



Environmental factors influencing ground-nesting bee communities in an urban landscape: implications for conservation

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Abstract

Habitat loss and degradation of nesting habitats due to agricultural and urban development is considered one of the key factors causing pollinator decline worldwide. Nesting habitat requirements and availability is a strong determinant to which wild bee species are prevailing in urban spaces and knowledge of habitat requirements is therefore fundamental for successful conservation management. Although urban environments can host relatively diverse wild bee communities, ground-nesting bees and associated cleptoparasitic bees are disadvantaged, primarily due to a scarcity of suitable nesting resources. Further, conservation efforts for wild bee habitat (re)creation are largely focused on aerial nesters, despite the proportionally greater diversity and higher vulnerability of ground-nesting bees. The aim of this study was to investigate how environmental factors, including the age and size of sand patches, sand grain size, soil temperature, and the proportion of ground litter-cover vs. bare ground, have shaped ground-nesting bee community structure in an urban landscape. This was done by evaluating wild bee diversity and abundance across various sites with a range of qualities in Uppsala, Sweden. This study revealed a drastic 85% loss of suitable sandy habitat over a 75-year period due to urbanization. Based on the results of this study, we recommend a conservation approach for urban developers to lessen the negative impacts of urbanization on wild bee diversity and abundance. This includes the establishment of numerous bare ground sandy sites with medium size sand grain, and periodical management of vegetation to sustain bare sandy soil patches.

Keywords Wild bees · Cleptoparasitic bees · Indicator taxon · Sand habitat · Habitat age · Ground cover · Biodiversity · Bee conservation · Landscape management · Urban planning

Introduction

Wild bee species are declining in abundance, species diversity and species richness in various parts of the world (Biesmeijer et al. 2006; Burkle et al. 2013; Cameron et al. 2011; Morales et al. 2013; Rhodes 2018; Williams and Osborne 2009; Zattara and Aizen 2021). These declines have had a direct and negative impact on flowering plant reproduction, which in turn has caused cascading effects in ecosystem food webs and ultimately a reduction in biodiversity worldwide (Kaiser-Bunbury et al. 2010; Pauw 2007; Ramos-Jiliberto et al. 2020; Sánchez-Bayo and Wyckhuys 2019) and has adversely affected human food security (Parreño et al. 2022; van der Sluijs et al. 2016).

Habitat loss and degradation of nesting habitats due to agricultural and urban development is considered one of the key factors causing pollinator decline worldwide (Potts et al. 2010; Tilman et al. 2001). Expanding urbanization replaces natural habitats and most of the original ecosystems are

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locally lost, resulting in drastic deterioration of biodiversity and local extinctions of many native species (McKinney 2006; Seto et al. 2012). Urban environments can sustain a certain degree of biodiversity, especially if it is considered in city planning by creating green spaces and if conservation management is in effect (Bazelet and Samways 2011; Beninde et al. 2015; McKinney 2006; Nilon 2011; Pardee and Philpott 2014). When it comes to wild bee communities, knowledge of habitat requirements is fundamental for successful biodiversity conservation management and adaptation to urban development (Christmann 2019; Threlfall et al. 2017).

Wild bees exploit a range of different substrates for nesting; dead wood, plant stem cavities, crevices in stones and trees, man-made structures such as buildings and fences, empty snail shells, and various types of soil are used by different species (Falk, 2015). Depending on their nesting requirements, wild bees can thus be divided into aerial and ground nesters. Ground nesting bees excavate their own underground tunnel systems in the soil (fossorial), and account for around 70% of bee species worldwide, which nesting behaviours are known (Cane and Neff 2011; Harmon-Threatt 2020). Aerial nesting species are most often favoured in urban habitats through the so called ‘urban-filtering’, which offers various vertical structures that provide ample nesting opportunities (Ayers et al. 2021). In contrast, large amounts of impervious surfaces and compressed soils associated with urban landscapes have the opposite effect and are detrimental to ground-nesting species (Quistberg et al. 2016; Threlfall et al. 2017). Cleptoparasitic bees do not construct nests and instead invade the nest of a host bee species to lay an egg which hatches and consumes the food provisioned by the host bee, often killing the host brood in the process (Falk, 2015). Cleptoparasitic bees are one level up in the trophic web, as they are entirely dependent on, and vulnerable to shifts in, the presence and abundance of their host species (Finke and Denno 2004). This makes cleptoparasitic bee species diversity and abundance a potentially great bioindicator (Pearson 1994) for the stability of wild bee assemblages, even in early stages of habitat disturbances (Sheffield et al. 2013). Species diversity and quality of the habitat surveyed, can be assessed by the cleptoparasitic load (CL), or parasite-to-host ratio (Archer 1995; Calabuig and Calabuig 2000), which proposes that a high ratio of cleptoparasites indicates stability of a bee community (Calabuig and Calabuig 2000).

Nesting habitat requirements and availability are strong determinants to which wild bee species are prevailing in urban space (Buchholz and Egerer 2020; Potts et al. 2005, 2010). Although some studies reveal that urban environments can host relatively diverse wild bee communities compared to other human altered landscapes, such as intensified

