Ground-nesting bees in the age of urbanization

– quality of sandy habitat and wild bee diversity in Uppsala, Sweden

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Abstract

Wild bees are indispensable pollinators of most flowering plants and agricultural crops, and thus are vital components of functioning ecosystems and provide essential ecosystem services to humans. This study primarily aimed to discover the environmental features of nesting habitat that are mostly associated with wild ground-nesting and associated cleptoparasitic bee species diversity in urban landscape. As wild bee species diversity and abundance continue to decline in the age of urban development, it is necessary to deepen our knowledge about the nesting habitat preferences of ground-nesting bees. Six environmental variables (sand patch size, age, sand grain size, soil temperature, litter cover and bare ground) were measured at ten sandy soil patches in the study area in south of Uppsala, Sweden. Colour pan traps were deployed at each site to capture wild bees on four different occasions during spring/summer of 2019. To have species data comparison even two reference sites at bee species rich sand and gravel quarries outside the city were selected for survey. It was found that highest species richness was at sand patches that had ‘medium’ compared to ‘coarse’ type of sand. Litter cover was negatively associated with species diversity. Likewise, although opposite to expectations, habitat size was negatively associated with species diversity. Sand grain size, litter cover and bare ground were the factors that shaped urban bee community. Bee data was additionally employed to assess whether cleptoparasitic bees could predict the diversity of host species and thus act as a potential indicator taxon. The results showed a positive trend, although not statistically significant. Cleptoparasitic load (CL) measure was used to assess the sand patches established specifically for insects and suggested that newly created habitats may be colonized by stable and diverse bee communities within a matter of several years. Moreover, the estimated temporal change of open sandy soil availability in the study area throughout 75-year period showed a drastic decline; less than 15% of sandy habitat was available in 2019 compared to 1945. Based on the results of this and previous studies, recommendations of additional nesting habitat creation to assist and increase wild bee diversity in urban landscape were provided.

Keywords: ground-nesting bees, cleptoparasites, indicator taxon, sand, sandy habitat, urbanization, urban development, sand grain size, habitat size, habitat age, litter cover, bare ground

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Abbreviations

CA	Correspondence Analysis
CCA	Constrained (Canonical) Correspondence Analysis
CL	Cleptoparasitic load
ENS	Effective number of species
GLM	Generalized Linear Model
SAR	Species-are Relationship

1. Introduction

1.1. Overview of to the study

Knowledge of habitat requirements for wild bee communities is fundamental for successful management and adaptation to urban development (Threlfall et al. 2015; Christmann 2019). This study evaluates multiple environmental factors that define nesting habitat of ground-nesting and associated cleptoparasitic bees. As Shelford's Law of Tolerance explains, the occurrence and abundance of an organism is defined by environmental gradient, where each species prospers at its environmental optimum, but when the values exceed or go below the optimum values, species struggle and cannot survive (Shelford 1911). In present study, species diversity metrics are applied to evaluate habitat qualities in attempt to find an environmental optimum of nesting habitat that is suitable for the greatest diversity of ground-nesting and cleptoparasitic bees.

Ground cover features (vegetation, litter cover (dead leaf and grass) and exposed bare ground), soil texture (e.g., sand grain size) and soil temperature are some of the major habitat characteristics influencing preferences of nesting site selection (Antoine & Forrest 2021). Open bare ground is often considered an attractive feature for ground-nesting bees (Falk 2015). Vegetation and dead plant matter covering the soil can be attractive to some species, while repel others (Breed 1975; Packer & Knerer 1986). Soil texture is a critical factor for many ground-nesting bees when selecting a place to nest, often being associated with sandy or sandy loam habitats (Cane 1991). Moreover, nesting habitat is most often associated with sunny and warm areas (Stone 1994; Weissel et al. 2006; Forrest et al. 2019).

It is generally inferred that size of the suitable habitat is positively associated with species richness (Conor & McCoy 2001) and is thus included as an environmental factor in the study. The species-area relationship (SAR) is a frequently studied pattern in ecology, describing a tendency of species richness to increase with increasing habitat size (Lomolino 2001). A few studies have found that size of sand and limestone quarry areas is a significant determinant of wild bee species richness (Krauss et al. 2009; Twerd et al. 2019). Additionally, age of the sandy habitat is evaluated as another potentially defining factor of species diversity. The historical effects, such as age of the habitat, on species diversity are scarce and less documented, often based on theoretical studies. As metacommunity theory suggests, local species richness can be affected by length of time since the establishment of a community (Mouquet et al. 2003). Older habitats may host diverse species assemblages with some relict species unlike more recently established habitats.

Furthermore, the study explores the potential role of cleptoparasitic bees as an indicator taxon for bee community as proposed in studies by Sheffield et al. (2013a, 2013b). Cleptoparasitic load (CL) measure is applied to explore differences in some sites of interest. Lastly, this study addresses 75 years of urban development and its impact on sandy habitat from 1942 to present (2017-2019) in the southern part of Uppsala, Sweden.

The study area comprises ten sandy soil sites that are either natural or artificially created. Four of these sand patches have been recently established specifically for sand-nesting insects as habitat compensation in response to urban development. Remaining six sand patches occurred either naturally or have been created artificially for other purposes than conservation (e.g., recreational).

1.2. Background

1.2.1. Wild bees as effective pollinators

Wild bees are a diverse order of pollinators, comprising around 70,000 pollinator species described to date. Although Lepidoptera is more diverse with over 141,000 pollinator species (Ollerton 2021), bees are by far the most effective pollinators (Garibaldi et al. 2013; Wardhaugh 2015). Pollination is a process where pollen is transferred from male anther of a flower to a female part stigma of the same or another individual flower. The resulting fertilization produces seeds and/or fruits. While many bee-pollinated plants can also self-pollinate if not visited by bees, eventually that causes inbreeding depression (Michener 2007). Thus, cross-pollination is most often favoured type of plant reproduction, and bees play large part of it.

Some morphological features account for successful bee-driven pollination (Falk 2015). Many bees have branched body hair with electrostatic charge properties that attract pollen while foraging. Active pollen collecting bees may have a pollen brush ‘scopae’. Some wild bee species exhibit sonication behaviour, the ability to vibrate flight muscles, which aid pollination of certain plant species (King & Buchmann

2003). Moreover, the effectiveness in pollination can also be defined by ‘floral constancy’, the term describing species which have coevolved dependency on single or several plant species (monolectic or oligolectic) (Falk 2015; Ollerton 2017).

1.2.2. Valuable pollinators for humans and natural ecosystems

There are approximately 20,500 bee species recorded globally to date (many not described yet, thus real number is greater), of which around 50 species are domesticated used mostly in agriculture (Potts et al. 2016; Ascher & Pickering 2020). Wild and managed bees are crucial for sustaining most flowering native plant species populations in almost all terrestrial ecosystems (Biesmeijer et al. 2006; Burkle et al. 2013; Lowenstein et al. 2015) as well as flowering crops grown for food production (Garibaldi et al. 2013; Blitzer et al. 2016). Despite the common practice of utilizing managed bees for enhanced pollination of various food crops grown in agricultural landscapes, wild bees contribute substantially to overall crop production, in some cases being irreplaceable by domestic bees (Garibaldi et al. 2011; Garibaldi et al. 2013; Mallinger & Gratton 2014). The diversity of wild bees is largely concurrent with sustainable crop pollination and diversity of flora in general (Kaiser-Bunbury et al. 2010; Carvalheiro et al. 2011). It is undoubtedly difficult, if even possible, to assign a monetary value to any living organism, but if one attempts to estimate the importance of animal-driven pollination for food crops alone, the worth in value approximates of 153 billion Euros annually and is further increasing by year (Gallai et al. 2009; Bauer & Wing 2016). In addition to provisioning human populations with nutritious food, wild bees are valuable for indirect ecosystem service contributions such as pest and disease control as well as soil formation (Matias et al. 2017). Without doubt wild bees are vital components of functioning ecosystems in various landscapes, driving the pollination of most flowering plant species and hence maintaining the biodiversity within natural ecosystems (Ollerton et al. 2011).

1.2.3. Decline of wild bee diversity and abundance

The global collapse of insect pollinators has become one of the most worrisome phenomena and has received a substantial awareness from the public and scientific community (Kevan & Viana 2003; Dirzo et al. 2014; Lever et al. 2014; Rhodes 2018; Zattara & Aizen 2021). Loss of pollination services has direct negative impact on fitness and reproduction of majority flowering plants and hence can have cascading effects within food webs, reducing overall biodiversity (Pauw 2007; Kaiser-Bunburry et al. 2010; Sánchez-Bayo & Wyckhuys 2019; Ramos-Jiliberto et al. 2020). Wild bee decline, both in abundance and species diversity, has been recorded in various parts of the world (Biesmeijer 2006; Williams & Osborne 2009; Cameron et al. 2011; Burkle et al. 2013; Morales et al. 2013). In Sweden alone, a third of wild bee species are threatened and red listed, calling for conservation action (Borgström et al. 2018). Several major key factors that often act in synergy have been identified as driving forces of bee population declines worldwide: (1) loss and degradation of habitat as a result of agricultural practices and urban development; (2) climate change; (3) exposure to pesticides and other pollutants; (4) pests and pathogens; (5) loss of genetic diversity (Potts et al. 2010; Meeus et al. 2018; Mathiasson & Rehan 2020; Soroye et al. 2020). Specialist and rare species, as well as those of higher trophic levels (e.g., cleptoparasitic species) and cavity nesters are particularly vulnerable to the changes in their environment (Biesmeijer et al. 2006).

1.2.4. Ground-nesting bee biology

Virtually all bee species depend on floral food resources of pollen and nectar, and the depth of knowledge regarding the species-specific floral requirements is comparatively well studied. However, wild bee species exhibit significant variation in life-history traits as well as ecological adaptations. This is especially true to nesting biology and differences in nesting substrate preference and requirements among species. Unfortunately, nesting resource requirements for wild bees remain largely understudied compared to bee pollinator foraging ecology, thus research on this topic is particularly encouraged by the scientific community and conservation focused bodies (Antoine & Forrest 2021).

Wild bees have evolved to exploit a range of different substrates for building their nests; 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 a variety of species (Falk 2015). Depending on their nesting requirements, bees can thus be divided into aerial and ground nesters. As name suggests, aerial nesters build their nests above the ground and comprise a quarter of wild bee species. In contrast, ground nesters excavate their own nests in the soil (fossorial), and account for around 70% of species (note: only a fraction of known bee species nesting biology has been described to date) (Cane & Neff 2011; Harmon-Threatt 2020). It is a diverse group of bees that are members of families Andrenidae, Apidae, Melittidae, Oxaeidae, Halictidae, Colletidae, Megachilidae and Anthophoridae. For the purpose of this study, the term ‘ground-nesting bee’ will be referred to all wild bee species that dig their own underground tunnel systems and nests. Hence bumblebees (*Bombus* spp.; Apidae), which often nest below ground but in the pre-existing cavities (such as old rodent burrows), are excluded from the term in this study.

Majority of ground-nesting bees are solitary bees. That means that solitary bee females construct and provision nests for their brood on their own. In contrast, social bees have various degrees of social structure complexity, and eusocial behaviour is a well-defined one. Eusocial queen (fertile female) is assisted by her offspring (female workers) to build, provision and defend the nests. Several ground-nesting *Lasioglossum* and *Halictus* species exhibit primitive eusocial behaviour (Falk 2015). Bumblebees and honeybees have considerably more complex social structures. Some solitary bees, however, can be found nesting in large aggregations. Such non-social communal nesting behaviour has reciprocal benefits such as defence and more efficient nest founding (Danforth et al. 1996).

Ground-nesting bees usually exploit open soil habitats for nesting and generally show preference to areas with minimal or low vegetation, sloped ground and at least some degree of sun exposure (Antoine & Forrest 2021). Soil type and its compaction can also define which fossorial species may choose to build their nests; while a few species prefer compact clay ground for building nests, majority of ground nesters are associated with softer, sandy ground (Potts & Willmer 1997). Female bees excavate tunnels that lead to brood cells with a varying degree of complexity depending on the species. Based on the current knowledge, the depth of nests varies immensely among species, ranging from as shallow as 1 cm to as deep as 530 cm (Cane & Neff 2011). However, many species excavate nests on average at 10-20 cm depth. The mother bee often uses glandular secretions to cover the walls of the brood cells which provides protection against microbial infestation as well as prevents water penetration (Cane 1981; Almeida 2008). Once the brood cells are provisioned with rich food reserves from flower nectar and pollen, bee lays fertilized egg and seals the cell. Depending on species, bee will either continue making new cells, or will excavate new tunnels creating one-celled nests elsewhere (Antoine & Forrest 2021). These fossorial bees spend most of their life underground and undergo several developmental stages from egg to larval and pupal (Cane 1991). Depending on species and other factors such as time of the year and environmental conditions (e.g., temperature), pupa will either proceed to develop into an adult that emerges the same flight season, or will, most often, overwinter and emerge only the following year to complete its life cycle as an adult bee (Falk 2015; Harmon-Threatt 2020; Antoine & Forrest 2021).

1.2.5. Cleptoparasitic bees

Cleptoparasitic bees (also referred to cuckoo bees) are the so-called ‘apex’ of bees’ communities. Cleptoparasites belong to the highest trophic level and thus depend entirely on the presence and abundance of their hosts (Finke & Denno 2004). Cleptoparasitic bees are mainly associated with solitary bees, although some social Halictinae are also known to be hosts (Michener 2007). There are around 2,500 cleptoparasitic bee species described worldwide (Michener 2007). The most diverse groups are represented by subfamily Nomadinae (approx. 800 species in the genus *Nomada*), Halictidae by genus *Sphecodes* and Megachilidae by genus *Coelioxys* (Rozen 2001; Michener 2007). While a few are species-specific, most cuckoo bees parasitise multiple host species (and even from several genera), although in general our current knowledge on parasite-host relationships is inadequate (Falk 2015). So-called blood bees of genus *Sphecodes* are associated mainly with members of genera *Lasioglossum, Halictus* and *Andrena*. Nomad bees (*Nomada* spp.), on the other hand, predominantly attack *Andrena* species, although some are also known to take advantage of bees from genera *Melitta, Lasioglossum, Panurgus* and *Eucera*. (Falk 2015).

