bedrock were characterized by such species as *Veronica officinalis, Deschampsia flexuosa, Sedum telephium* and *Solidago virgaurea*, and sheep fescue dry meadows were characterized by *Veronica chamaedrys, Stellaria graminea, Centaurea jacea* and *Campanula patula*. There was considerable overlap between early (purple ellipse) and late (red ellipse) ruderal habitats, with such characteristic species as *Artemisia vulgaris, Scrophularia nodosa* and *Vicia cracca*.

The bee ordination (Fig. 3) reached an optimal solution after 20 iterations with a goodness of fit value for urbanization of $r^2 = 0.4618$ ($P = 0.011$) and for habitat of $r^2 = 0.3743$ ($P < 0.038$). Bees showed a continuous response to urbanization more-or-less vertically through the ordination (Fig. 3A). *Andrena semilaevis* Pérez, 1903, *Lasioglossum fratellum* (Pérez, 1903), *Bombus pascuorum* (Scopoli, 1763), and *Eucera longicornis* (Linnaeus, 1758) were least tolerant of urbanization and *Andrena nigroaenea* (Kirby, 1802) and *Bombus terrestris* (Linnaeus, 1758) were the most tolerant. The responses to habitat types (Fig. 3B) showed less clear separation according to habitat type than for vegetation, implying that more bee species use a greater variety of habitats than plant species do. The sheep fescue dry meadow assemblage was characterized by such species as *A. semilaevis* and *Sphecodes pellucidus* Smith, 1845. The greatest extent of overlap was between dry meadow on bedrock and late ruderal, with such species as *Chelostoma rapunculi* (Lepeletier, 1841), *Bombus hypnorum* (Linnaeus, 1758) and *Halictus tumulorum*. The early ruderal habitats were favoured by such species as *Bombus soroeensis* (Fabricius, 1776), *Nomada roberjeotiana* Panzer, 1799 and *Eucera longicornis.*

In (B), the habitat types are marked with ellipses representing a 95% CI for each habitat type. The green ellipse to the left of the centre represents sheep fescue dry meadow, which was favoured by *Andrena semilaevis* and *Sphecodes pellucidus*; the elongated purple ellipse at the lower right represents early ruderal, favoured by *Eucera longicornis*. Dry meadow on bedrock (blue) and late ruderal (red) are more-or-less concentric, indicating a high level of similarity in their species composition.

In the GLMM species analysis, there was a positive relationship between areas with the lowest level of urbanization and number of bee individuals, and a near significant positive effect on number of species. At the species level, there was a highly significant negative association between *Lasioglossum lucidulum* and meadows on bedrock (Habitat 3), which had a near-significant association with *Lasioglossum leucopus* (Table 1). For the trait groups, both the polylectic kleptoparasites (PK) and the oligolectic species significantly favoured sites with the lowest level of urbanization. None of the trait groups showed significant associations with any of the habitat types.

Discussion

The results of this study suggest that the grassland habitats of Helsinki support a relatively modest bee fauna. The sampling method used, however, of pan-trap sampling for 24 h periods at fortnightly intervals, is not very intensive compared to continuous pan-trapping (Heliölä et al., 2004) or Malaise-sampling (Paukkunen, 2020), and also the range of urban habitats sampled here was limited. Thus our results (Appendix B) provide a sample of the species using these habitat types rather than a comprehensive survey of the bee fauna of the Helsinki Metropolitan Region. Continuous sampling with a combination of Malaise traps, pan traps and transect counts in two botanical gardens, Kaisaniemi (2600 individuals, 52 species) and Kumpula (1100 individuals, 57 species), in central Helsinki, recorded three red-listed species (*Lasioglossum nitidiusculum* (Kirby, 1802), *Megachile lagopoda* (Linnaeus, 1761) and *Andrena coitana* (Kirby, 1802)). That study has also shown that the urban bee fauna in Helsinki comprises bumblebees, solitary bees and domestic honeybees in approximately equal proportions (Paukkunen, 2020). Sampling of High Nature Value HNV meadow habitats in rural parts of southern Finland in 2004, using continuous sampling with yellow pan-traps, recorded an average of 35 bee species per site (Paukkunen, 2009). In comparison, our study, based on periodic sampling with pan-traps, seems to underrepresent numbers of bumblebees and domestic honeybees, as well as scarce and threatened species, which were not recorded in this study. Another issue regarding the use of pan-traps is that their catches have been found to be negatively proportional to the amount of flowers present, as they compete with the flowers for the attention of the bees (Cane, Minckley, & Kervin, 2000; Prendergast, Menz, Dixon, & Bateman, 2020; Roulston, Smith, & Brewster, 2007).