agricultural landscapes (Hall et al. 2017; Theodorou et al. 2020), ground-nesting bees and associated cleptoparasites are disadvantaged, primarily due to a scarcity of suitable nesting resources in urban landscapes (Beninde et al. 2015; López-Urbe et al. 2015; Quistberg et al. 2016; Threlfall et al. 2017). Ground cover features (i.e. vegetation, litter cover by dead leaves or grass, or exposed bare ground), soil texture (e.g. sand grain size), and soil temperature are some of the major habitat characteristics influencing preferences of nest site selection for ground-nesting bees (Antoine and Forrest 2021; Cane 1991). Open bare ground, often associated with sunny and warm areas, is considered an important attractive feature for ground-nesting bees (Falk, 2015; Forrest et al. 2019; Stone 1994; Weissel et al. 2006). However, such structures are not always appreciated by the park managers and citizens that wish to cover the ground with either dense vegetation or as paved surfaces. Vegetation and dead plant matter covering the soil can be attractive to some ground-nesting bee species and repel others (Breed 1975; Packer and Knerer 1986). The specificity of nesting site preferences among species stresses the need of existing habitat protection as well as additional bare sandy soil habitat creation in urban spaces to prevent further species decline and local extinctions. Habitat restoration and creation for wild bees can have a positive effect on their abundance and diversity (Tonietto and Larkin 2018), but existing literature on conservation efforts for wild bee nesting habitat (re)creation is largely focused on aerial nesters, despite the proportionally greater diversity and higher vulnerability of ground nesting bees (Dicks et al., 2010; Payne et al. 2024).

The aim of this study was to produce knowledge that can be beneficially applied to wild bee conservation management to help increase and/or maintain bee diversity in urban landscapes by optimizing nesting habitat qualities, specifically for ground-nesting bees. To do this, we evaluated various sandy habitats in an urban environment and explore which environmental factors shape bee communities, including the age and size of the sand patches, sand grain texture, soil temperature, and the proportion of ground litter-cover versus bare ground. We investigate the temporal change in nesting habitat supply in our study area during the recent decades, as well as how bee diversity and abundance relates to age of present sand patches. Within our study area we surveyed ten sand patches, of which five were recently created (new sites) by urban developers for conservation and five were older (old sites) sandy habitats. We investigate how bee diversity and community structure varies between these sites of different qualities and evaluate this bee conservation management approach. Finally, we assess the concept of employing cleptoparasitic bees as an indicator taxon for the stability of ground-nesting bee communities.

Materials and methods

Study area and site selection

The study was conducted in 2019 in Uppsala, Sweden, a city of approximately 17.62 km² and subject to increasing urban development (Fig. 1). The city is within the nemoboreal zone, and the surrounding landscape consists of a mixture of agricultural fields and forests. The soils in the region primarily consist of moraine or rock hills, with post-glacial clay deposits found in between (Geological Survey of Sweden; www.sgu.se). However, through the city there is an esker, “Uppsalaåsen” where we placed our study area (Fig. 1), because the esker is sandy with several sandy areas around it formed after the glaciation.

To locate study sites, and how they have developed during the last decades, we searched areas with open bare sand from aerial photographs from 1942, 1965, 1992 (greyscale analog, scanned and orientated) and 2017 (digital infrared), during the spring of 2019. As guidance for imagery interpretation, soil deposit was used (jordart, from Jordartskartansgrunderlag produced by Geological Survey of Sweden,

SGU). Landscape interpretation of aerial images was done in stereo mapping using DAT/EM Summit evolution 7.4. All bare sand patches were located, systematically mapped, and defined by creating polygons in ArcMap 10.5.1. Sites were then selected from a map generated by GIS analysis interpretations of the most recent orthophoto (year 2017) using QGIS 2.18.17. program. The sites were then visited for inspection during the spring 2019 to determine suitability for the study. Sand patches located within 100 m were regarded as one site, since this distance is the shortest flight distance of various wild bees between nesting and foraging locations (Gathmann and Tschardt 2002; Hofmann et al. 2020; Zurbuchen et al. 2010a; Zurbuchen, Landert, Zurbuchen et al. 2010a, b).

A total of ten sites were selected for this study (Fig. 1; Table 1). Four of the sites had been created by the municipality and urban developers specifically for ground-nesting bees and other insects. Three of these sites (N3, N4 and N5) were created in August 2016 for conservation of the solitary bee *Colletes cunicularius* and its associated cleptoparasite blister beetle, *Apalus bimaculatus* (Widenfalk et al. 2018). The fourth site (BP) was established for general



Fig. 1 The location of the sampling sites in Uppsala, Sweden (left). The complete study area is outlined within the red polygon in the south of Uppsala (right). Study sites are within the red polygon and marked

with blue (new sites) or yellow triangles (old sites). Red triangles R1 and R2 denote external reference sites. A key to the site identification codes is found in Table 1

Table 1 Descriptive summary of the study sites along with the environmental variables measured