Cleptoparasitic bees do not construct nests nor provision their brood. Instead, adult cuckoo female bee invades a nest of a host and oviposits its own egg (Michener 2007). Depending on the species, it may mean entering the nest while it is still being provisioned by a host or destroying the already sealed cell. Likewise, adult females of some species kill host's egg or larva, and in some species it's the cuckoo grub that kills the host's brood (Rozen 2001; Falk 2015). Once hatched from an egg, the invader's larva develops by consuming provisions collected by the host bee.

Some research proposes to recognize life history traits of bees and recommend applying guild profiles (non-taxonomic functional group) as baselines for assessing wild bee communities (Sheffield et al. 2013a; Sheffield et al. 2013b). The vulnerability of cleptoparasitic bees to any shifts in species richness and density of their host communities makes them first to respond. Moreover, the greater species diversity and abundance of cuckoo bees are, the more stable and species rich the wild bee assemblage often is (Sheffield et al. 2013b). Additionally, cleptoparasitic bees are more easily recognizable than most other wild bee guilds (Michener 2007). These factors make cleptoparasitic bee guild a potentially great bioindicator (Pearson 1994), and assessment of cuckoo bees in wild bee communities can provide valuable information on the health of wild bee assemblages in even early stages of habitat disturbances (Sheffield et al. 2013b).

The are several different ways in which cleptoparasitic bees can help to interpret the diversity and state of bee communities as well as habitat quality. For instance, absence of cleptoparasites in the surveyed community might indicate the instability of bee populations and / or that the population established only recently (Calabuig 2000). The presence of cleptoparasites can also hint of the existing host species that have not been sampled in a survey (O'Toole & Ismay 1995). Moreover, the overall species diversity of a community, as well as the quality of the habitat surveyed may be assessed by the cleptoparasitic load (CL) measure (parasite and host ratio) (Archer 1995; Calabuig 2000). It is expected that ca 15-20% of cleptoparasitic bee species constitute stable bee assemblages (Wcislo & Cane 1996; Twerd & Banaszak-Cibicka 2019). High ratio of cleptoparasites indicates stability of the communities and vice versa (Calabuig 2000).

1.2.6. Urbanization and wild bee diversity

Habitat loss and degradation due to agricultural and urban development is considered one of the key factors causing pollinator decline worldwide (Tilman et al. 2001; Potts et al. 2010). Expanding urbanization replaces natural habitats and most of the original ecosystems are locally lost, resulting in drastic deterioration of biodiversity and local extinctions of many native species (McKinney 2002; Seto et al. 2012). Nevertheless, urban environment can sustain a certain degree of biodiversity, especially if it is considered in city planning by creating green spaces and conservation management is in effect (McKinney 2002; Bazelet & Samways 2011; Nilon 2011; Pardee & Philpott 2014; Beninde et al. 2015).

Vegetation in urban environment is often considered a foundation element for a range of ecosystem services that urban population receives; among many is a significant reduction in air and water pollution, flood control, regulation of temperature and improved physical and mental public health (Fuller et al. 2007; Weber et al. 2014; Säumel et al. 2016; Stevenson et al. 2020). Pollinators, in particular wild bees, are essential components in sustaining the biodiversity of trees and flowering plants in these anthropogenic landscapes (Stevenson et al. 2020). Moreover, they are responsible for pollinating various food crops grown within urban agricultural systems and thus contribute to overall food security (Lin et al. 2015; Lowenstein et al. 2015). Additionally, high diversity of urban wild bee populations can act as a potential source of pollinators to surrounding agricultural landscapes (Goulson et al. 2010).

Despite that habitat fragmentation and shrinking habitat have a negative impact on wild bees (Aizen & Feinsinger 1994; Aguilar et al. 2006; Lopez-Uribe et al. 2015), urban wild bee diversity and abundance can be considerably high compared to other human altered landscapes (Beninde et al. 2015; Hall et al. 2017; Theodorou et al. 2020). If the requirements of floral and nesting resources are met, viable and species diverse populations of wild bees can be sustained in urban environments. Naturally, floral resource is a key factor shaping pollinator community structure and population viability (Petanidou & Vokou 1990). However, nesting trait is another strong determinant to which wild bee species are prevailing in urban space (Potts et al. 2005; Potts et al. 2010; Buchholz & Egerer 2020). Aerial nesting species are most often favoured in urban habitats through the so called ‘urban-filtering’, which offers various vertical structures and provide ample of nesting opportunities (Ayers & Rehan 2021). On the other hand, large amounts of impervious surfaces and compressed soils have the opposite effect and are detrimental to ground-nesting species (Threlfall et al. 2015; Quistberg et al. 2016). Negative effect on species diversity and bee health has been observed in various studies (Potts et al. 2010; Neame et al. 2012; Fortel et al. 2014). Researchers stress that negative impact of urbanization on ground-nesting bees has been underestimated (Fitch et al. 2019). Consequently, it is important to consider and assist this group of bees disadvantaged by urban expansion.

1.3. Aims of the study

Regarding the above discussed importance of wild bee diversity to humans and natural ecosystems as well as the challenges these pollinators face, particularly in urban environments, this study aims to produce some insights on nesting preferences of ground-nesting bees. The aim of this study is to evaluate which sandy habitat qualities in an urban environment are reflected by species diversity metrics of ground-nesting wild bees. Moreover, the study explores which environmental factors shape bee communities.

The acquired knowledge can be beneficial for wild bee conservation management and help to increase and/or maintain bee diversity in urban landscapes by optimizing nesting habitat qualities. For instance, the results of age factor can suggest whether older sites are irreplaceable for bees and if creation of new habitats is a valuable conservational practise for urban bee populations. Size of the habitat factor can suggest whether smaller sized sand sites can be sufficient for diverse bee assemblages or if sand patches created in the future should be larger to accommodate diversity. Ground cover factor results may imply whether a certain vegetation management is necessary to maintain nesting habitats. Knowing the preferable sandy soil texture based on sand grain size analysis would allow to choose an appropriate soil material when creating nesting habitats to attract diverse bee communities.

Furthermore, cleptoparasitic bees that entirely depend on ground-nesting bee hosts are evaluated as an indicator taxon. Lastly, the change of sandy habitat availability over 75-year period in the study area is assessed. Hence, the objectives of this study can be represented by following questions:

(1) Is the diversity of ground-nesting and associated cleptoparasitic bees related to any of the studied environmental factors (habitat age and size, sand grain size, ground cover features and soil temperature)?

(2) Does this study support the concept of employing cleptoparasitic bees as an indicator taxon for ground-nesting bee community?

(3) Has the available sandy habitat changed since 1942 in the study area?

(4) What recommendations can be provided to conservation management bodies to promote wild bee species diversity in urban environment?

2. Materials and methods

2.1. The study area

The study has been conducted in Uppsala, Sweden (Fig. 2.1). It is a city ca 70 km north of capital Stockholm. Located in the northern temperate zone and affected by the Gulf Stream, Sweden experiences four seasons with harsh winters (especially the northern parts) and warm summers. The study area comprises approximately 17.62 km^2 (Fig. 2.2) and it has been subjected to an increasing urban development.

Figure 2. 1. Map showing Scandinavian countries and the location of Uppsala (red dot) in Sweden.

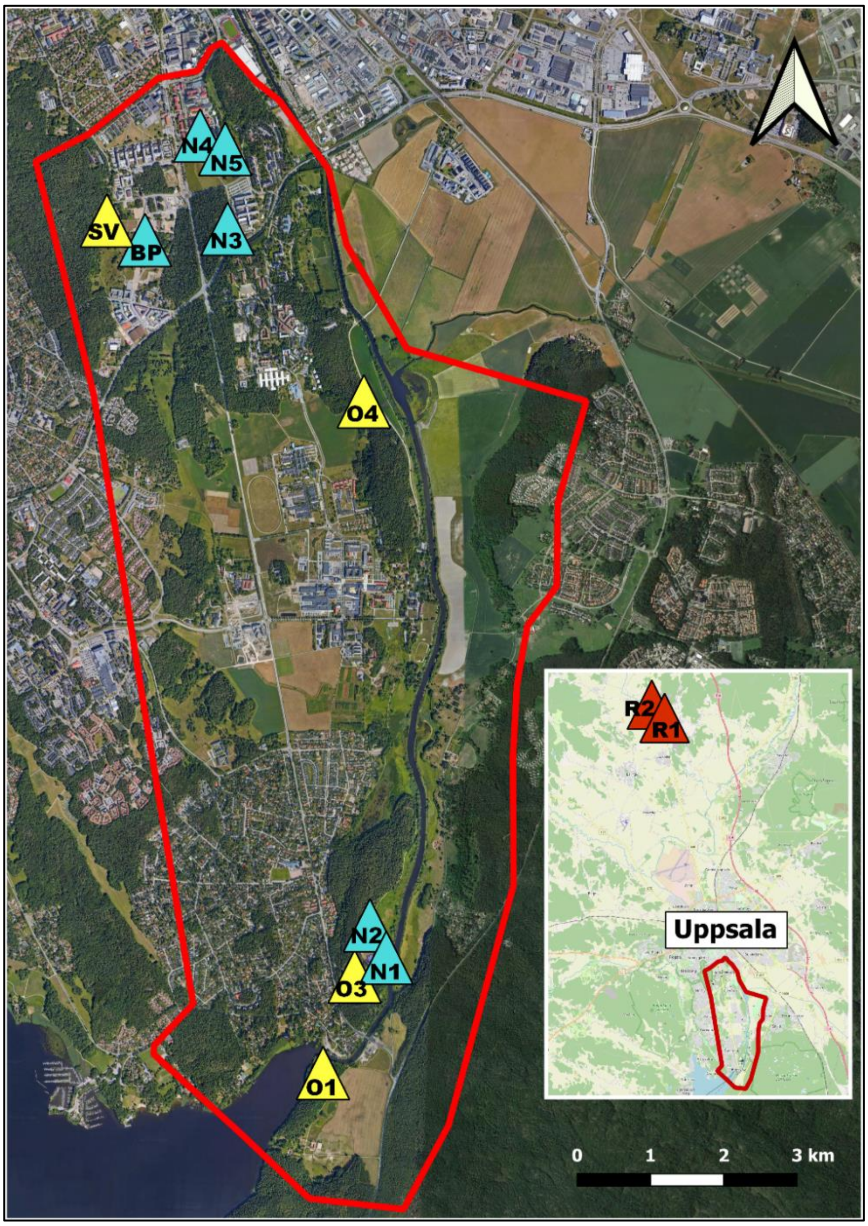

Figure 2. 2. Map showing the study area in the south of Uppsala, Sweden, and the location of two reference sites (red triangles R1 and R2) in the smaller map on the right. Red polygon represents the study area; yellow triangles are 'old' and blue triangles are 'new' sand patches.

2.2. Selection of study sites

Since it was important to determine the age of each sand patch in this study, GIS tools were applied not only to locate sandy areas, but also to determine the approximate age. Aerial photographs from 1942, 1965, 1992 (greyscale analog, scanned and orientated) and 2017 (digital infrared) were used for this purpose. All aerial photographs obtained for the surface analysis were taken in the same month of a year (May) in order to account for conditions of greenery cover that could affect the land surface interpretations (shadows, canopy cover etc.). As guidance for imagery interpretation, soil deposit (jordart, from Jordartskartansgrundlager produced by Geological Survey of Sweden, SGU) was used. 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. These interpretations of historical orthophotos were carried out by Anders Björkén, SLU.

Sites for the inventories were then selected from a map generated by GIS analysis interpretations of the most recent orthophoto (year 2017) using QGIS 2.18.17 program. Because the analysis discovered a very limited number of such potential sand patches, every patch was visited doing ground control inspections and determined whether it is suitable for the study (i.e., if the sandy soil patch was correctly identified by orthophoto interpretations, and if it is still present in spring/summer 2019). Sand patches that were located close to each other (within 100 meters) were regarded as one site. The distance of 100 m was chosen regarding shortest flight distance of various wild bees between nesting and foraging sites (Gathmann & Tscharntke 2002; Zurbuchen 2010; Zurbuchen et al. 2010a, 2010b; Hofmann et al. 2020).

Initially 11 sand patches were selected for the study, but due to recurring trap destruction, one site was excluded from the study, resulting in a total of ten sand patches (Fig. 2.2). Moreover, two additional sites at sand and gravel quarries that are known to be species rich habitats of various ground-nesting bees were chosen as reference sites in the North of Uppsala, approx. ten kilometres from the closest city developments (Fig. 2.2). The main reason for surveying these sites was to have comparable bee species data from sandy soil habitats that are unrelated to urban factors. No environmental variables were measured at reference sites.

Four sand sites sampled in the study were created specifically for soil nesting bees and other insects by municipality and urban developers. In August 2016 three sandy habitats have been created for conservation of the solitary bee *Colletes cunicularius* and its associated cleptoparasite blister beetle (*Apalus bimaculatus*) (Widenfalk et al. 2018). It was the first known attempt in Sweden to translocate the sand as a conservation approach with the aim to move the bees at the larval life-cycle stage.

These sites in text are referred to as 'N3', 'N4' and 'N5' patches. A fourth site, referred further in text as 'BP', was established for general ground-nesting bee diversity preservation purpose in the newly built residence area. It was the most recent sand patch created just before the first bee flight season when bee trapping was carried out in 2019 spring/summer. The sand used for translocation was taken from the nearby sand mound, another study site referred to in text to as 'SV' site (Fig. 2.3). Historically, SV was utilized by former military practises and is known as particularly species rich site of insects associated with sandy habitat, especially bees. The translocation of sand was carried out in December 2018 by moving the frozen blocks of sand. The summarized information of all sand patches with location coordinates is available in the Appendix A.

Figure 2. 3. Sand moved from SV site on the left to the BP site on right.

2.3. Habitat assessment – environmental variables

2.3.1. Size and age of sand patches

GIS tools were used to determine size and age of each sand patch. Total surface area of the sand patches was calculated by considering the terrain inclination using raster calculator in FME (Feature Manipulation Engine). The age of sand patches was categorized as 'new' or 'old' by the aerial photographs from GIS analysis from different years. Sand patches were categorized as 'new' if they were only present in 2017-year ortophoto (and were confirmed during ground control in 2019), but not in 1942 and/or 1965 aerial photographs. Patches were categorized as 'old' if those identified in ortophoto of 2017 were also present in 1942 and/or 1965-year aerial photographs, meaning they were at least 52-77 years old (example in Fig. 2.4). QGIS 2.18.17 program was used for this purpose.