The bee fauna of semi-natural grassland habitats in Finland has not been well studied. Whilst there have been numerous studies of vascular plants (e.g. Luoto et al., 2003; Pykälä, Luoto, Heikkinen, & Kontula, 2005) and butterflies of semi-natural grasslands (e.g. Pöyry, Paukkunen, Heliölä, & Kuussaari, 2009) and roadside verges (e.g. Saarinen, Valtonen, Jantunen, & Saarnio, 2005), the only published study of bees is one of bumblebees (*Bombus* spp) in urban parks in the city of Helsinki, which were sampled along transects (Bäckman & Teräs, 1999).

Land-use planning is a major issue in urban regions, and a key goal of urban planning is the retention of adequate UGI for the provision of Ecosystem Services (ES) and Nature-based solutions (NBS) (Ralla, Kabisch, & Hansen, 2015; Tzoulas et al., 2020). Urban grasslands are recognized for their contribution to plant and insect diversity, aesthetic value and their role in supporting the provision of such services as pollination (Norton et al., 2019; Southon, Jorgensen, Dunnett, Hoyle, & Evans, 2017). There is therefore a need for reliable information on the potential value of different components of UGI (Jalkanen, Vierikko, & Moilanen, 2020) and factors affecting species diversity in different taxa (Hunter & Hunter, 2008), to guide the planning process.

In Finland, as in much of Europe (Carboni et al., 2015), semi-natural grassland habitats are highly threatened (Kontula & Raunio, 2019) and many associated plant and insect

Table 1. Results of GLMM analysis of the predicted probability of occurrence of number of bee species (species richness), number of bee individuals (abundance), the three most abundantly recorded species, *Lasioglossum leucopus, Bombus lucorum* coll. and *Halictus tumulorum*, and three trait groups: polylectic ground-nesting (PG), polylectic cavity-nesting (PC) and kleptoparasites (PK). The columns indicate level of urbanization (Urban1 = low; Urban2 = intermediate and Urban3 = high urbanization) and habitat type (Habitat1 = early ruderal; Habitat2 = late ruderal; Habitat3 = sheep fescue meadow and Habitat4 = dry meadow on bedrock). Urban1 (low level of urbanization) and Habitat1 (early ruderal) are represented by the intercept. Statistically significant values are indicated in bold font.

		Intercept	Urban2	Urban3	Habitat2	Habitat3
Bee species	Coef.	1.985	0.053	0.431	−0.257	0.264
	(SE)	(0.193)	(0.206)	(0.229)	(0.265)	(0.178)
	P-value	<0.001	0.798	0.060	0.333	0.139
Bee individuals	Coef.	2.809	0.140	0.526	−0.611	0.193
	(SE)	(0.207)	(0.244)	(0.251)	(0.322)	(0.201)
	P-value	<0.001	0.565	**0.036**	0.057	0.338
Lasioglossum leucopus	Coef.	−2.156	−0.060	0.627	−1.265	0.906
	(SE)	0.547	0.596	0.606	0.846	0.491
	P-value	<0.001	0.920	0.301	0.135	0.065
Lasioglossum lucidulum	Coef.	−2.346	0.491	−18.959	1.007	−2.379
	(SE)	0.610	0.481	427.038	603.923	0.645
	P-value	<0.001	0.308	0.965	0.999	<**0.001**
Bombus lucorum coll.	Coef.	−4.450	0.091	−0.533	−0.280	−0.174
	(SE)	1.116	0.612	0.759	0.971	0.554
	P-value	<0.001	0.882	0.483	0.773	0.754
Halictus tumulorum	Coef.	−3.765	−0.760	0.672	0.288	0.915
	(SE)	0.789	0.680	0.612	0.695	0.561
	P-value	<0.001	0.264	0.272	0.678	0.103
Group PG	Coef.	1.518	−0.205	0.163	−0.006	−0.230
	(SE)	0.270	0.317	0.349	0.368	0.278
	P-value	<0.001	0.518	0.641	0.986	0.409
Group PC	Coef.	0.446	0.050	0.461	0.074	−0.189
	(SE)	0.447	0.506	0.546	0.533	0.430
	P-value	0.318	0.921	0.399	0.889	0.659
Group PK	Coef.	−0.429	1.190	1.572	−0.163	−0.141
	(SE)	0.625	0.647	0.676	0.502	0.422
	P-value	0.493	0.493	**0.020**	0.746	0.738
Group OL	Coef.	−1.174	0.725	2.066	−1.320	0.893
	(SE)	0.831	0.736	0.731	0.865	0.601
	P-value	0.158	0.325	**0.005**	0.127	0.137