SITE ID	PATCH AGE	ARTIFICIAL /NATURAL	AREA NAME, DESCRIPTION, AND PURPOSE OF ESTABLISHMENT IF APPLICABLE.	SOLAR EXPOSURE	SAND TYPE	LITTER COVER (%)	BARE GROUND (%)	GROUND TEMP. (°C)	PATCH SIZE (RAW/LOG) (M ²)	GPS COORDINATES
N1	New	Artificial	Sunnersta, winter alpine skiing slope.	Complete	Coarse	2.43	86.30	18.83	7816/ 3.89	131086.1, 6630977.3
N2	New	Artificial	Sunnersta, winter alpine skiing slope.	Complete	Coarse	2.92	83.87	18.00	754.86/ 2.88	131077.34, 6631147.41
N3	New	Artificial	Kronparken, public park with mix tree cover, established by sand translocation for the conservation of <i>C. cunicularius</i> & <i>A. bimaculatus</i> (August 2016)	Semi	Medium	7.71	59.00	15.95	32/ 1.51	130112.46, 6635880.74
N4	New	Artificial	Pollacksbacken, public park with mix tree cover and open field, established by sand translocation for the conservation of <i>C. cunicularius</i> & <i>A. bimaculatus</i> (August 2016)	Complete	Medium	4.21	64.79	17.55	68.04/ 1.83	129897.29, 6636469.13
N5	New	Artificial	Pollacksbacken, public park with mix tree cover and open field, established by sand translocation from nearby Skjutvallen (SV) for the conservation of <i>C. cunicularius</i> & <i>A. bimaculatus</i> (December 2018)	Complete	Medium	4.79	52.29	16.93	72.02/ 1.86	130044.03, 6636404.90
BP	New	Artificial	Biparken, Rosendal. Open area with sandy soil translocated from SV site.	Complete	Medium	1.00	88.75	17.05	561.03/ 2.75	129465.5, 6635978.3
O1	Old	Natural	Kungshamn Naturreservat. Slope in mix forest by river.	Semi	Coarse	7.86	90.57	14.83	232.09/ 2.37	130757.5, 6630146.1
O3	Old	Natural	• Sunnersta. Open area with sandy soil and human disturbance.	Complete	Coarse	1.58	86.62	17.00	2506.79/ 3.40	130920.7, 6630791.7
O4	Old	Natural	Linnestigen. Sandy slope area in the mix forest.	Semi	Coarse	13.03	81.61	15.93	1438.93/ 3.16	131031.58, 6634792.70
SV	Old	Artificial	Skjutvallen, Rosendal. Old sand pile, historically used for military shooting training.	Semi	Medium	3.24	84.09	18.00	1637.72/ 3.21	129322.2, 6636090.8
R1	Old	Artificial	Gozzis, Lövsalöt. Sand and gravel quarry.							127102.7, 6650137.0
R2	Old	Artificial	Högstaåsen. Sand and gravel quarry.							126821.6, 6651071.5

ground-nesting bee diversity preservation purposes in a newly built residential area, by translocating frozen blocks of sand from a nearby site (SV) in December 2018. Historically, the SV site was utilized by military practices and is known as a particularly rich site for insects associated with sandy habitats, particularly bees. All sites, including SV, that were present in historical aerial photographs and were still present in 2019 were used in this study and categorised as ‘old’ sites.

An additional two reference sites ‘R1’ and ‘R2’, were selected at sand and gravel quarries located approximately 10 km north of Uppsala’s developmental area and known to be species rich habitats for various ground-nesting bees (Fig. 1; Table 1; Cederberg B. & Nilsson A.N., 2002, Diversity of wild bees at Tunåsen and Uppsala mounds, Uppsala, unpublished report to Uppsala municipality). These sites were included to compare species data from habitats unrelated to urban factors, environmental variables were not measured there.

Habitat assessment - environmental variables

To assess the patch age and overall temporal change of open sandy soil availability from 1942 until present (2017–2019), all sand patches in each of the four studied time periods were summed to give one value (in m²). An estimate for year 2019 was made based on field validation, which slightly readjusted the estimation acquired from GIS analysis of the year 2017 orthophoto. Patches that turned out to be falsely identified as sand by GIS analysis (ca. 246 m²), unsuitable for ground-nesting insects (volleyball court, ca. 134 m²), or

already gone due to urbanization by year 2019 (ca. 1,222 m²), were subtracted from the total sand area estimate of GIS analysed orthophoto of year 2017 (ca. 16,884 m²). A new sand patch in 2019 (Biparken, ca. 522 m²) was added to the total value of sand area and the total percentage of the sand area for each time-period was estimated. The sand patches ranged in size from 32 m² to 7816.6 m² (Table 1).

In 2019, for each study site, we collected data on six environmental variables: patch size, patch age, sand grain size/type, ground temperature, proportion of litter cover and proportion of bare sand (Table 1). Each patch size was determined using the Feature Manipulation Engine (FME) software, utilizing the raster calculator tool with digital elevation models (DEMs) to account for variation in terrain slope when calculating the total surface area. The age of sand patches was assessed by the aerial photographs from GIS analysis from different years (QGIS 2.18.17). They were categorized as ‘new’ if they were only present in 2017 orthophotos or as ‘old’ if they were also present in the 1942 and/or 1965-year aerial photographs, meaning they were at least 52–77 years old (Table 1).

Sand grain size was estimated as an average of two soil samples collected from each sand patch at the surface, and at a depth of 20 cm below the surface ($n=20$ samples). The samples were air-dried and sieved through meshes of different sizes (diameter in mm) that correspond to specific categories of grain size based on Wentworth size classification (Fletcher & Bryan, 1912; Wentworth 1922). Only two categories of sand grain size were represented in the samples of this study: medium (0.25–0.5 mm) and coarse (0.5–1.00 mm; Table 1).

Ground temperature was measured with a digital thermometer at each sand patch location on four occasions (May 22, June 01, June 23, and August 03, 2019) at three depth levels in the soil: 0 cm, 10 cm, and 20 cm. The mean recorded temperature at 10 cm and 20 cm depth correlated to each other significantly ($t=17.8$, $df=46$, $p<0.001$) so only the temperature measured at 20 cm depth was used for statistical analyses, since most ground nesters excavate their nests relatively deep and thus the surface temperature is less relevant (Cane and Neff 2011). An average of the temperature at each sand patch for the four different occasions was used in the analyses (Table 1).

The percentage of bare ground availability in sand patches, a commonly applied environmental variable when studying ground-nesting bees, was estimated using a quadrat sampling method on two occasions throughout the summer coinciding with bee inventories (June 05, and July 05, 2019). Seven quadrats were used at sites $<250\text{ m}^2$ and 19 quadrats were used at patches larger than 250 m^2 . Each quadrat ($50\times 50\text{ cm}$) was placed on the sand patches and the percentage of total vegetation, litter ground cover and bare ground, within each quadrat, was visually estimated always by the same observer. Data collected on both sampling occasions were pooled and averaged (Table 1).