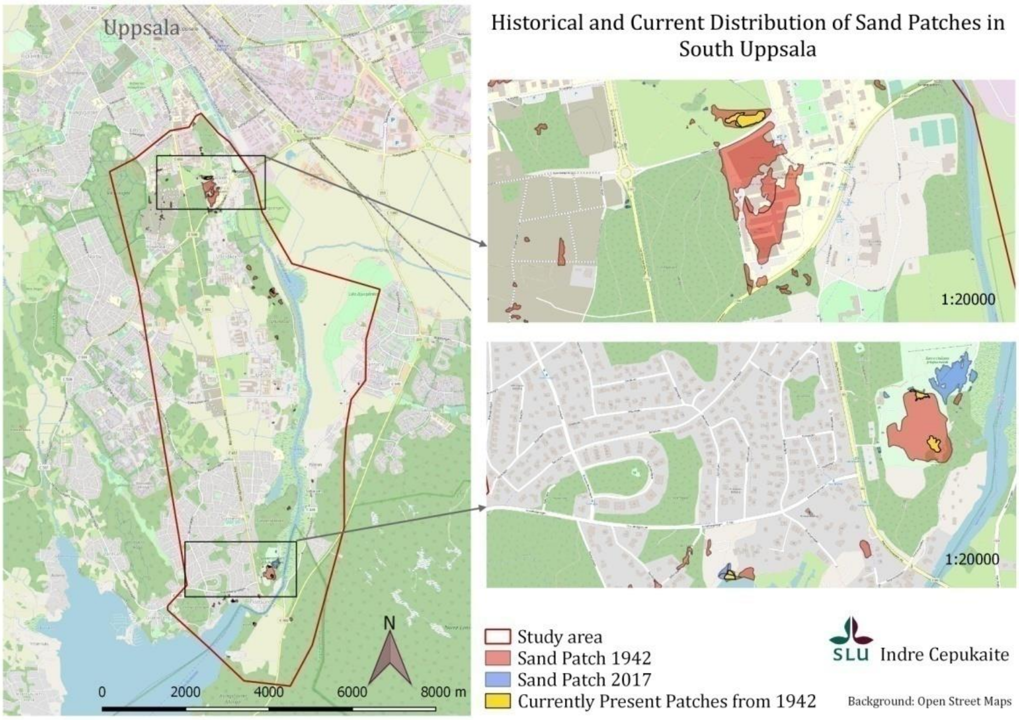

Figure 2. 4. Example of sand patch age categorization in the study area (red line polygon). Red polygons show the existing open sandy soil areas that were present in 1942, the blue polygons the sand patches that were present in 2017, and yellow the sand patches present in 2017 that date back at least to 1942.

2.3.2. Soil sampling and substrate characterization

Average sand grain size at each sand patch was measured and categorized based on four sand category classes (Table 2.2) (Fletcher & Bryan 1912). Two soil samples at each sand patch were collected at the gradient of 0-20 cm depth (n = 20 samples). Soil samples were thoroughly air-dried, and dry sieve analysis was performed. Sieves of different mesh sizes (diameter in mm) that correspond to a specific category of sand grain size based on Wentworth size classification (Wentworth, 1922) (Table 2.1) were used as following: 2 mm, 1 mm, 0.5 mm, 0.25 mm and 0.125 mm.

Table 2. 1. Adapted from Wentworth (1922), the table presents sand categories based on sieve mesh diameter size (mm).

Mesh Size (mm)	Sand Category
> 2.00	Gravel
2.00 - 1.00	Very coarse sand grain
1.00 - 0.5	Coarse sand grain
0.5 - 0.25	Medium sand grain
0.25 - 0.125	Fine sand grain
0.125-0.0625	Very fine sand grain
< 0.0625	Silt and clay particles

For each sample the initial dry weight was noted and then the soil was sieved manually by shaking sieves with using equal effort at each stage (timing to 4 minutes per sieve). After each shaking session dry weigh of soil remaining on the sieve was measured. Due to the lack of equipment, the finest particles of the soil were not measured, thus the final pan measure (the percentage of soil that was sieved through the 0.125 mm sieve) was assumed to contain ‘very fine’ sand, as well as finest components clay and silt.

Both samples taken at each sand patch were averaged to have a single measure. Then each averaged sample, that represents each study sand patch, was categorized based on sand grain size using the classification of soil material scheme (Table 2.2). It was assumed that soil samples contain no more than 20% of silt and clay. The assumption seemed reasonable considering that relatively small fraction of soil was left after sieving soil samples through the finest sieve (0.125 mm).

Table 2. 2. Adapted from Fletcher and Bryan (1912) (United States Bureu of Soils), table represents classification of soil material. This classification is based on assumption that soil contains no more than 20% of silt and clay material.

Sand Category	Requirements
Coarse sand	More than 25% ‘very coarse’ and ‘coarse’ sand, and less than 50% any other lower grade.
Medium sand	More than 25% ‘very coarse’, ‘coarse’ and ‘medium’ sand, and less than 50% ‘fine’ sand.
Fine sand	More than 50% ‘fine’ sand, or less than 25% ‘very coarse’, ‘coarse’ and ‘medium’ sand.
Very fine sand	More than 50% ‘very fine’ sand.

The results acquired from sieving analysis showed that only two types of sand were present at the sand patches: ‘medium’ and ‘coarse’ sand. To support these results, an alternative measure was also done by plotting particle-size distribution graph (percent soil passing versus the sieve mesh size) using Microsoft Excel (Appendix B). To plot the graph, the cumulative mass retained (CMR) (g) on each sieve is calculated first, and then the cumulative percent of soil retained on each sieve is estimated following the equation:

$$\boldsymbol{Cumulative\ \%\ retained = \frac{W(CMR)}{W(Total)} \times 100\%}$$

$W_{(CMR)}$ - weight (g) of soil retained on the particular sieve (CMR);
$W_{(Total)}$ - total weight of the sample.

Following, the cumulative percent of soil passing each sieve is calculated by subtracting the cumulative percent retained from 100% as summarized below:

$$\boldsymbol{Cumulative\ \%\ passing = 100\% - Cumulative\ \%\ retained}$$

2.3.3. Sand patch ground temperature and solar exposure

Ground soil temperature was measured with a digital thermometer (accuracy ± 1°C) by taking three soil temperature measures at each sand patch on four occasions (May 22, June 01, June 23, and August 03, 2019) at three depth levels: 0 cm, 10 cm, and 20 cm. The mean recorded temperature (of the three samples at each sand patch) at 10 cm and 20 cm depth correlated to each other significantly (t = 17.8, df = 46, $p < .001$). Hence, only the temperature measured at 20 cm depth was used for statistical analyses, since the majority of ground nesters excavate their nests relatively deep (Cane & Neff 2011). Furthermore, temporal temperature data collected on four different occasions was visualised in a plot and it was concluded that the correlation between sampling occasions is apparent. Thus, mean temperature of all four measuring occasions was calculated. This resulted in one averaged temperature measure (at 20 cm depth) for each sand patch (n = 10) that was used in further statistical analyses.

Solar exposure was estimated visually at each study site and assigned to one of the three categories: (i) complete exposure (none or close to no significant shading on the sand patch at midday), (ii) semi-exposure (some but not complete shading on the sand patch at midday), and (iii) no exposure (complete or close to complete shading on the sand patch at midday). However, no patches were described by the third category, hence only ‘complete’ and ‘semi’ exposure categories were considered in the study. Estimations were done around midday, the warmest time of the day. Categories reflect the intensity of the direct sunlight each site receives throughout the day by considering the shading from surrounding natural and other structures (trees, buildings etc).

2.3.4. Sand patch ground cover

Sand patch ground cover was estimated using a quadrat sampling method on two occasions throughout the summer coinciding bee trapping sessions (June 05, and July 05). Quadrates (50 x 50 cm) were placed on the sand patches aiming to capture the variation of vegetation and litter cover (leaf and plant dead matter) (Fig. 2.5).

Figure 2. 5. Example of quadrat (50 x 50 cm) sampling at the sand patch. (Photo: F. Ferreira)

The number of sampling plots were related to the area of the patch. Seven quadrates were used at sites < 250 m^2 and 19 quadrates at patches larger than 250 m^2. The percentage of total vegetation and litter ground cover within each quadrat was visually estimated. The percentage of bare ground was further calculated by deducting vegetation and litter percentage from a total 100%. Data collected on both sampling occasions were pooled and averaged in order to have one measure of vegetation cover (%), litter cover (%) and bare ground (%) per each sand patch. The summary of all environmental variables is presented in the table below (Table 2.3).

Table 2. 3. Summary of all the environmental variables.

Site ID	**Sand type**	**Patch age**	**Solar exposure**	**Litter cover (%)**	**Bare ground (%)**	**Ground temp. (°C)**	**Patch size (raw/log) (m^2)**
N1	Coarse	New	Complete	2.43	86.30	18.83	7816.6 / 3.89
N2	Coarse	New	Complete	2.92	83.87	18.00	754.86 / 2.88
N3	Medium	New	Semi	7.71	59.00	15.95	32 / 1.51
N4	Medium	New	Complete	4.21	64.79	17.55	68.04 / 1.83
N5	Medium	New	Complete	4.79	52.29	16.93	72.02 / 1.86
BP	Medium	New	Complete	1.00	88.75	17.05	561.03 / 2.75
O1	Coarse	Old	Semi	7.86	90.57	14.83	232.09 / 2.37
O3	Coarse	Old	Complete	1.58	86.62	17.00	2506.79 / 3.40
O4	Coarse	Old	Semi	13.03	81.61	15.93	1438.93 / 3.16
SV	Medium	Old	Semi	3.24	84.09	18.00	1637.72 / 3.21

2.4. Wild bee trapping and species identification

Wild bee species data was collected using colour pan traps. Coloured bowls (usually yellow and white, sometimes also blue) filled with water are successfully used for catching insects, particularly members of Hymenoptera (Campbel & Hanula 2007; Nielsen et al. 2011).

For this study, pan traps were made from yellow and white plastic buckets which were cut to approx. 11 cm height and were 22.5 cm in diameter (approx. volume of 4,160 ml). Traps were filled with two thirds of water and mixed with a drop of fragrance- and colour-free washing detergent to reduce the surface tension. Two sets of pan traps were placed at each site (a 'set' here means one yellow and one white pan). The same number of traps at each sand patch was used despite the extreme patch size variation (Fahrig 2013).

Pan traps were placed in the vegetation on or in a proximity to the selected sand patches (within 10 m), placing them near dead wood, small slopes or other natural structures if available (Fig. 2.6). Yellow and white pan traps were deployed approx. 1-2 meters apart, setting each set of traps as far from each other within the study patch area as judged reasonable.

Figure 2. 6. A set of pan traps placed directly at the sand patch (left) and at the understory at the nearby sand patch (right). (Photo: F. Ferreira)

To capture the seasonal variation, trapping was carried out on four different occasions during late spring and following summer months (May 21-23; May 30-June 01; June 21-23; August 01-03, year 2019). Pan trapping was carried out on dry and sunny days with preferably low winds. Traps were active between 48 and 52 hours. To have all traps active as similar length of time as possible they were collected in the same order as they were set. In the field, insect samples were collected to tubes with ethanol 75% solution. Shortly after sample collection, all bee specimens were dried and pinned for later species identification.

All bee samples, except for the bumblebees (*Bombus* spp.) which were excluded from this study due to the differences in nesting ecology, were identified to species level. Main source for species identification used was ‘Field Guide to the Bees of Great Britain & Ireland’ (Falk 2015), as well as artportalen.se website which offers up to date information on majority of species occurrences in Sweden. Specimens that were difficult to identify were verified by the professor Anders Nilsson, Uppsala University. Lastly, each bee species was assigned to its nesting guild (ground and aerial nesting bees) based on wild bee species life history information presented in two literature sources (Falk 2015; Westrich 2018).

2.5. Data analyses

2.5.1. Species diversity measures

It is generally advised to report at least several diversity measures in studies that dwell on biodiversity subjects (Heino et al. 2008; Morris et al. 2014). In the present study I have used: species richness (S), Shannon-Wiener (H) and Gini-Simpson’s (1-D) diversity indices. Only ground nesting and associated cleptoparasitic bees’ data were used. Bees caught on all four trapping occasions at each sand patch were pooled together to have a single species abundance data per sand patch. Calculations were done with Microsoft Excel program.

Despite the popularity of these diversity indices in the field of community ecology, comparing diversities between different communities is often a problematic practice as they are measures of uncertainty rather than true diversities *per se* (Jost 2006, 2007, 2009). Major issue is that these indices have strong non-linearity properties. To overcome this, Shannon and Gini-Simpson can be transformed into effective number of species (ENS), also known as Hill numbers, which is the number of equally abundant species necessary to produce the same value of a diversity measure. Conversion allows diversity to be measured in units of number of species irrespectively on which index it is based on, thus comparable even across different metrics. This measure can be derived from any diversity index by a simple conversion and is advised to be presented in the studies of ecological diversity (Morris et al. 2014). However, caution must be taken when interpreting ENS just like with any diversity indices (Cao & Hawkins 2019). For the present study of ground-nesting bee diversity, Shannon and Gini-Simpson indices were converted to ENS and these two measures, together with species richness, were used in the statistical analyses (Table 2.4).

Table 2. 4. Formulas of diversity indices and their conversion to true diversities (ENS).

Index	**Formula**	**Conversion to ENS**
Shannon-Wiener (H)	$x \equiv -\sum_{i=1}^{S} p_i \ln p_i$	e^H
Gini-Simpson (1-D)	$x \equiv 1-\sum_{i=1}^{S} p_i^2$	1/x

S – species richness (number of species);

p_i – relative abundance of species i;

e – exponential of Shannon-Wiener.

In order 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. Species data collected at reference sites were not included for the rarefaction. Diversity metric calculations and conversions were done with Microsoft Excel, and rarefaction was generated with RStudio program.

2.5.2. Analysis of environmental variables

Generalized linear models (GLMs) were performed to analyse the associations between species diversity measures (response variables) and environmental (explanatory) variables. This was done with RStudio program.

Some explanatory variables were excluded from the analyses to avoid problems with multicollinearity and overfitting the model. The vegetation cover was excluded from the analyses since it showed strong correlation with bare ground (%) ($t = -7.77$, $df = 10$, $p < .001$). The measure of bare ground was chosen because it is commonly applied as an environmental variable when studying ground nesting bees (Potts et al. 2005; Grundel et al. 2010). Likewise, solar exposure was excluded as it nearly significantly correlated with ground temperature ($t = 2.15$, $df = 8$, $p = 0.06$). Sand patches with full sun exposure had higher ground temperature than patches with semi-exposure.