taxa are endangered (Hyvärinen et al., 2019). Grassland habitats are critically important for the support of populations of pollinating insects. Other urban habitats, such as parks (Bäckman & Teräs, 1999), gardens (Ahrné, Bengtsson, & Elmqvist, 2009; Goddard, Dougill, & Benton, 2010) and ruderal habitats (Martins, Gonzalez, & Lechowicz, 2017), are also known to support pollinators, though little research has been performed on their potential for supporting insect diversity, particularly regarding declining species and stenotopic species, such as oligolectic species in the case of bees.

Whilst the urban green infrastructure of the Helsinki region is primarily forested, meadow habitats have been managed for the enhancement of biodiversity and the provision of ecosystem services, such as pollination, since the 1990s (Manninen et al., 2010). The municipalities of the capital region have implemented a policy of identifying semi-natural grassland habitats and managing them for biodiversity (Venn et al., 2015). Our results suggest that urbanization has an effect on both plant composition and bee assemblages, with both taxa containing species that are sensitive to urbanization, others that are tolerant and a considerable number of species lying between those extremes (Figs. 2A, 3A). Dry meadows on bedrock, sheep fescue dry meadows and ruderal habitats are distinctive on the basis of their vegetation but despite apparent differences between early and late ruderal habitats, there is considerable overlap in their vegetation composition (Fig. 2B). Regarding bees (Fig. 3B), there is separation of the assemblage of sheep fescue meadows and early ruderal habitat, though surprisingly strong overlap between the assemblages of dry meadow on bedrock and late ruderal. We presume that the reason for this is that the bee species forage over a larger area than individual sites (Gathmann & Tscharntke, 2002; Zurbuchen, 2010), as a result of which the assemblages of each meadow depend considerably on the habitats and resources outside the site, as well as those within. Solitary bee species in particular have relatively small foraging ranges and whilst individual sites may be important for them, also the availability of suitable patches of vegetation within the foraging range of their nest determines their capacity to persist. It is therefore the combination of optimal and sub-optimal habitat within this range that determines which bee species can persist (Gathmann & Tscharntke, 2002). This suggests that also ruderal habitats will support the persistence of those species capable of utilizing the resources they provide, which is likely to predominantly benefit polylectic species.

There is considerable variation in the habitat preferences of bee species, with generalistic species, such as *Lasioglossum leucopus*, occurring in all of the studied habitats and others, such as *Andrena nigroaenea* and *Megachile versicolor* Smith, 1844, restricted to meadows on bedrock, whilst *Bombus pascuorum* and *Lasioglossum fratellum* were only recorded from sheep fescue dry meadows. It is therefore important to safeguard the provision and management of such habitats, and late successional habitats in general, for the benefit of scarcer and more stenotopic species, which might be entirely dependant on those habitats.

The vast majority of species recorded in this study were ground-nesting species (*n* = 22), compared to seven cavity-nesting species and six kleptoparasites. This contrasts with the results of a number of studies from other regions that reported a similar majority of cavity-nesting bee species in Arizona (Cane, Minckley, Kervin, Roulston, & Williams, 2006), New York (Matteson, Ascher, & Langellotto, 2008), UK (Bates et al., 2011) and Brazil (Zanette, Martins, & Ribeiro, 2005). These differences could be due to regional differences in urban habitat structure or different proportions of these traits in regional species pools. Fetridge, Ascher, and Langellotto (2008) and Matteson et al. (2008) have suggested that ground-nesting bee species are likely to be more vulnerable to the effects of urbanization, though Helsinki has a relatively high proportion of green infrastructure (di Marino & Lapintie, 2018), which may provide better opportunities for ground-nesting bee species. Our results do support the general trend of only few oligolectic and kleptoparasitic species occurring in urban regions (Banaszak-Cibicka & Żmihorski, 2012; Fetridge et al., 2008; Frankie et al., 2005; Matteson et al., 2008).