Wild bee inventory and species identification

The bees were collected using pan traps (Campbell and Hanula 2007; Nielsen et al. 2011). Two sets of pan traps were used at each site. Each set included one yellow and one white plastic bucket of approx. 11 cm height and 22.5 cm diameter (approx. volume of 4,160 ml). They were filled to two thirds with water, mixed with a drop of fragrance- and colour-free washing detergent to reduce the surface tension. The traps were placed at each sand patch in vegetation on or near the selected sand patches (within 10 m), and yellow and white pan traps were placed 1–2 m apart, setting each set of traps as far from each other as reasonably possible within the study patch area. The traps were placed in the sites for 48–52 h on four occasions ranging from late spring to summer (May 21–23; May 30–June 01; June 21–23; August 01–03, 2019). In the field, insect samples were collected from the pan traps in tubes with 75% ethanol. Shortly after, the bee specimens were dried and pinned for species identification.

All bee samples, except for the bumblebees (*Bombus* spp.), were identified to species level using Falk (2015) and confirmed using the artportalen.se website which offers up to date information on majority of species occurrences in Sweden. Each bee species was also assigned to its nesting guild (ground-nesting an associated cleptoparasitic bees or

aerial nesting bees) based on wild bee species life history information (Falk, 2015; Westrich 2018).

Data analyses

Only ground-nesting bees and associated cleptoparasitic bees were analysed in all analyses. All bees from each patch were pooled, giving a single species abundance measure per sand patch. Species diversity was calculated with three diversity indices: species richness (S), Shannon-Wiener (H), and Gini-Simpson's (1-D) (Heino et al. 2008; Morris et al. 2014). To overcome issues with the strong non-linearity of Shannon and Gini-Simpson's indices, they were transformed to the effective number of species (ENS), which is the number of equally abundant species necessary to produce the same value of a diversity measure (Morris et al. 2014). To examine the completeness of sampled ground-nesting bee species community, the percentage of singletons (species represented by single individuals) was calculated. Additionally, an individual-based rarefaction curve was generated, although not including species data collected from the two reference sites (R1, R2). Diversity metric calculations and conversions were done with Microsoft Excel, and rarefaction was generated with Rstudio Team 2019.

Generalized linear models (GLMs) were performed to analyse the associations between species diversity measures (response variables) and the six environmental (explanatory) variables (Table 1) using Rstudio Team 2019. Data was visually (Q-Q plots) and statistically (Shapiro-Wilk test) inspected for normal distribution. Explanatory variables that fit the GLMs were selected based on lowest AIC (Akaike Information Criterion) values.

Unimodal ordination analyses were performed to explore if species composition was affected by the six environmental variables (Table 1). Species that occurred in only one site were eliminated from the analysis. First, unconstrained correspondence analysis (CA) was carried out to visualise species composition and sand patch relations to each other. Constrained (canonical) correspondence analysis (CCA) was then performed to analyse which environmental variables effected species composition. Monte Carlo permutation test was used to test whether these environmental variables could explain a significant amount of variation ($p>0.05$). Significant variables were added to the model by forward selection until none of the remaining variables could contribute significantly.

A Poisson Generalized Linear Model (GLM) was used to test whether the number of cleptoparasitic bee species predicts the species richness of ground-nesting bees. The model was fit using cleptoparasitic species richness as the predictor variable and ground-nesting bee species richness as the response variable. In addition, cleptoparasitic load

Table 2 A summary of estimated wild bee species diversity indices at the sand patches: species richness (S), Shannon-Wiener (H), Gini-Simpson (1-D), as well as effective number of species (ENS) derived from H and 1-D. The most species rich and diverse sites are coloured in green and the least species rich and diverse site is coloured in yellow

Sand patch	S	H	1-D	ENS (H)	ENS (1-D)
N1	7	1.272	0.604	3.567	2.522
N2	11	2.210	0.875	9.118	8.000
N3	25	2.607	0.893	13.554	9.318
N4	13	2.352	0.885	10.510	8.667
N5	17	2.619	0.911	13.723	11.227
BP	9	2.010	0.836	7.461	6.095
O1	8	1.859	0.809	6.420	5.233
O3	7	1.831	0.815	6.240	5.400
O4	2	0.637	0.444	1.890	1.800
SV	20	2.175	0.801	8.804	5.018
R1	14	1.472	0.546	4.359	2.203
R2	9	2.010	0.836	7.461	6.098

(CL), which is a parasite-to-host ratio (Archer 1995), was calculated for each sand patch.

Results

Bee species composition and diversity

A total of 665 individual bees were collected including 44 honeybees (*Apis mellifera*), 107 bumblebees (*Bombus* spp.), and 520 wild solitary bees (Supplementary Table I). The latter constituted 57 species, of which 34 species were ground-nesting bees (358 individuals), including 7 bee species that are exclusively nesting in sand (46 individuals), and 9 cleptoparasitic bee species (100 individuals). The most abundant ground-nesting bee species were *Lasioglossum morio* (80 individuals), *L. semilucens* (48 individuals), *L. leucopus* (38 individuals) as well as the cleptoparasitic bee *Nomada lathburiana* (39 individuals). Three species (*Andrena bicolor*, *A. subopaca* and *Dasygaster hirtipes*) were only recorded in the reference sites. Therefore, 40 species (34 ground-nesting bees+9 cleptoparasitic bees– 3 species found only at reference site=40) were used in the analyses. Twelve species occurred as singletons accounting for 30% of species, and one species occurred in only one site (*N. flavoguttata*). The greatest species richness and diversity, for ground-nesting bees and associated cleptoparasitic bees, was found at the sand patches 'N3' and 'N5', respectively, while the lowest species richness and diversity was found at the 'O4' sand patch (Table 2).