Finally, six environmental variables were chosen for the GLM models; four continuous: sand patch size (log-transformed, m^2), bare ground (%), litter cover (%), soil temperature (at 20 cm depth) (°C), and two categorical (both binary): sand patch age (‘new’, ‘old’), sand grain size (‘medium’, ‘coarse’) (Table 2.3). Variables were visually (Q-Q plots) and statistically (Shapiro-Wilk test) inspected for normal data distribution. Gaussian (= normal) distribution was assumed in the GLMs. Explanatory variable selection was made both by forward selection and backward elimination. Best set of explanatory variables that fit the GLMs were selected based on the lowest AIC (Akaike Information Criterion) values.

2.5.3. Wild bee species composition and environmental variables

Unimodal ordination analyses were performed to explore wild bee species composition and community’s response to the environmental variables. Singleton species were eliminated from the dataset resulting in total of 27 species for the analyses. First, unconstrained correspondence analysis (CA) was carried out to visualise species composition and sand patch relations to each other. Following, constrained (canonical) correspondence analysis (CCA) was performed to analyse which environmental variables shape the wild bee community. Forward stepwise selection was carried out to select the environmental variables for the CCA model. In total six environmental variables (sand patch size (log-transformed, m^2), bare ground (%), litter cover (%), soil temperature (at 20 cm depth) (°C), sand grain size (‘medium’, ‘coarse’), and age of the sand patch (‘new’, ‘old’)) were used in forward selection. Whether environmental variables and canonical axes (one and two) could explain a significant amount of variation ($p < .05$) was tested by Monte Carlo permutation tests (499 permutations). Two biplots for CA (species- and sites-oriented) (Appendix C) and a triplot (species-oriented) for CCA were plotted (Fig. 3.7).

2.5.4. Cleptoparasitic bees as indicator taxon

A non-parametric Spearman’s rank-order correlation test was performed to test whether cleptoparasitic bee species richness can predict the ground-nesting bee species richness. Correlation test was done between species richness of ground-nesting bees and species richness of only cleptoparasitic bees. Moreover, cleptoparasitic load (CL), which is a parasite and host ratio as described by Archer (1995), was calculated for each sand patch. It was used to assess the bee community in the sand patches specifically created for insects, as well as the old SV site from which the sand was translocated and used to establish a nesting habitat for bees in site BP.

2.5.5. Temporal change of sandy soil availability

To assess the 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 in order to have one value (in m^2) per each time period. Additionally, an estimate for year 2019 has been made based on ground control results, which slightly readjusted the estimation acquired from GIS analysis of year 2017. Patches that turned out to be falsely identified as sand by GIS analysis (ca. 246 m^2), unsuitable for ground-nesting insects (volleyball court, ca. 134 m^2) or already gone due to urbanization by year 2019 (ca. 1,222 m^2) were subtracted from the total sand area estimate of GIS analysed orthophoto of year 2017 (ca. 16,884 m^2). Additionally, a new sand patch (Biparken, ca. 522 m^2) was added to the total value of sand area. The total percentage of the sand area in each time period was estimated.

3. Results

3.1. Wild bee species and diversity

A total of 665 bee individuals were collected: 44 domestic honeybees (*Apis mellifera*), 107 bumblebees (*Bombus* spp.), and 520 other wild bees. The latter constituted of 57 species, out of which 34 species are ground-nesting bees (358 individuals), including 7 species of exclusively sand-nesting bees (46 individuals), and 9 species of associated cleptoparasitic bees (100 individuals). The most numerous ground-nesting bee species are *Lasioglossum morio* (80 individuals), *L. semilucens* (48 individuals), *L. leucopus* (38 individuals) as well as cleptoparasitic bee *Nomada lathburiana* (39 individuals).

Out of 43 bee species (ground-nesting and associated cleptoparasitic bees), three species (*Andrena bicolor*, *A. subopaca* and *Dasypoda hirtipes*) were only recorded in the reference sites. Therefore, the total number of species used for analyses was 40, out of which 29% are associated cleptoparasites. In total 12 species occurred as singletons accounting for 30% of species, and one species occurred in only one site (*N. flavoguttata*). The individual-based rarefaction curve has only slightly begun to flatten (Fig. 3.2).

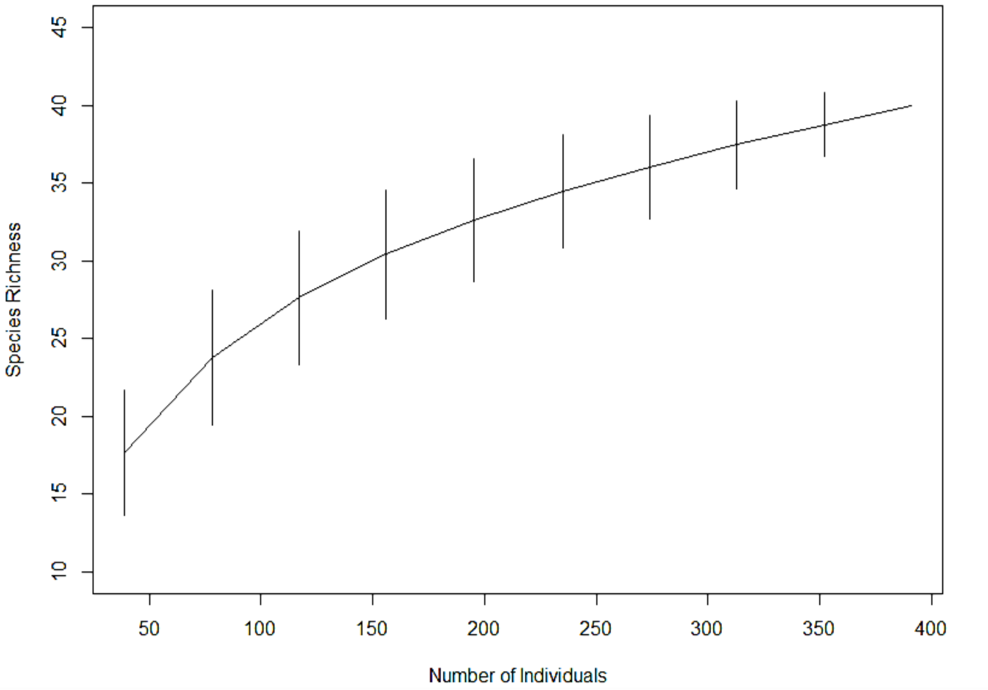

Figure 3. 1. Individual-based rarefaction curve of species richness by the number of individuals collected in all the samples (except reference sites). Bars represent 95% confidence intervals from standard deviation (standard effort of the estimate).

The sand patch N3 had the highest species richness (S = 25) (Table 3.1), and N5 was the most species diverse patch (H = 2.619, 1-D = 0.911). In contrast, the lowest species richness and diversity was found in the sand patch O4 (S = 2, H = 0.637, 1-D = 0.444). For the full collected bee species list and summary see Appendix D.

Table 3. 1. 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 and the least species rich and diverse sites are colored in grey.

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

3.2. Diversity and environmental variables

Sand grain size, size of the sand patch and litter cover were the variables that significantly explained diversity values in GLMs (Table 3.2). However, which environmental variable explained what diversity metrics varied depending on diversity metric itself. Moreover, both GLMs with and without cleptoparasitic bees in the dataset also provided somewhat different results (Table 3.2).

Table 3. 2. Condensed results from GLM based on full wild bee dataset and data without cleptoparasitic bees. Table shows 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. P*-value is provided.*

Dataset in GLM	**Species richness**		**Shannon ENS**		**Simpson ENS**	
	sig. variables	*p-value*	*sig. variables*	*p-value*	*sig. variables*	*p-value*
Full dataset	sand	.014	size	.022	size	.009
			litter	.017	litter	.008
Without cleptoparasitic bees	size	.007	size	< .001	size	.002
			litter	.011		

Sand grain size significantly affected species richness in GLM with dataset of both ground-nesting and associated cleptoparasitic bees (Table 3.2). Species richness tends to be higher in a 'medium' type of sand (Fig. 3.3). Size of the sand patch and litter cover were both negatively associated with Shannon ENS and Simpson ENS (Fig 3.4).

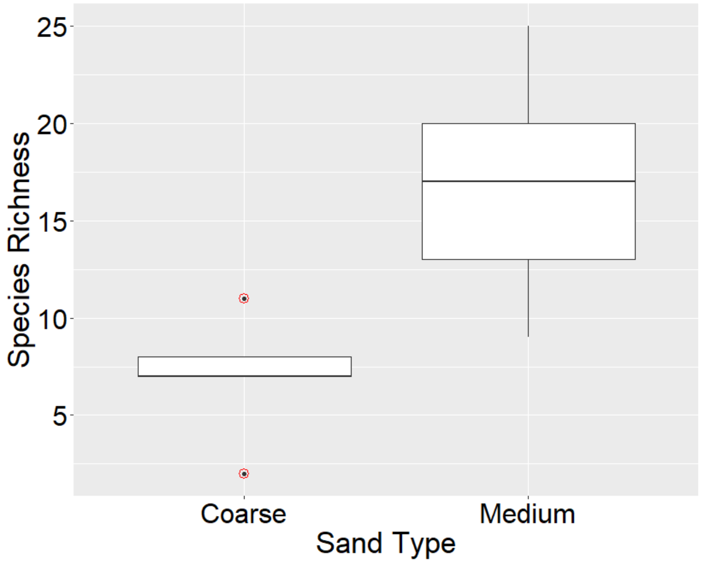

Figure 3. 2. Box and whisker plots above illustrate distribution of species richness (left) and Shannon ENS (right) values among sites with 'coarse' and 'medium' type of sand. Lower and upper

whiskers show the spread of the values, red circles represent possible outliers. Produced with dataset of both ground-nesting and associated cleptoparasitic bees.

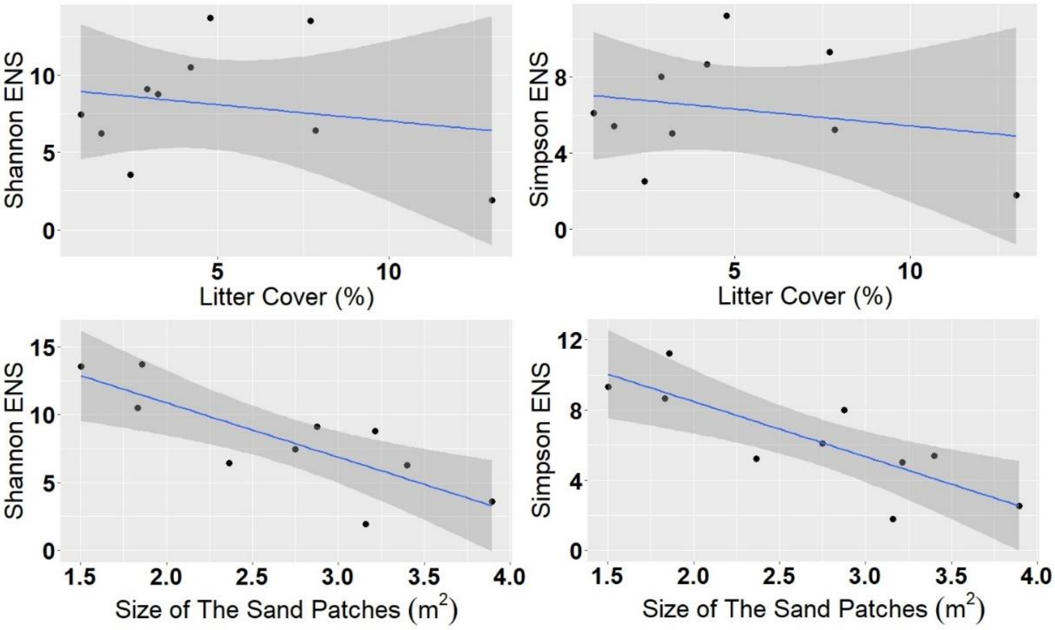

Figure 3. 3. Distribution of litter cover (%) (top) and size of the sand patches (logged, m^2) (bottom) values plotted against Shannon ENS and Simpson ENS values. Darker grey area represents 95% confidence interval. Produced with dataset of both ground-nesting and associated cleptoparasitic bees.

When cleptoparasitic bees were excluded from the analysis, only size of the sand patch and litter cover remained significant (Table 3.2). Size of the sand patch had negative association with species richness, Shannon ENS and Simpson ENS (Table 3.2, Fig. 3.5). Litter cover was negatively associated with Shannon ENS (Fig. 3.5). More detailed results from all GLMs are presented in Appendix E.

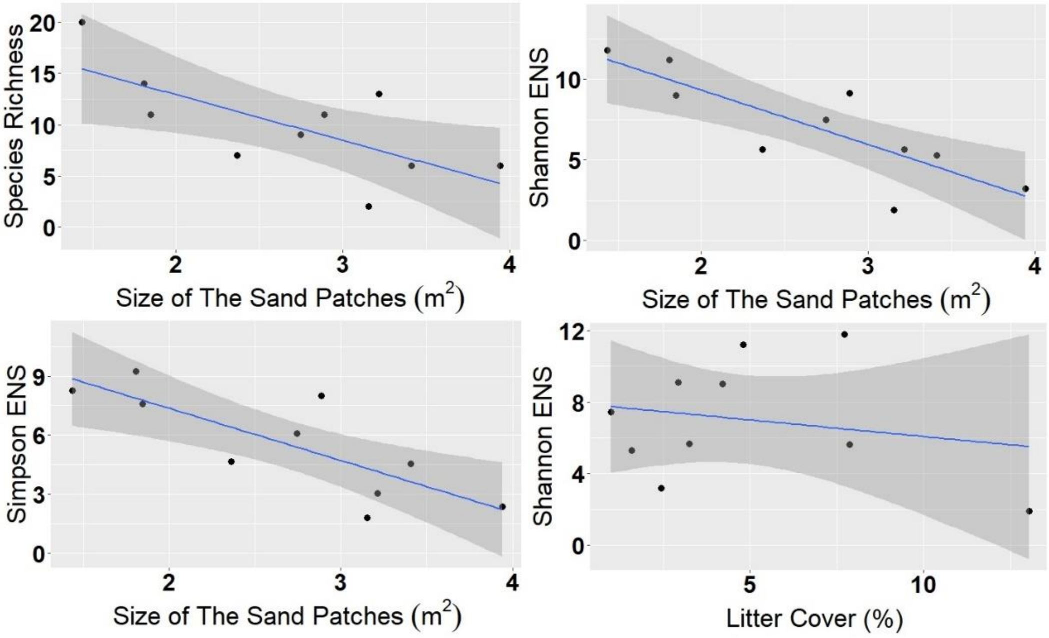

Figure 3. 4. Distribution of size of the sand patches (logged, m^2) plotted against species richness, Shannon ENS and Simpson ENS values (top and bottom left) and litter cover (%) plotted against Shannon ENS values (bottom right). Darker grey area represents 95% confidence interval. Data with excluded cleptoparasitic bees.