Urbanization intensity is clearly an important factor affecting bee diversity, as sites with the lowest level of urbanization had more bee species and more individuals, and were also favoured by polylectic kleptoparasites (PK) and oligolectic species. This suggests that sites that are relatively isolated and inaccessible are particularly valuable for vulnerable taxa.

Our results seem to support the suggestion of urban assemblages containing a high proportion of generalist species (Kotze, Venn, Niemelä, & Spence, 2011), though there is a need for more intensive studies of urban bee assemblages and comparisons with rural assemblages before firm conclusions can be made. Multitaxa studies also reveal that there are considerable differences between the vulnerability of different insect taxa to urbanization in the UK (Bates et al., 2011), Poland (Dylewski, Maćkowiak, & Banaszak-Cibicka, 2019), Russia (Eremeeva & Shushchev, 2005) and Belgium (Verboven, Uyttenbroeck, Brys, & Hermy, 2014), for instance. These regional differences in urban pollinator assemblages emphasize the need for further regional studies, such as the present study from Helsinki. Studies of carabid beetles in Helsinki show that urban grassland habitats support highly diverse assemblages (Venn et al., 2013), though butterflies seem to be highly sensitive to urbanization, with only few species persisting in urban regions (Kuussaari et al., 2020). This is the first study to investigate bee assemblages of semi-natural grassland habitats in a Finnish city.

Conclusions and recommendations

We recommend that future studies of urban bee populations should be implemented at a broader geographical scale and consider networks of habitats within the UGI, rather than individual sites, and also account for the effects of species traits and preferences for specific habitat types. Clearly the conservation of open habitats with low levels of urbanization is beneficial for bee diversity, as is the conservation of traditional meadow habitats, such as the sheep fescue dry meadows and meadows on bedrock studied here. Ruderal habitats also have value for bees. This study shows that the majority of bee species in the urban fauna of Helsinki were found from only one or two habitat types, which emphasizes the necessity of providing diverse UGI for the maintenance of insect diversity and assemblages of pollinating insects in particular. There is also a need to collect data on less well-studied taxa of pollinating insects, such as Diptera, which occur abundantly in pan-trap material but which are yet to be studied for Helsinki. We endorse the need for further work to conserve, manage and expand meadow networks and conduct further studies of less well-known taxa.

Low-intensity sampling of bee fauna is not adequate for generating comprehensive data on scarce species or on species diversity but does give valuable data on the community composition and relative value of different sites and habitats for bees.

Polylectic ground-nesting species are more resilient, as they tolerate high levels of urbanization and utilize early successional habitats. This implies that conservation efforts should focus on oligolectic and cavity-nesting species, as well as kleptoparasites, which are more vulnerable to urbanization and less able to benefit from early successional habitats. To support diverse communities of pollinator insects such as bees, it is necessary to incorporate a diverse range of habitats with forb vegetation, such as the meadow and ruderal habitats studied here. This should also include retention of deadwood and vegetation with hollow stems, which provide nesting sites for cavity-nesting species. We assume that provision of insect hotels would also be beneficial, as long as the cavities they provide are sufficiently intact and long enough to function as nest cavities.

In Helsinki, a network of meadow habitats has been incorporated into the urban green infrastructure and managed for plant and insect diversity in particular. The city has several areas devoted to allotments and gardens, and both residents and municipal officials are aware of the importance of pollinating insects. However, for effective provision of pollination, it is necessary to consider how this service could be provided more effectively. Regarding the maintenance of diverse populations of bees as pollinators, attention clearly needs to be focussed on oligolectic and cavity-nesting species. This can best be achieved through increasing the provision and connectivity of semi-natural grasslands. Furthermore, as semi-natural grasslands are generally vulnerable to both overgrowth and encroachment from adjacent woody vegetation, and are often isolated and poorly connected, we recommend managing them first and foremost to maximize their surface area and connectivity.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2023.03.003.

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