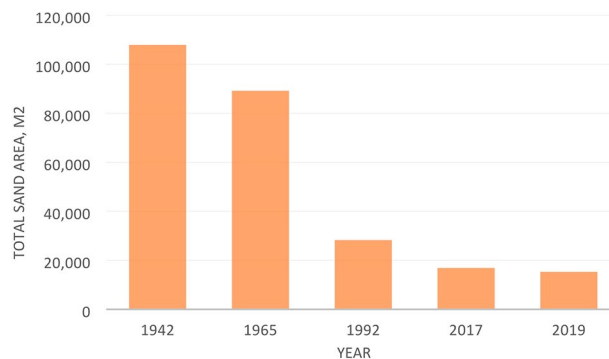


Fig. 2 Temporal change, between 1942–2019, of open sandy soil availability (m²) in the study area in Southern Uppsala, Sweden

Temporal change of available sandy patches

Open sandy soil within the total study area (polygon in Fig. 1) has declined substantially over time (Fig. 2). The percent of sand habitat that remains is estimated to only 14.8% of the total sand area that was present in 1942.

Diversity and environmental variables

Sand grain size, size of the sand patch and the litter cover significantly explained diversity values within the full dataset (Table 3). However, this varied depending on the diversity metric used and whether cleptoparasitic bees were included or excluded from the dataset (Table 3). For the full dataset, sand grain size significantly affected species richness, which tended to be higher with a 'medium' sand grain type (Table 3; Fig. 3) The size of the sand patch and the litter cover were both negatively associated with the Shannon-Wiener (H), and Gini-Simpson's (1-D) diversity metrics

Table 3 Condensed results from the GLM analysis using either the full wild bee dataset and the dataset without cleptoparasitic bees showing only those explanatory variables that could provide statistically significant evidence explaining each species diversity measure (species richness, Shannon ENS and Simpson ENS) in each GLM model

Dataset in GLM	Species richness		Shannon ENS		Simpson ENS	
	Significant variables	<i>p</i> -value	Significant variables	<i>p</i> -value	Significant variables	<i>p</i> -value
<i>Full dataset</i>	Sand grain size	0.014	Patch area size	0.022	Patch area size	0.009
			Litter cover	0.017	litter cover	0.008
<i>Without cleptoparasitic bees</i>	Patch area size	0.007	Patch area size	<0.001	Patch area size	0.002
			Litter cover	0.011		

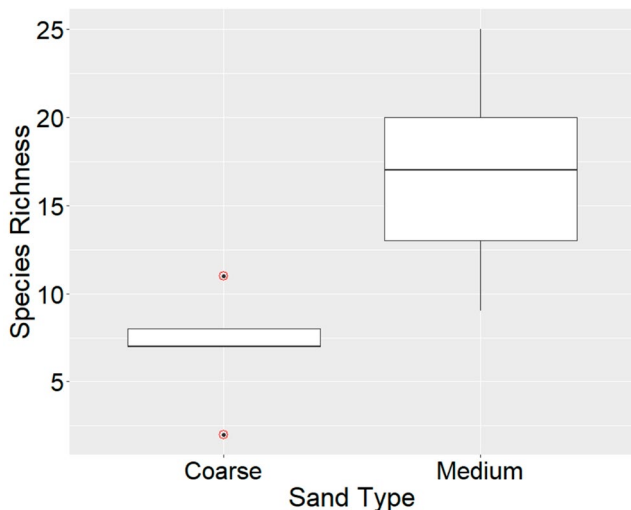


Fig. 3 Box plot illustrating the distribution of species richness values in sites with ‘coarse’ and ‘medium’ sand grain size. Lower and upper whiskers show the spread of values with red circles representing outliers. Produced from the dataset including cleptoparasitic bees

(Fig. 4). When the cleptoparasitic bees were excluded from the dataset only size of the sand patch and litter cover remained significant (Table 3), both were negatively associated with species richness (Fig. 4).

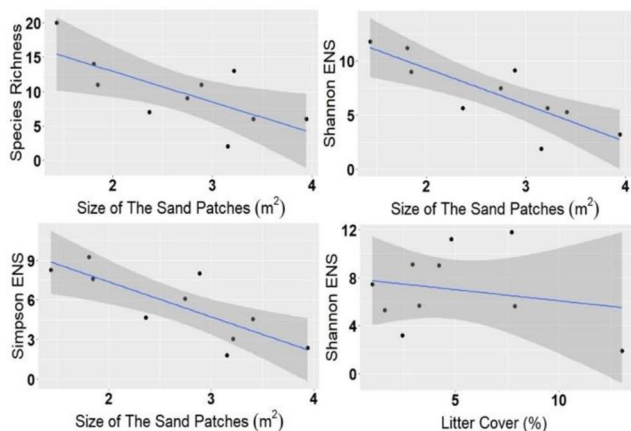


Fig. 4 Distribution of values for litter cover (%) and size of the sand patches (logged, m²) plotted against either Shannon ENS, Simpson ENS or species richness. The left figures are produced from the data-

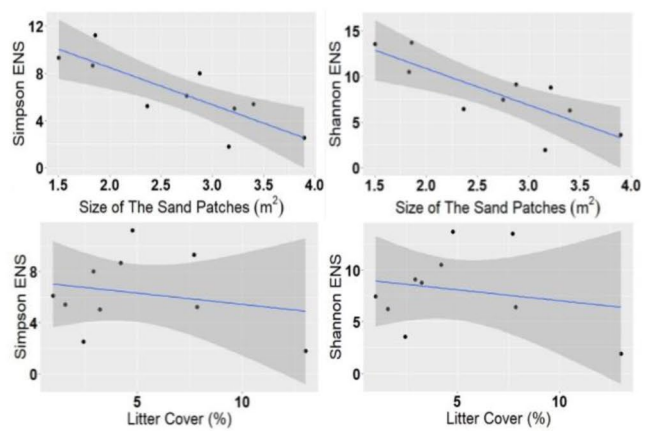
Bee species composition and environmental variables

Forward selection in the CCA selected sand grain size, bare ground, and litter cover as explanatory environmental variables of bee species data. Monte Carlo permutation tests produced the following *p*-values: model *p*=0.002; CCA axis one *p*=0.006 and CCA axis two *p*=0.014; sand grain size *p*=0.002, litter cover *p*=0.004, and bare ground *p*=0.014.