3.3. Wild bee species composition and environmental variables

Forward selection in the CCA selected three explaining variables: sand grain size, bare ground, and litter cover. Monte Carlo permutation tests produced following *p*-values: model *p*=.002; CCA axis one *p*=.006 and CCA axis two *p*=.014; sand grain size *p*=.002, litter cover *p*=.004, bare ground *p*=.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 suggested some trends of species alignment along selected environmental variables (Fig. 3.7). Not many species cluster near ‘coarse’ type of sand, while most species cluster towards ‘medium’ type of sand. A range of species seem to associate with litter coverage, and just a few species are more associated with bare ground.

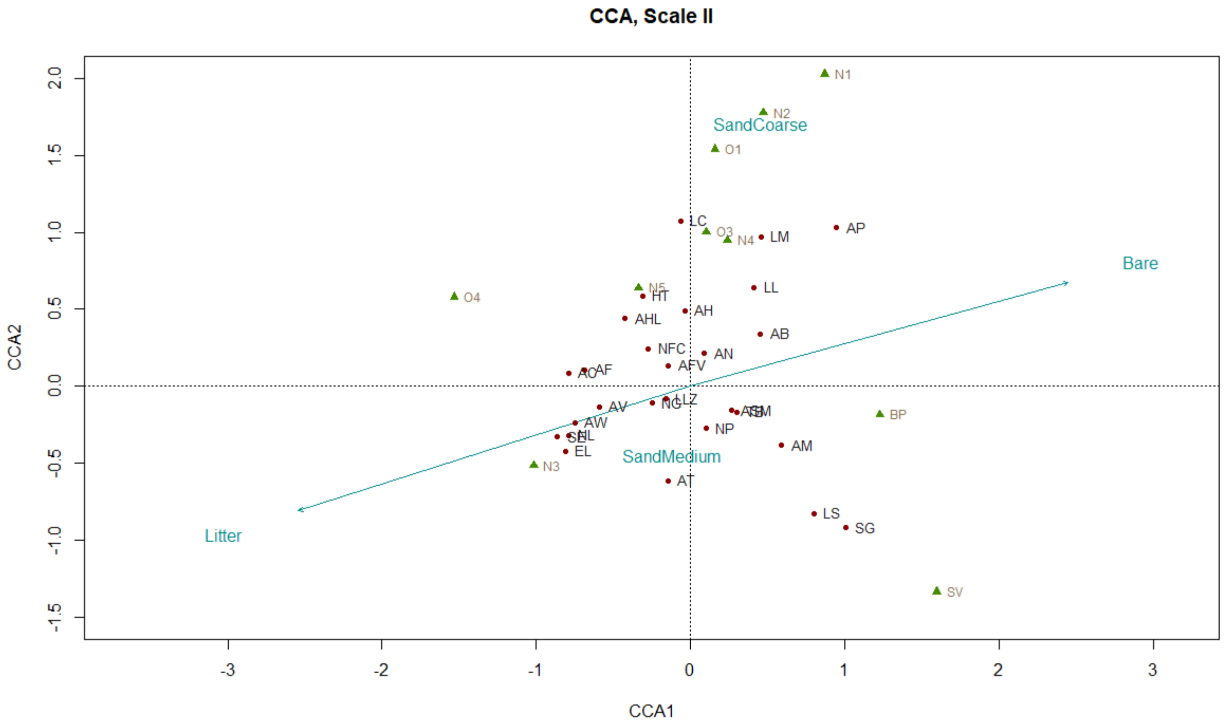

Figure 3. 5. CCA triplot of wild bee species composition plotted with species-oriented scaling (II), showing axes 1 and 2; sites marked as green triangular shapes and species as red circles. Abbreviated IDs of both sites and species are located on the right side of the marks. Environmental variables explaining the variance in species composition - sand ('coarse' and 'medium'), litter cover (%) and bare ground (%) are also presented in the plot; litter cover and bare ground are presented with arrows, which lengths represent strength, and location of species to the arrows shows the strength of association. As 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. Full species names and sites of abbreviated IDs in the graph can be found in Appendix F and A, respectively

3.4. Cleptoparasitic bees as indicator taxon

There was a nearly significant positive correlation of species richness between ground-nesting and cleptoparasitic bees (Fig. 3.6) (Spearman's rank correlation; S = 125.07, *p* = .057). Cleptoparasitic load varied between 0-36%, indicating quite an extreme range of values between the sand patches (Table 3.3).

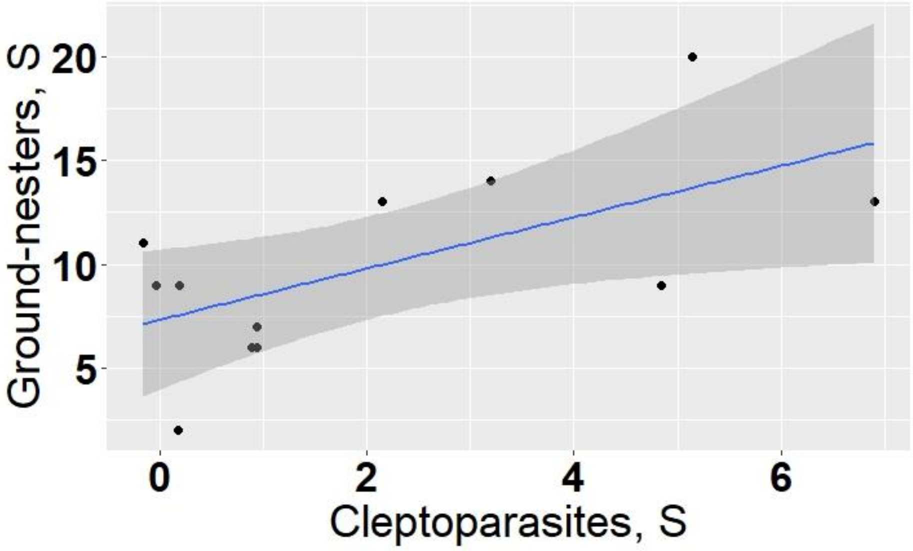

Figure 3. 6. Correlation of cleptoparasitic and ground-nesting wild bee species richness (S) in ten study sites and two reference sites (total n=12). Darker grey area represent 95% confidence interval.

Table 3. 3. A summary table of ground-nesting (hosts - H) and cleptoparasitic bee (C) species richness at each study site, with a final column presenting the cleptoparasitic load CL (percentage ratio).

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

3.5. Temporal change of sandy soil availability

Open sandy soil has declined substantially over time in the study area (Fig. 3.1). The present sandy habitat (mean value of 2017 GIS analysis estimate and readjusted estimate of 2019) estimates to only 14.8% of the total area that was present in 1942.

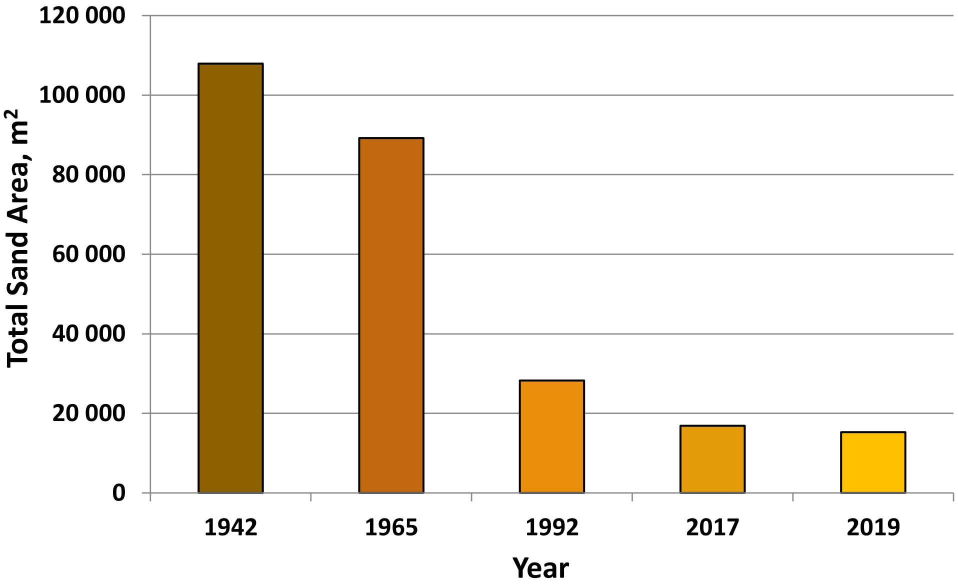

Figure 3. 7. Overall temporal change (1942-2019) of open sandy soil availability in the study area (m^2), Southern Uppsala, Sweden.

4. Discussion

The results suggest that sand grain size, as well as size of the sand patch and litter cover were significant factors affecting the diversity of bees. Interestingly, the size of the sand patch had an opposite relation to diversity than was expected, suggesting a negative trend between the variables. Sand grain size, litter cover and bare ground affected species composition of the bee community as revealed by CCA. Moreover, current study could not confidently support the role of cleptoparasitic bees as an indicator taxon. Cleptoparasitic load measure was used to assess differences between some sand patches of interest. This study also revealed a drastic loss of sandy habitat in the study area due to urbanization. Furthermore, the results also provide some guidance for conservation management of wild bees in the urban landscape when diversity is a fundamental focus.

It is important to consider that following interpretations were made on results derived from potentially insufficient data. Rarefaction curve has only slightly begun to flatten (Fig. 3.2). It indicates that further sampling would have increased number of species discovered, especially more rare species. Likewise, large percentage of singleton species (30%) indicate that sites were not sufficiently sampled based on recommended less than 21% (Lopez et al. 2012). Nonetheless, reference sites showed similar diversity as at urban sites (Table 3.1), and communities were similar with only three out of 43 species found at reference sites, suggesting that urban sites were representative in terms of species diversity.

4.1. Diversity and environmental factors

4.1.1. Sand grain size

One of the three significant variables affecting the diversity of ground-nesting bees as revealed by GLM and CCA analyses is sand grain size. Species richness was notably higher in patches with ‘medium’ than in those with ‘coarse’ grain sand (Fig. 3.3). Moreover, the analyses of species composition showed that many species were associated with ‘medium’ sand and no species closely associated with ‘coarse’ sand (Fig. 3.7).

Higher species richness in a ‘medium’ compared to ‘coarse’ sand is not surprising since many ground-nesting bee species are associated with softer sandy soil (Cane 1991; Potts & Willmer 1997; Harmon-Threatt 2020). It is possible that preference for ‘medium’ over ‘coarse’ sand by many species simply is that excavating in such soils is more time and energy efficient, as well as less abrasive to bee mandibles and wings (Potts & Willmer 1997).

Secondly, moisture levels in the soil are critical for developing brood. Many species even create a hydrophobic membrane on the inside walls of the brood cells by applying Dufour’s gland secretions (Duffield et al. 1982; Cane & Carlson 1984). This both helps to maintain moisture homeostasis within the nest cells and offers protection against water entering the cell from the surrounding environment (May 1972; Roubik & Michener 1980). Importantly, it seems to be effective over a wide range of edaphic and climatic conditions (Cane 1991). Moreover, moisture is a necessary dietary component of weight gain in bee larvae (May 1972). Cane & Love (2021) found that larval provisions of nectar have hygroscopic properties and absorb water vapour from the surrounding soil which are necessary for brood’s diet and development.

The rate of moisture transportation (or water retention) is determined by particle size distribution of the soil. To put it simply, the greater proportion of larger sized particles constitutes the soil, the faster drainage of the water. For instance, coarse sand has a rapid, while clay, sandy silt a slow rate of water permeability (O’Green 2013). Sandy soil in general has a quick water drainage, although factors such as organic matter, sand, silt and clay ratio affect the drainage (O’Green 2013; Schaetzl 2013). Unfortunately, the lack of consideration to true ratio of sand to silt to clay in this study does not allow to determine accurate soil’s capacity to conduct and hold water in the studied sites. Nevertheless, based on crude sand grain size categorization, one can still predict that ‘coarse’ grade sand should provide faster water conduction than ‘medium’ sand. Water drainage is important to reduce risks of waterlogging nest cells, as well as excess moisture that can cause deadly fungal infections and spoil food provisions (Stephen 1965; Ordway 1984; Packer & Knerer 1986; Potts & Willmer 1997). However, fast water drainage means that soil dries out quickly, potentially causing brood desiccation (Potts & Willmer 1997). Thus, while ‘medium’ grade sand still provides good water drainage, it also maintains necessary humidity for the developing brood in the soil at better balance than the ‘coarse’ grade sand. Sandy soil can thus be considered a suitable nesting habitat for many species if it is neither too moist nor too dry (Potts & Willmer, 1997; Tsiolis 2018).

None of the study sites had other grades of sand than ‘coarse’ and ‘medium’ (as defined in Table 2.2). Therefore, one can only presume what nesting preferences would have been revealed if there was a complete graded range of sandy soil textures available to compare with. In general, extremely sandy soils are not attractive to many species as loose sand cannot support architectural integrity of a nest, especially if nesting in larger aggregations (Antoine & Forrest 2021). Various studies have discovered clear preferences of ground-nesting bees initiating nests in sandy soil of certain sand, silt and clay proportions which keep architecture stable enough even when dry or disturbed (Cane 1991; Potts & Willmer 1997; López-Uribe et al. 2015; Harmon-Threatt 2020). For instance, while some species are more associated with coarser soils, others show nesting preferences for loams of sandy clay or silt loams (Cane 1991). And while the extent to which soil texture determines nesting site selection for many bee species is still unclear (Fortel et al. 2016), the creation of additional nesting habitats with 'medium' grade sand in urban environment is likely to benefit the diversity of bees. It is, however, important to consider that a variety of habitats can benefit a greater range of species if those that thrive in a narrower environmental optimum are also considered. Often these are specialist species that are the most vulnerable to habitat loss.

Interestingly, sand grain size was not an important variable when cleptoparasitic bees were excluded from the analyses. The simple reason of this result can be that sample size of the dataset was significantly reduced. Even though ground-nesting and cleptoparasitic bees have obvious life-history trait differences, they are closely coevolved and the diversity of cleptoparasitic bees is tightly associated with the diversity and abundance of host species (Finke & Denno 2004). And although cleptoparasites do not choose nesting soil texture *per se*, the choice is made by default of their associated hosts. Thus, one can conclude that it is indeed sensible to consider cleptoparasitic bees in the dataset together with ground-nesting bees when assessing bee diversity.

4.1.2. Litter cover

Both species diversity and composition were affected by litter cover. Shannon ENS and Simpson ENS had a negative association with litter cover (Fig. 3.4). Dataset without cleptoparasitic bees revealed similar result, although only Shannon ENS was explained by litter cover (Fig. 3.5). Litter cover was also a significant explanatory variable in CCA analysis. However, majority of species were located not far from graph's origin, indicating that associations were weak (Fig. 3.7).

The studies investigating litter cover and bee nesting habitats are scarce, and conclusions are generally made from species-specific studies. Nests covered by the fallen leaves may provide some protection against parasites than those exposed on the bare ground, as the study of *Halictus ligatus* bees by Packer and Knerer (1986) suggests. Moreover, dead vegetation covering the soil may help to regulate soil temperatures (Antoine & Forrest 2021). On the other hand, Breed (1975) noted that ground-nesting *Lasioglossum rohweri* bees have not been observed nesting in the sites with dead leaf and plant matter covering the soil even when nearby areas were occupied in large aggregations. One can assume that finding nest entrances for a bee might be difficult on such sites covered with vegetation and leaf litter. At least some ground-nesting bees use learned distances of visual landmark cues to locate their nests (Brünnert et al. 1994). This might be challenging if the ground is largely covered by dry leaves, which may also shuffle around on windy days. Moreover, if the ground is heavily covered by dead leaf and vegetation matter, it can simply obstruct discovering ground that would be attractive nesting habitat otherwise. In this study, however, litter cover was not particularly extensive, ranging between the total ground cover of 1.00-13.03 % (Table 2.3).

Despite the negative association of litter cover and diversity revealed in GLM analysis, some bee species were associated with litter cover even though the associations were likely week due to closeness to graph's origin (Fig. 3.7). Hence, one can conclude that while greater litter cover is not particularly attractive factor to many ground-nesting bees, it may benefit or simply do not affect other species. However, the real benefits/drawbacks of such relatively low percentage of litter cover in this study are questionable. Experimental studies are needed to better understand how leaf and vegetation litter affects nesting choices of a wider range ground-nesting bees.

4.1.3. Size of a sand patch

This study suggests that smaller sand patches are associated with a greater bee diversity and increasing size shows a decreasing trend of diversity (Fig. 3.4, 3.5). The results are opposite to expectations based on the ecological species-area relationship (SAR) pattern where species diversity tends to increase with increasing habitat size (Lomolino 2001). SAR, as defined in Connor & McCoy paper (2001), is 'the dependence of the number of species in a sample region on the area or size of the region'. The concept is explained by several biological mechanisms that are not mutually exclusive and may act independently or together (Connor & McCoy 1979): (1) habitat diversity hypothesis suggests that greater species richness in larger areas is due to the fact that larger areas have a greater variety of habitats than smaller areas (Williams 1964); (2) the area per se hypothesis proposes that stochastic extinction events are less likely to occur in larger areas, hence species have a greater chance of persisting than in smaller habitats where local extinctions are more probable (Simberloff 1976), and (3) passive sampling hypothesis predicts that sample size increases in larger areas, hence larger sample size ultimately represents more species than sample obtained in the smaller area (Rosenzweig 1996). There are also other concepts such as edge effects and resource concentration hypothesis attempting to explain SAR across various taxa (Connor & McCoy 2001).

The SAR pattern, studied across various taxonomic groups of organisms, has also been supported by several wild bee studies. Krauss et al. (2009) have assessed wild bee communities in 24 limestone quarries of various sizes. They found that bee species diversity could be predicted by habitat size, with larger quarries representing more diverse bee communities. Likewise, Twerd et al. (2019) have found that the size of sand quarry was a primary explanation of wild bee species richness and abundance showing a positive correlation. Although present study did not carry out analysis to specifically test SAR, the negative correlation of sand patch size and species diversity suggests that results of this study does not support SAR.

Since sandy soil is a scarce resource for ground-nesting bees, smaller patches might be more densely occupied and crowded while bees nesting at larger areas are more spread out. In the study area the sizes of sand patches varied substantially, with smallest measuring 32 m^2 and largest 7816.6 m^2 of total area (Table 2.3). Thus, reasonable explanation could be that statistical error occurred from the unbalanced sampling effort. The same number of pan traps was deployed at each sand patch irrespective to its size. Although this type of sampling is considered reasonable (Fahrig 2013), due to the nature of species distribution in large vs. small areas the undersampling of such large patches might have occurred. Since the power of statistical tests essentially depends on sample size, type I statistical error might have occurred suggesting the negative correlation when in fact it might be a positive (or none) correlation (Nakagawa & Cuthill 2007; Knudson & Lindsey 2014).

It is also possible, that pan trap placement has affected the bee catch in the traps. For instance, placement of the pan traps in the sites where floral resources are abundant can result in a much lower catchment compared to the areas where flowering vegetation is scarce (Westerberg et al. 2021). In the case of this study, one of the largest sites ‘O3’ was an open public area and trap placement on the sandy patch for targeting ground-nesting bee catchment was impossible. Therefore, traps were placed close by in the particularly flower abundant parts of the area to hide the them from public since trap destruction was a reoccurring issue. That might have significantly reduced chances of capturing ground-nesting and cleptoparasitic bees and somewhat affected the results.

Additionally, as correlation not equal to causation, other underlaying factors could have influenced such questionable results. Even though the multicollinearity issue was considered prior statistical analyses by reducing a number of independent variables, other factors such as nature of sandy habitats could have potentially correlated with patch size. For instance, majority of large areas were either naturally occurring, or created for recreational purposes, without having in mind soil nesting insects. In contrast, all four sand patches that were purposedly created to assist soil nesting bees were mostly smallest areas. Hence, considering these dubious diversity and habitat size results one should be particularly cautious when interpreting or relying on these results.

Despite the reasons behind these results, it is nevertheless encouraging to discover that even small sand patches can host relatively diverse wild bee communities. In the urban areas, the creation of additional numerous but small habitats might be a feasible conservational approach. However, it is important to consider that such small habitats are more prone to stochastic events that might cause local bee extinctions (Losos & Ricklefs 2010). Also, due to high edge-to-area rations, the regrowth of vegetation might occur relatively rapid (Haddad et al. 2015), thus the continuous management to sustain such small habitats would be necessary.

4.1.4. Bare soil

Although bare soil did not explain variation of diversity metrics in GML analyses, the CCA suggested that bare soil is a significant factor shaping the ground-nesting bee community (Fig. 3.7). A few species are associated to bare ground, although as with litter cover, the associations are considered rather weak due to closeness to graph's origin.

Bare or sparsely vegetated soil is often considered as an attractive feature for ground-nesting bees and creation of bare ground has been practically implemented as a conservation method (Gregory & Wright 2005; Falk 2015; Widenfalk et al. 2018). Exposed soil is amongst defining factors of local pollinator diversity repeatedly suggested by various studies (Severns 2004; Potts et al. 2005; Sardiñas & Kremen 2014; Quistberg et al. 2016; Theodorou 2017; Wenzel et al. 2020). There are multiple reasons that could explain this attractiveness. For instance, sparse or lack of vegetation does not shade the ground, thus soil warms up faster and maintains higher temperatures compared to densely overgrown soil. Sun exposure also affects external activities of bees as warmed up by direct sunlight they can begin nest excavation and foraging routine sooner and more effectively (Stone 1994; Weissel et al. 2006; Barbosa et al. 2013). Furthermore, dense root biomass of vegetation can impede nest excavation process and expanding roots can damage or destroy bee nests, as well as obstruct the emergence of the brood (Wuellner 1999). Moreover, extensive root systems can change edaphic conditions as they absorb soil moisture, potentially disadvantaging brood development (Packer & Knerer 1986). Additionally, dense vegetation may obscure nest entrance making it more difficult for bees to locate the nest (Wuellner 1999). Wesserling & Tscharntke (1995) observed that vegetation removal on sandy patches has increased density of ground-nesting bees and wasps. In the study of ground-nesting alkali bees (*Nomia melanderi*) by Stephen & Evans (1960), the removal of vegetation cover clearly benefited the bees as population increased by 300%. Several other species-specific studies observed that bees prefer to nest in an open, sparsely vegetated soil (Breed 1975; Wuellner 1999; Potts & Willmer 1997).

Alternatively, the study by Twerd & Banaszak-Cibicka (2019) did not find any associations with bee diversity and bare soil in the urban environment. There is also evidence that some species prefer to nest under vegetation cover (Packer & Knerer, 1986). Particularly in dry and loose sand environments vegetation root systems may actually help to maintain architectural integrity of the nests (Potts & Willmer 1997; Antoine & Forrest 2021). Some species simply have broader nesting habitat preferences, and their occurrence is not explained by a degree of exposed soil (Kim et al. 2006). It is also unclear what degree of bare ground is acceptable to a variety of bees. Moreover, it is also worthwhile considering that it is not always clear whether exposed ground is an actual bee nesting preference or an observational bias (Harmon-Threatt 2020; Antoine & Forrest 2021). Even though bare soil in this study has not explained the diversity of bees, some species are associated with it (Fig. 3.7), and exposed soil should be considered as an important nesting habitat feature as supporting evidence from various studies suggest.

4.1.5. Age of the sand patch

In this study, the age of the sand patch and ground temperature variables did not explain any variation of diversity metrics nor showed evidence affecting bee community composition.

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, 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 were made by Krauss et al. (2009), where researchers have studied 24 limestone quarries across 120 years age gradient. Bee richness and community structure was not influenced by the age of the quarry. Alternatively, Potts et al. (2005) have studied bee communities in habitats regenerating after fire and found that ground-nesting bee diversity decreases with the age of post-fire habitat, and then increases once again at the oldest post-fire sites. These findings suggest that age of the habitat and its importance to bee community may depend on the nature of habitat disturbance and following structural changes such as secondary succession (Cook et al. 2005). Although wild bees seem to not be affected by their nesting habitat age in this study, it is important to consider that older sites may be of high importance to plants and other organisms that have low dispersal abilities such as reptiles (Reinhardt et al. 2005; Krauss et al. 2009).

4.2. Cleptoparasites as indicator taxon

It is particularly interesting to compare cleptoparasitic load (CL) between SV and BP study sites. Here one essentially compares two communities, one that is bee species rich inhabiting an old site (SV), and one from a recently established site (BP). SV had 35% of cleptoparasitic load compared to 0% in BP (Table 3.3). The absence of cleptoparasitic bees in BP confirms the assumption that newly established communities may not be yet inhabited by cleptoparasites (Calabuig 2000). In contrast, the other three recently created sites (N3, N4 and N5) had comparatively stable cleptoparasitic load, ranging from 13-20% (Table 3.3). However, these three sites were created two years earlier than BP. This suggests that successful colonization of diverse bee assemblages in newly created nesting habitats may happen rather rapidly within a course of few years. Of course, it is important to consider that other factors such as foraging resources, connectivity between the habitats in a fragmented landscape as well as presence of species in the surrounding habitats affect the colonization rate and success (Boscolo et al. 2017; Griffin & Haddad 2021).

There was a nearly significant correlation (p=.057) between ground-nesting and associated cleptoparasitic bee species richness (Fig. 3.6). The sample size in this study is small (n=12), and as mentioned above, the power of a statistical test largly depends on sample size (Nakagawa & Cuthill 2007; Knudson & Lindsey 2014). It is possible that because of small sample size type II error occurred suggesting absence of a relationship when in fact there is one. Moreover, the result (p=.057) is very close to a statistically significant .05 p-value, indicating that probability of a relationship between the two bee guilds is rather high. Also, the correlation test of species richness (disregarding species densities and evenness) may simply be not sufficient to answer this question and more sophisticated statistical approach is necessary (Sheffield et al. 2013b).

4.3. Urbanization – loss of nesting habitat

Although some studies reveal that urban environment can host relatively diverse wild bee communities as compared to other human altered landscapes, ground-nesting bees and associated cleptoparasites are disadvantaged primarily due to scarce nesting resources in urban landscapes (Beninde et al. 2015; Lopez-Uribe et al. 2015; Threlfall et al. 2015; Quistberg et al. 2016; Hall et al. 2017; Theodorou et al. 2020). In the study area of southern Uppsala, sandy soil has declined substantially over the 75-year period (Fig. 3.1). The sandy habitat in 2019 estimates to less than 15% of the total area that was present in 1942. That has undoubtedly impacted ground-nesting bee communities as the availability of suitable nesting habitat shrank dramatically over time, although comparative bee data is lacking. The study by Cardoso and Gonçalves (2018) assessed the change of wild bee diversity over the course of 34-years of urbanization. Researchers found that wild bee species richness reduced by 45%, with ground-nesting bees being particularly affected by urban expansion. That, together with the results presented in this study, stress 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.

4.4. Recommendations for conservation management

Habitat restoration and creation for wild bees have a positive effect on wild bee abundance and diversity (Tonietto & Larkin 2018). Despite the proportionally greater diversity of ground nesting bees compared to aerial nesters, the existing literature of conservational efforts for wild bee nesting habitat (re)creation is largely focused on aerial nesters (Dicks et al. 2010). The existing studies show that creation of additional nesting habitats for ground-nesting bees in human altered landscapes has positive effects for diverse ground-nesting bee assemblages (Wesserling & Tscharntke 1995; Edwards 1998; Severns 2004; Gregory & Wright 2005). This study contributes with additional knowledge of nesting preferences of ground-nesting bees. The drastic loss of sandy soil in the study area emphasizes the urgent need of conservational action to assist this vulnerable and often dismissed group of wild bees.