The first two CCA axes together explained 43% of the variance in the bee species data (total inertia 1.7959; eigenvalues 0.3909 and 0.3761 for CCA axes one and two, respectively). The variable-scaled (species-oriented) CCA triplot suggests some trends of species alignment along selected environmental variables (Fig. 5). Most species cluster towards ‘medium’ type of sand with not many species cluster near ‘coarse’ sand type and a range of species seem to be associate with litter coverage, while just a few species were more associated with bare ground (Fig. 5).

Cleptoparasitic bees and indicator taxon

The cleptoparasitic load varied between 0 and 36% indicating a large variation of parasitic bees in the different sand patches (Table 4). There was a statistically significant positive relationship between species richness of ground-nesting



set including both ground-nesting and associated cleptoparasitic bees and the right figures produced from the dataset including only ground-nesting bees. Darker grey area represents 95% confidence interval

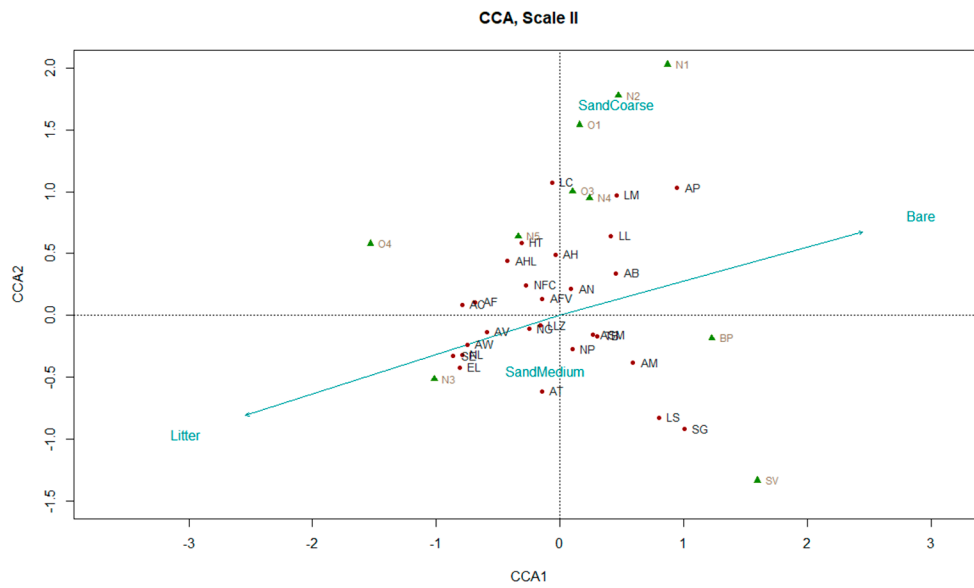


Fig. 5 CCA triplot of wild bee species composition plotted with species-oriented scaling (II), showing axes 1 and 2. Sites are marked as green triangles, species are marked as red circles, and the names for the abbreviated IDs can be found in supplementary Table 1. The environmental variables explaining the variance in species composition are: sand

(‘coarse’ and ‘medium’); and litter cover (%) or bare ground (%). Litter cover and bare ground are presented with arrows, which length represent the strength of the association. As a categorical variable, sand type is presented in the graph without arrows, closeness of species to the either sand grain type represents the strength of association

Table 4 A summary of species richness of ground-nesting host bees (H) and cleptoparasitic bees (C) at each study site, along with the calculated cleptoparasitic load CL (%)

Site Id	No. of hosts (H)	No. of cleptoparasites (C)	Cleptoparasitic LOAD (100*C/(H+C)) %
N1	6	1	14
N2	11	0	0
N3	20	5	20
N4	13	2	13
N5	14	3	18
BP	9	0	0
O1	7	1	13
O3	6	1	14
O4	2	0	0
SV	13	7	35
R1	9	5	36
R2	9	0	0

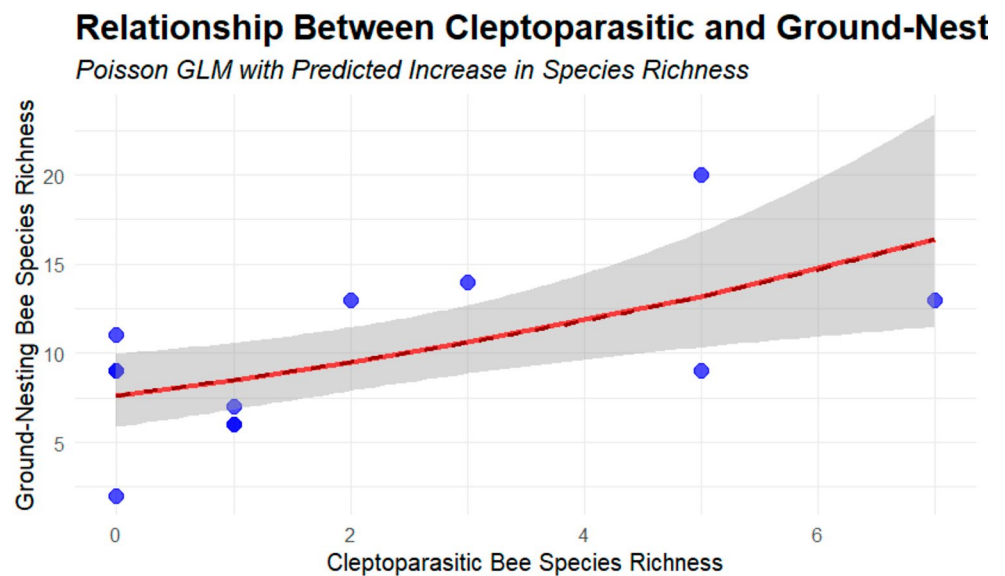
bees and cleptoparasitic bees (Fig. 6; SE=0.037, z=2.98, p=0.00291). The coefficient of cleptoparasitic species richness was 0.11, suggesting that for each additional cleptoparasitic bee species, the species richness of ground-nesting bees increases by 11.5% ($\exp(0.11) \approx 1.115$; Fig. 6). The cleptoparasitic load was higher at old sites (35% CL at SV) compared with the newest established site (0% CL at BP), but was comparatively intermediate at sites that were created only 2 years earlier than BP (e.g. CL ranging from 13 to 20% at N3, N4, and N5; Table 4).

Discussion

This study revealed a drastic loss of suitable sandy habitat for ground nesting bees in the study area due to urbanization over a 75-year period. Historical aerial photographs revealed that the available sand area of southern Uppsala had decreased by 85% since 1942. The previous sandy areas are now covered by buildings and paved roads. A reasonable expectation would be that older sand patches can represent more diverse bee communities with some relict species that have established populations over a long period of time. However, the age of the sand patch in this study did not explain variation of bee diversity metrics. It seems that bees are capable of effectively inhabiting new sand sites and the age of nesting habitat is of no obvious importance. Similar conclusions have been made in studies of bees in Germany and U.K. (Krauss et al. 2009; Potts et al. 2005). This is perhaps not surprising as species thriving in these types of successional habitats would need to be rather opportunistic. (Krauss et al. 2009; Potts et al. 2005). It is therefore more likely that the importance of habitat age to bee community and diversity depends on the nature of its disturbances (Cook et al. 2005). Although this study lacks corresponding bee diversity data over time in this region, this dramatic reduction in sand area has undoubtedly impacted ground-nesting bee communities by limiting the availability of suitable nesting habitat.

In this study, the smaller sand patches were associated with the greatest bee diversity and increasing size in

Fig. 6 Correlation of cleptoparasitic and ground-nesting wild bee species richness (S) in ten study sites and two reference sites (total $n = 12$). The blue points are the data points, the red line is the predicted relationship from the Poisson GLM, showing the increase in ground-nesting bee species richness as cleptoparasitic species richness increases. The grey shading is the model fit with 95% confidence intervals



sand patches was related to decreasing bee diversity. This is opposite to the expectations of the ecological species-area relationship (SAR) pattern, which postulates that species diversity tends to increase with increasing habitat size (Lomolino 2001), and contrasts with previous studies showing patch area size as a primary explanation for bee species diversity and abundance (Krauss et al. 2009; Twerd et al. 2019). A possible explanation for this disparity could be that all four of the small sand patches in this study were purposely created to assist ground nesting bees, in contrast to the larger sand patches, which were naturally occurring or created for recreational purposes without specifically having soil nesting insects in mind. Sandy soil is a scarce resource for ground-nesting bees, particular in urban environments, so smaller patches might be more densely occupied and crowded while bees in larger areas may be more spread out leading to unbalanced sampling. Alternatively, the same number of pan traps were used at each site regardless of the patch size, and while this is considered a reasonable sampling strategy (Fahrig 2013), it could have led to an underestimation of bees in larger patches in this study. Despite this unexpected result and its possible explanations, it is nevertheless encouraging that small sand patches can host a relatively diverse wild bee community. This demonstrates that the creation of numerous but small habitats in urban areas could be a feasible conservation approach, if they are implemented in connection to floral resources for the bees nutritional requirements of pollen and nectar (Gathmann and Tscharrntke 2002; Hofmann et al. 2020).

Litter cover affected bee diversity negatively in this study, suggesting that litter cover is not a particularly attractive feature for many ground nesting bees. However, litter cover was not particularly extensive in this study, ranging between the total ground cover of 1.00-13.03% making it

difficult to assess the full benefits or drawbacks of this environmental factor. Studies investigating litter cover and bee nesting habitats are scarce and conclusions are generally made from species-specific studies (Breed 1975; Brännert et al. 1994; Packer and Knerer 1986).

Bare ground, or sparsely vegetated soil, is often considered an attractive feature for ground-nesting bees and the creation of bare ground has been implicated as a practical conservation method (Gregory and Wright 2005; Widenfalk et al. 2018). Exposed soil is a defining factor of local pollinator diversity as shown repeatedly in other studies (Potts et al. 2005; Quistberg et al. 2016; Sardiñas and Kremen 2014; Severns 2004; Theodorou et al. 2017; Wenzel et al. 2020), with several species-specific studies observing that bees prefer to nest in an open, sparsely vegetated soil (Breed 1975; Potts and Willmer 1997; Wuellner 1999). However, conclusions from studies vary. Removal of vegetation for conservation purpose benefited ground nesting alkali bees (*Nomia melanderi*) with an increase in their population by 300% (Stephen and Evans 1960). In contrast bee diversity and bare soil in urban environments, (Twerd and Banaszak-Cibicka 2019) did not have any associations in another study (Twerd and Banaszak-Cibicka 2019). Some species may simply have broader nesting habitat preferences (Kim et al. 2006), and it is not always clear if bare ground is preference or an observational bias (Antoine and Forrest 2021; Harmon-Threatt 2020). Even though bare ground did not explain bee diversity in this study, it was a significant factor shaping bee species community, at least for a few species (Fig. 5). This result together with supporting evidence from other studies suggests that exposed soil should be considered an important nesting habitat feature. However, more experimental studies are necessary to better understand how litter-cover or bare-ground affects nesting choices,

particularly for a wider range of ground-nesting bees or to determine if there are potential threshold values, above which the amount of bare ground does not explain variation in species diversity and abundance.