The suitable wild bee habitat should be provided and maintained by landowners and conservation managers working in urban development sectors. The existing sandy soil areas in city environment should be treated as vital nesting habitats for ground-nesting bees, and if possible, preserved. However, the creation of additional nesting habitats in urban environment are necessary to reduce the negative effects of landscape fragmentation (Cane et al. 2006; Fitch et al. 2019) as well as to increase the total available nesting habitat area. Establishment of numerous bare ground sites across urban landscape with finer sand material (‘medium’ sand grain size) that provides fast drainage but maintains a certain degree of soil humidity is recommended. This study cannot provide the advice on the size of sandy patches that should be created due to dubious results. Nevertheless, the study does show that even small size sand patches provide a valuable nesting resource for diverse wild bee assemblages. Additionally, vegetation management should be implemented to periodically remove the layer of plant matter from the sand patches once the vegetation successionally starts to colonize the sites. As the age of nesting sites for ground-nesting bees seem to not be of significant importance, the creation of new patches should be effective in attracting diverse bee communities in following season and years.

As various other studies suggest, sandy patches should be preferably located in southern sides, and the proximity to foraging resources is of crucial importance (Potts et al. 2005; Antoine & Forrest 2021). Although this study does not explore the fragmentation effects on bee diversity, research shows that it is essential to account for both foraging and nesting sites that are connected so that distances between the two types of habitats effectively match bee flight abilities (Rader et al. 2011; Carvell et al. 2012; Zurbuchen 2010; Zurbuchen et al. 2010a, 2010b). The creation and restoration of preferable nesting habitats for wild bees should lessen the negative impacts of urbanization and benefit overall wild bee diversity (Vanbergen 2013). However, it is important to highlight that diversity measure should not be the only ‘go-to’ conservation approach. A diverse community may represent a habitat that is not suitable for specialist and rare bee species. Instead, a more holistic attitude should be taken considering vulnerable and endangered species which may have very different habitat requirements and narrower environment optimum. It is essential to consider overall habitat heterogeneity and create opportunities for various species finding their niche in urban landscapes.

5. Conclusions and future study recommendations

A few environmental variables showed to have a strong association with species diversity metrics: sand grain size, litter cover and size of the sand patch. In patches where sand was defined as ‘medium’, higher species richness was observed when compared to patches with ‘coarse’ type of sand. Lower percentage of litter cover on the sand patch was associated with a greater bee diversity. Size of the sand patch was negatively associated with species diversity, opposite of expectation based on SAR. Ground-nesting bee community seemed to be largely influenced by three variables: sand grain size, litter cover and bare ground. More species clustered around ‘medium’ type of sand than the ‘coarse’ sand. The influence of litter cover and bare ground on bee community is rather ambiguous but does suggest that some species prefer a rather exposed ground for nesting, while other species potentially are benefited or simply not influenced by litter cover.

Relatively stable cleptoparasitic load was apparent after three years from habitat establishment in the newly created sites, suggesting that stable communities established rather fast in such sites. The guild of cleptoparasitic bees has a potential to act as an indicator taxon, although the positive association between the number of cleptoparasitic bee species and the number of ground-nesting bees was not statistically significant (Fig. 3.4). Further studies with a greater sample size are necessary before confidently implementing cleptoparasites as bee community and habitat quality indicators in practice.

The study area has been subjected to increasing urbanization which resulted to alarming loss and degradation of sandy habitats. Barely 15% of the total sandy habitat was present in 2019 since 1942. The results highlight the importance of additional sandy habitat implementation for ground-nesting bees and other associated insects in this urban environment.

Recommendations to conservation management would be to focus on establishing additional bare ground patches with finer sand material (‘medium’ sand is appropriate). Even relatively small habitats can host a great diversity of ground-nesting and associated cleptoparasitic bees in urban environment as this study shows. Therefore, if larger areas cannot be dedicated for nesting habitat creation, even small patches are very valuable as they will be colonized by a diversity of wild bees. Considering the trend of substantial loss of sandy habitat, numerous sand patches should be established to reduce negative impacts of landscape fragmentation. Moreover, some implemented vegetation management by periodically removing the vegetation from the sand patches may benefit the overall ground-nesting bee diversity. It is crucial to consider plentiful and diverse floral resources in a proximity to nesting habitats.

Recommendations for the future research of ground-nesting bee nesting preferences would be to conduct a study with significantly higher sample size. That is especially important for evaluating sand patch size and bee diversity relationship (SAR). Moreover, adding foraging resources as another environmental variable should be a critical step to improve the understanding of overall nesting habitat requirements. Additionally, a complete particle distribution analysis of soil should be conducted in the future study. Knowing the actual preferences of majority ground-nesting bees on sand, clay and silt ratio would provide a more accurate picture of optimal range of soil texture for bees. Other soil properties such as compaction of the soil, porosity, acidity (pH), humidity and organic matter are worth considering to determine the environmental optimum for wild bee diversity.

To further improve our knowledge of ground-nesting bee nesting biology, it would be valuable to carry out a temporal study over a course of few years, since it is known that bee populations experience yearly fluctuations (Frankie et al. 1998). Such data would not only account for seasonal, but also yearly variation in bee populations. Moreover, it would be interesting to observe the dynamics of bee community establishment over time, especially in the ‘new’ sand patches. Ultimately it comes down to costs and time, which should be adequately considered whether the purpose of the study outweighs the costs.

6. References

Aguilar, R., Ashworth, L., Galetto, L. & Aizen, M.A. (2006). Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters*. 9, 968-980.

Aizen, M.A. & Feinsinger, P. (1994). Habitat fragmentation, native insect pollinators, and feral honey-bees in Argentine chaco serrano. *Ecological Applications.* 4, 378-392.

Almeida, E.A.B. (2008). Colletidae nesting biology (Hymenoptera:Apoidea). *Apidologie*. 39(1), 16-29. https://doi.org/10.1051/apido:2007049

Antoine, C.M. & Forrest, J.R. (2021). Nesting habitat of ground-nesting bees: a review. *Ecological Entomology*. 46(2), 143-159. https://doi.org/10.1111/een.12986

Archer, M.E. (1995). Aculeate wasps and bees (Hymenoptera: Aculeata) of Blaxton Common in Watsonian Yorkshire with the introduction of a new national quality system. *Naturalist.* 120, 21-29.

Ascher, J.S. & Pickering, J. (2020). Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide=Apoidea_species [2021-01-02]

Ayers, A. & Rehan, S. (2021). Supporting Bees in Cities: How Bees Are Influenced by Local and Landscape Features. *Insects*. 12(2), 128. 10.3390/insects12020128.

Barbosa, F., Alves, R., Souza, B. & Carvalho, C. (2013). Nest architecture of the stingless bee Geotrigona subterranea (Friese,1901) (Hymenoptera: Apidae: Meliponini). *Biota Neotropica*. 13 (1), 147-152.

Bauer, D.M. & Wing, I.S. (2016). The macroeconomic cost of catastrophic pollinator declines. *Ecological Economics.* 126, 1-13. https://doi.org/10.1016/j.ecolecon.2016.01.011

Bazelet, C.S. & Samways, M.J. (2011). Relative importance of management vs. design for implementation of large-scale ecological networks. *Landscape Ecology*. 26, 341-353. https://doi.org/10.1007/s10980-010-9557-z

Beninde, J., Veith, M., & Hochkirch, A. (2015). Biodiversity in cities needs space: A meta-analysis of factors determining intra-urban biodiversity variation. *Ecology Letters*. 18(6), 581-592. https://doi.org/10.1111/ele.12427

Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J. & Kunin, W.E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science.* 313, 351-354. https://doi.org/10.1126/science.1127863

Blitzer, E.J., Gibbs, J., Park, M.G. & Danforth, B.N. (2016) Pollination services for apple are dependent on diverse wild bee communities. *Agriculture Ecosystems & Environment*. 221, 1-7. https://doi.org/10.1016/j.agee.2016.01.004

Borgström, P., Ahrné, K. & Johansson, N. (2018). Pollinatörer och pollinering i Sverige. Naturvårdsverket rapport 6841. ISBN 978-91-620-6841-7

Boscolo, D., Tokumoto, P., Ferreira, P., Ribeiro, J. & Silveira dos Santos, J. (2017). Positive responses of flower visiting bees to landscape heterogeneity depend on functional connectivity levels. *Perspectives in Ecology and Conservation*. 15(1), 18-24. https://doi.org/10.1016/j.pecon.2017.03.002

Breed, M.D. (1975). Life cycle and behavior of a primitively social bee, *Lasioglossum rohweri* (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society*. 48, 64-80.

Brünnert, U., Kelber, A. & Zeil, J. (1994). Ground-nesting bees determine the location of their nest relative to a landmark by other than angular size cues. *Journal of Comparative Physiology A.* 175, 363-369. https://doi.org/10.1007/BF00192995

Buchholz. S. & Egerer, M.H. (2020). Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationships. *Biodiversity and Conservation.* 29, 2779-2801. https://doi.org/10.1007/s10531-020-02003-8

Burkle, L.A., Marlin, J.C. & Knight, T.M. (2013). Plant-pollinator interactions over 120 years: loss of species, co-occurrence, and function. *Science.* 339, 1611-1615.

Calabuig, I. (2000). Solitary bees and bumblebees in a Danish agricultural landscape. PhD-thesis. University of Copenhagen, Copenhagen.

Campbell, J.W. & Hanula, J.L. (2007). Efficiency of Malaise traps and coloured pan traps for collecting flower visiting insects from three forested ecosystems. *Journal of Insect Conservation*. 11, 399-408.

Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F. & Griswold, T.L. (2011). Patterns of widespread decline in North American bumble bees. *PNAS.* 108(2), 662-667. https://doi.org/10.1073/pnas.1014743108

Cane, J.H. (1981). Dufour's gland secretion in the cell linings of bees (Hymenoptera: Apoidea). *Journal of Chemical Ecology*. 7(2), 403-410.

Cane, J.H. & Carlson, R. (1984). Dufour's gland glycerides from *Anthophora*, *Emphoropsis* (Anthophoridae) and *Megachile* (Megachilidae) bees (Hymenoptera: Apoidea). *Comparative Biochemistry and Physiology*. 78B, 769-772.

Cane, J.H. (1991). Soils of ground-nesting bees (Hymenoptera: Apoidea): texture, moisture, cell depth and climate. *Journal of the Kansas Entomological Society*. 64(4), 406-413.

Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H. & Neal, M. (2006). Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications*. 16(2), 632-644. DOI:10.1890/1051-0761(2006)016[0632:CRWADB]2.0.CO;2

Cane, J. H. & Neff, J. L. (2011). Predicted fates of ground-nesting bees in soil heated by wildfire: Thermal tolerances of life stages and a survey of nesting depths. *Biological Conservation*. 144(11), 2631-2636. https://doi.org/10.1016/j.biocon.2011.07.019

Cane, J.H. & Love, B.G. (2021). Hygroscopic larval provisions of bees absorb soil water vapor and release liquefied nutrients. *Apidologie* 52, 1002-1016. https://doi.org/10.1007/s13592-021-00883-5

Cao, Y. & Hawkins, C.P. (2019). Weighting effective number of species measures by abundance weakens detection of diversity responses. *Journal of Applied Ecology*. 56(5), 1200-1209. https://doi.org/10.1111/1365-2664.13345

Cardoso, M.C. & Gonçalves, R.B. (2018). Reduction by half: the impact on bees of 34 years of urbanization. *Urban Ecosystems*. 21**,** 943-949. https://doi.org/10.1007/s11252-018-0773-7

Carvalheiro, L.G., Veldtman, R., Shenkute, A.G., Tesfay, G.B., Pirk, C.W.W., Donaldson, J.S. & Nicolson, S.W. (2011). Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters*. 14(3), 251-259. https://doi.org/10.1111/j.1461-0248.2010.01579.x

Carvell, C., Jordan, W., Bourke, A., Pickles, R., Redhead, J. & Heard, M. (2011). Molecular and spatial analyses reveal links between colony-specific foraging distance and landscape-level resource availability in two bumblebee species. *Oikos*. 121, 734-742. DOI:10.1111/j.1600-0706.2011.19832.x

Christmann, S. (2019). Do we realize the full impact of pollinator loss on other ecosystem services and the challenges for any restoration in terrestrial areas? *Restoration Ecology*. 27, 720-725. https://doi.org/10.1111/rec.12950

Connor, E.F. & McCoy, E.D. (1979). The statistics and biology of the species–area relationship. *The American Naturalist*. 113, 791-833.

Connor, E.F. & McCoy, E.D. (2001). Species–Area Relationships. *Encyclopaedia of Biodiversity*. 5. 397-411. DOI 10.1016/B0-12-226865-2/00252-2

Cook, W.M., Yao, J., Foster, B.L., Holt, R.D. & Patrick, L.B. (2005). Secondary succession in an experimentally fragmented landscape: community patterns across space and time. *Ecological Society of America*. 86(5), 1267-1279.

Danforth, B.N., Neff, J.L. & Barretto-Ko, P. (1996). Nestmate relatedness in a communal bee, Perdita texana (Hymenoptera: Andrenidae), based on

DNA fingerprinting. *Evolution*. 50, 276-284. https://doi.org/10.1111/j.1558-5646.1996.tb04491.x

Dicks, L.V., Showler, D.A. & Sutherland, W.J. (2010). *Bee conservation: Evidence for the effects of interventions.* Exeter: Pelagic Publishing.

Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B. & Collen, B. (2014). Defaunation in the Anthropocene. *Science.* 345, 401-406. DOI: 10.1126/science.1251817

Duffield, R.M., Laberge, W.E., Cane, J.H. & Wheeler, J.W. (1982). Exocrine secretions of bees. IV. Macrocyclic lactones and isopentenyl esters in Dufour's gland secretions of Nomia bees (Hymenoptera: Halictidae). *Journal of Chemical Ecology*. 8(2), 535-543.

Edwards, M. (1998). Monitoring of bare ground for use by heathland insects. Unpublished report to the West Sussex Heathlands Project.

Fahrig, L. (2013). Rethinking patch size and isolation effects: the habitat amount hypothesis. *Journal of Biogeography.* 40, 1649-1663.

Falk, S. (2015). *Field Guide to the Bees of Great Britain and Ireland.* British Wildlife Pub.; UK ed. edition. ISBN: 9781910389034

Finke, D.L. & Denno, R.F. (2004). Predator diversity dampens trophic cascades. *Nature*. 429, 407-410.

Fitch, G., Glaum, P., Simao, M.-C., Vaidya, C., Matthijs, J., Iuliano, B. & Perfecto, I. (2019). Changes in adult sex ratio in wild bee communities are linked to urbanization. *Scientific Reports.* 9, 3767. https://doi.org/10.1038/s41598-019-39601-8

Fletcher, C.C. & Bryan, H. (1912). *Modification of the method of mechanical soils analysis.* Bulletin of the U.S. Department of Agriculture Vol. 84.