Higher species richness was found in sand patches with medium grain size compared to coarser grain size sand, in this study. This was not an unexpected result considering that many ground-nesting bee species are associated with a softer sandy soil (Cane 1991; Harmon-Threatt 2020; Potts and Willmer 1997). Sand grain size affects water retention and if the grain size is too small, there is a risk for water-logging nest cells or fungal infections due to high moisture levels, yet if the grain size is too large, the soil could dry out potentially causing brood desiccation (Potts and Willmer 1997). Thus, one could predict that the medium grain sand in this study, supporting higher species richness, would be preferred as it provides good water drainage, yet also maintaining a more balanced humidity for the developing brood than coarser sand could. Coarse or medium grain sand were the only sand types found in this study. Loose sand is generally not attractive to many bee species since it cannot support the architectural integrity of a nest, especially for bees nesting in aggregations (Antoine and Forrest 2021). The full extent to which sand texture determines nesting site selection for many bee species is still unclear (Fortel et al. 2016), but creating nesting habitats using medium grain sand in urban environments is likely to benefit bee diversity.

When the statistical analysis was tested with excluding cleptoparasitic bees, sand grain size was no longer an important variable for species richness. The simple explanation is most likely due to the reduction in sample size. Ground-nesting bees and cleptoparasitic bees differ in life-history traits but have tightly coevolved and the diversity of cleptoparasitic bees is highly associated with the diversity and abundance of their ground-nesting host species (Finke and Denno 2004). Even though cleptoparasites do not directly choose nesting soil, the choice is made by their associated host and so nesting habitats such as sand grain size, indirectly affect cleptoparasitic bee diversity, as the results of this study show.

The fact that cleptoparasitic bees were present in sites that were created only two years earlier suggests that the successful colonization of diverse bee assemblages in newly created nesting habitats may happen rather rapidly over a course of a few years. Factors such as foraging resources, connectivity between habitats in a fragmented landscape, and the presence of species in surrounding habitats, would affect the colonization rate and success of new habitats (Boscolo et al. 2017; Griffin and Haddad 2021). The results of this study provide strong support that an increase in cleptoparasitic bee species richness is associated with a significant increase in ground-nesting bee species richness, indicating that relationship between these two bee guilds is

rather high. However, the limited data set (locations $N=12$), and species richness model (disregarding species density and evenness), was insufficient to confidently determine the role of cleptoparasitic bees as an indicator taxon for assessing bee communities. Therefore, further research is needed to answer this question with a more sophisticated statistical approach (Sheffield et al. 2013).

Bee diversity and community structure was similar between the reference sites in this study and the urban sites investigated, with only 3 of the 43 species found only at the reference sites. This suggests that the urban sites were fairly representative in terms of species diversity in the area.

Implications for conservation

The dramatic loss of sandy soil in the study area since the 1940's emphasizes the need for conservation action to assist this vulnerable and often over-looked group of wild bees in urban landscapes. With such a drastic decline in habitat it is likely that some inhabiting species suffer from extinction debt, i.e. the habitat amount has already decreased below a threshold where the population is sustainable (Tilman et al. 1994). However, as long populations are still present in the area they might survive if habitat amounts are increased (Bulman et al. 2007).

Wild bee abundance and diversity can improve with habitat (re)creation (Tonietto and Larkin 2018), but most conservation efforts for wild bee nesting habitat is largely focused on aerial nesters (Dicks et al., 2010). The existing studies specifically on ground-nesting bee assemblages do however show that creation of nesting habitats in human altered landscapes has a positive effect on bee abundance and diversity (Gregory and Wright 2005; Severns 2004; Wesslerling and Tschamtké 1995). Based on the results of this study, We recommend the establishment of numerous bare ground sandy sites across urban landscapes with medium sand grain size as a conservation approach for improving ground-nesting bee diversity and abundance. Additionally, vegetation management should be implemented periodically to remove colonising plant matter from the sandy patches. This study cannot confidently make recommendation on the size of soil patches but does show that even small size sand patches provide valuable nesting resources for diverse wild bee assemblages. As the age of soil patches did not seem to be of significance for ground-nesting bees in this study, the creation of new patches should be effective in attracting diverse bee communities for following years. Ultimately, the creation and restoration of preferable nesting habitats for wild bees should lessen the negative impacts of urbanisation and benefit overall wild bee diversity (Vanbergen et al. 2013). However, measuring diversity should not be the only 'go-to' conservation approach. It is essential to consider overall habitat heterogeneity and create opportunities for various species to find their niche in urban landscapes.

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Author contributions IC designed, performed field surveys, species identification and data analysis, AB performed GIS analyses, LAW co-supervised the project, MJ conceptualized, designed, and supervised the project, BL conceptualized, funded and co-supervised the project. All authors contributed to the writing with the initial draft produced by IC. All authors read and approved the final manuscript.

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Data availability Data is provided within the manuscript or supplementary information files. The datasets used and/or analysed during the current study is available from the corresponding author (Barbara.locke@slu.se) on reasonable request. The dataset will also be stored in the Swedish National Data Service repository, [<https://doi.org/10.5878/h2hc-h513>].

Declarations

Competing interests The authors declare no competing interests.

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