Forrest, J.R.K., Cross, R. & CaraDonna, P.J. (2019). Two-year bee, or not two-year bee? How voltinism is affected by temperature and season length in a high-elevation solitary bee. *The American Naturalist*. 193(4), 560-574.

Fortel, L., Henry, M., Guilbaud, L., Guirao, A.L., Kuhlmann, M., Mouret, H., Rollin, O. & Vaissiere, E. (2014). Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. *PLoS ONE*. 9(8), e104679. https://doi.org/10.1371/journal.pone.0104679

Fortel, L.M., Guilbaud, H.L., Mouret, H. & Vaissière, B.E. (2016). Use of human-made nesting structures by wild bees in an urban environment. *Journal of Insect Conservation*. 20(2), 239-253.

Frankie, G.W., Thorp, R.W., Kirk, W.D.J., Rizzardi, M.A., Barthell, J.F., Griswold, T.L., Kim, J.-Y. & Kappagoda, S. (1998). Monitoring solitary bees in modified wildland habitats: Implications for bee ecology and conservation. *Environmental Entomology.* 27, 1053-1288.

Fuller, R.A., Irvine, K.N., Devine-Wright, P., Warren, P.H. & Gaston, K.J. (2007). Psychological benefits of greenspace increase with biodiversity. *Biology Letters.* 3(4), 390-394. https://doi.org/10.1098/rsbl.2007.0149

Gallai, N., Salles., J.-M., Settele, J. & Vaissière, B.E. (2009). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics.* 68(3), 810-821. https://doi.org/10.1016/j.ecolecon.2008.06.014

Garibaldi, L.A., Steffan-Dewenter, I., Kremen, C., Morales, J.M., Bommarco, R., Cunningham, S.A., Carvalheiro, L.G., Chacoff, N.P., Dudenhöffer, J.H., Greenleaf, S.S., Holzschuh, A., Isaacs, R., Krewenka, K., Mandelik, Y., Mayfield, M.M., Morandin, L.A., Potts, S.G., Ricketts, T.H., Szentgyörgyi, H., Viana, B.F., Westphal, C., Winfree, R., Klein, A.M. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters.* 14(10), 1062–1072. https://doi.org/10.1111/j.1461-0248.2011.01669.x

Garibaldi, L.A., Steffan-Dewenter, I., Winfree, R., Aizen, M.A., Bommarco, R., Cunningham, S.A., Kremen, C., Carvalheiro, L.G., Harder, L.D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V., Cariveau, D., Chacoff, N.P., Dudenhöffer, J.H., Freitas, B.M., Ghazoul, J., Greenleaf, S., Hipólito, J., Holzschuh, A., Howlett, B., Isaacs, R., Javorek, S.K., Kennedy, C.M., Krewenka, K.M., Krishnan, S., Mandelik, Y., Mayfield, M.M., Motzke, I., Munyuli, T., Nault, B.A., Otieno, M., Petersen, J., Pisanty, G., Potts, S.G., Rader, R., Ricketts, T.H., Rundlöf, M., Seymour, C.L., Schüepp, C., Szentgyörgyi, H., Taki, H., Tscharntke, T., Vergara, C.H., Viana, B.F., Wanger, T.C., Westphal, C., Williams, N., Klein, A.M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science.* 339(6127), 1608-1611. DOI: 10.1126/science.1230200

Gathmann, A. & Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal Ecology*. 71, 757-764. https://doi.org/10.1046/j.1365-2656.2002.00641.x

Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L. & Darvill, B. (2010). Effects of land use at a landscape scale on bumblebee nest density and survival. *Journal of Applied Ecology*. 47, 1207-1215. https://doi.org/10.1111/j.1365-2664.2010.01872.x

Gregory, S. & Wright, I. (2005). Creation of patches of bare ground to enhance the habitat of ground-nesting bees and wasps at Shotover Hill, Oxfordshire, England. *Conservation Evidence.* 2, 139-141.

Griffin, S.R. & Haddad, N.M. (2021). Connectivity and edge effects increase bee colonization in an experimentally fragmented landscape. *Ecogeography.* 44(6), 919-927. https://doi.org/10.1111/ecog.05299

Grundel R., Jean, R.P., Frohnapple, K.J., Glowacki, G.A., Scott, P.E. & Pavlovic, N.B. (2010). Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Society of America.* 20(6), 1678-1692. https://doi.org/10.1890/08-1792.1

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., Lovejoy, T. E., Sexton, J. O., Austin, M. P., Collins, C. D., Cook, W. M., Damschen, E. I., Ewers, R. M., Foster, B. L., Jenkins, C. N., King, A.

J., Laurance, W. F., Levey, D. J., Margules, C. R., Melbourne, B. A., Nicholls, A.O., Orrock, J.L., Song, D.X. & Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science advances*. 1(2), e1500052. https://doi.org/10.1126/sciadv.1500052

Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J., Baldock, K.C.R., Fowler, R., Frankie, G., Goulson, D., Gunnarsson, B., Hanley, M.E., Jackson, J.I., Langellotto, G., Lowenstein, D., Minor, E.S., Philpott, S.M., Potts, S.G., Sirohi, M.H., Spevak, E.M., Stone, G.N. & Threlfall, C. (2017). The city as a refuge for insect pollinators. *Conservation Biology*. 31(1), 24-29. DOI: 10.1111/cobi.12840

Harmon-Threatt, A. (2020). Influence of nesting characteristics on health of wild bee communities. *Annual Review of Entomology*. 65, 39-56. https://doi.org/10.1146/annurev-ento-011019-024955

Heino, J., Mykrä, H. & Kotanen, J. (2008). Weak relationships between landscape characteristics and multiple facets of stream macroinvertebrate biodiversity in a boreal drainage basin. *Landscape Ecology*. 23, 417-426.

Hofmann, M.M., Fleischmann, A. & Renner, S.S. (2020). Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. *Journal of Hymenoptera Research*. 77, 105–117. https://doi.org/10.3897/jhr.77.51182

Jost, L. (2006). Entropy and diversity. *Oikos*. 113(2), 363-375. https://doi.org/10.1111/j.2006.0030-1299.14714.x

Jost, L. (2007). Partitioning diversity into independent alpha and beta components. *Ecology*. 88(10), 2427-2439. https://doi.org/10.1890/06-1736.1

Jost, L. (2009). Mismeasuring biological diversity: Response to Hoffmann and Hoffmann (2008). *Ecological Economics*. 68(4), 925-928. https://doi.org/10.1016/j.ecolecon.2008.10.015

Kaiser-Bunbury, C.N., Muff, S., Memmott, J., Müller, C.B. & Caflisch, A. (2010). The robustness of pollination networks to the loss of species and interactions: a quantitative approach incorporating pollinator behaviour. *Ecology Letters*. 13(4), 442-452. https://doi.org/10.1111/j.1461-0248.2009.01437.x

Kevan, P.G. & Viana, B.F. (2003). The global decline of pollination services. *Biodiversity*. 4(4), 3-8. http://dx.doi.org/10.1080/14888386.2003.9712703

Kim, J., Williams, N. & Kremen, C. (2006). Effects of cultivation and proximity to natural habitat on ground-nesting native bees in California sunflower fields. *Journal of the Kansas Entomological Society*. 79(4), 309-320. http://dx.doi.org/10.2317/0507.11.1

King, M.J. & Buchmann, S.L. (2003). Floral sonication by bees: Mesosomal vibration by *Bombus* and *Xylocopa*, but not *Apis* (Hymenoptera: Apidae), ejects pollen from poricidal anthers. *Journal of the Kansas Entomological Society*. 76(2), 295-305. http://www.jstor.org/stable/25086116

Knudson, D.V. & Lindsey, C. (2014). Type I and Type II Errors in Correlations of Various Sample Sizes. *Comprehensive Psychology*. 3(1), 1-5. https://doi.org/10.2466/03.CP.3.1

Krauss, J., Alfert, T. & Steffan-Dewenter, I. (2009). Habitat area but not habitat age determines wild bee richness in limestone quarries. *Journal of Applied Ecology*. 46, 194-202.

Lever, J.J., Nes, E.H., Scheffer, M. & Bascompte, J. (2014). The sudden collapse of pollinator communities. *Ecology Letters.* 17(3), 350-359. https://doi.org/10.1111/ele.12236

Lin, B.B., Philpott, S.M. & Jha, S. (2015). The future of urban agriculture and biodiversity-ecosystem services: Challenges and next steps. *Basic and Applied Ecology.* 16(3), 189-201. https://doi.org/10.1016/j.baae.2015.01.005

Lomolino, M.V. (2001). The species-area relationships: new challenges for an old pattern. *Progress in Physical Geography: Earth and Environment.* 25(1), 1-21. https://doi.org/10.1177/030913330102500101

Lopez, L.C.S., Fracasso, M.P.A., Mesquita, D.O., Palma, A.R.T. & Riul, P. (2012). The relationship between percentage of singletons and sampling effort: A new approach to reduce the bias of richness estimates. *Ecological Indicators.* 14(1), 164-169. https://doi.org/10.1016/j.ecolind.2011.07.012.

Lopez-Uribe, M.M., Morreale, S.J., Santiago, C.K. & Danforth, N. (2015). Nest suitability, fine-scale population structure and male-mediated dispersal of a solitary ground nesting bee in an urban landscape. *PLoS ONE.* 10(5), 1-20. https://doi.org/10.1371/journal.pone.0125719

Losos, J.B. & Ricklefs, R.E. (2009). *The Theory of Island Biogeography Revisited.* Princeton University Press. ISBN: 9780691136530

Lowenstein, D. M., Matteson, K. C. & Minor, E. S. (2015). Diversity of wild bees supports pollination services in an urbanized landscape. *Oecologia*. 179(3), 811-821. DOI: 10.1007/s00442-015-3389-0

Mallinger, E. & Gratton, C. (2014). Species richness of wild bees, but not the use of managed honeybees, increases fruit set of a pollinator-dependent crop. *Journal of Applied Ecology.* 52(2), 323-330. https://doi.org/10.1111/1365-2664.12377

Mathiasson, M.E. & Rehan, S.M. (2020). Wild bee declines linked to plant-pollinator network changes and plant species introductions. *Insect Conservation and Diversity.* 13(6), 595-605. https://doi.org/10.1111/icad.12429

Matias, D.M.S., Leventon, J., Rau, A.-L., Borgemeister, C. & Wehrden, H. (2017). A review of ecosystem service benefits from wild bees across social contexts. *Ambio*. 46(4), 456-467. https://doi.org/10.1007/s13280-016-0844-z

May, D.G.K. (1972). Water uptake during larval development of a sweat bee, *Augochlora pura*. *Journal of the Kansas Entomological Society.* 45(4), 439-449.

McKinney, M.L. (2002). Urbanization, Biodiversity, and Conservation: The impacts of urbanization on native species are poorly studied, but educating a highly urbanized human population about these impacts can greatly improve species conservation in all ecosystems. *BioScience*. 52(10), 883-890. https://doi.org/10.1641/0006-3568(2002)052[0883:UBAC]2.0.CO;2

Meeus, I., Pisman, M., Smagghe, G. & Piot, N. (2018). Interaction effects of different drivers of wild bee decline and their influence on host-pathogen dynamics. *Current Opinion in Insect Science.* 26, 136-141. https://doi.org/10.1016/j.cois.2018.02.007

Michener, C.D. (2007). *The Bees of the World*. Johns Hopkins University Press, Baltimore. Second edition. ISBN-13: 9780801885730.

Morales, C.L., Arbetman, M.P., Cameron, S.A. & Aizen, M.A. (2013). Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment.* 11(10), 529-534. https://doi.org/10.1890/120321

Morris, E., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T., Meiners, T., Müller, C., Obermaier, E., Prati, D., Socher, S., Sonnemann, I., Wäschke, N., Wubet, T., Wurst, S. & Rillig, M. (2014). Choosing and using diversity indices: Insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*. 4(18), 3514-3524. https://doi.org/10.1002/ece3.1155

Mouquet, N., Munguia, P., Kneitel, J. M. & Miller, T. E. (2003). Community assembly time and the relationship between local and regional species richness. *Oikos.* 103, 618-626.

Nakagawa, S. & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: a practical guide for biologists. *Biological Reviews.* 82, 591-605.

Neame, L., Griswold, T. & Elle, E. (2012). Pollinator nesting guilds respond differently to urban habitat fragmentation in an oak-savannah ecosystem. *Insect Conservation and Diversity*. 6(1), 57-66. DOI 10.1111/j.1752-4598.2012.00187.x.

Nielsens, A., Steffan-Dewenter, I., Westphal, C., Messinger, O., Potts, S.G., Roberts, S.P.M., Settele, J., Szentgyörgyi, H., Vaissiere, B.E., Vaitis, M., Woyciechowski, M., Bazos, I., Biesmeijer, J.C., Bommarco, R., Kunin, W.E., Tscheulin, T., Lamborn, E. & Petanidou, T. (2011). Assessing bee species richness in two Mediterranean communities: importance of habitat type and sampling techniques. *Ecological Research.* 26(5), 969-983. https://doi.org/10.1007/s11284-011-0852-1

Nilon, C. (2011). Urban biodiversity and the importance of management and conservation. *Landscape and Ecological Engineering*. 7, 45-52. https://doi.org/10.1007/s11355-010-0146-8

O’Green, A.T. (2013). Soil water dynamics. *Nature Education Knowledge*. 4(5), 9.

Ollerton, J., Winfree, R. & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*. 120, 321-326. https://doi.org/10.1111/j.1600-0706.2010.18644.x

Ollerton, J. (2017). Pollinator diversity: distribution, ecological function, and conservation. *Annual Review of Ecology, Evolution, and Systematics*. 48, 353-376. https://doi.org/10.1146/annurev-ecolsys-110316-022919

Ollerton, J. (2021). *Pollinators & pollination. Nature & society*. Pelagic Publishing. ISBN 9781784272289.

Ordway, E. (1984). Aspects of the nesting behaviour and nest structure of *Diadasia opuntiae* Ckll. (Hymenoptera: Anthophoridae). *Journal of the Kansas Entomological Society*. 57, 216-230.

O'Toole, C. & Ismay, J.W. (1995). Report on the aculeate Hymenoptera and Diptera of Chafford Hundred, Essex, (Chafford Hundred Development, Penny Anderson Associates).

Packer, L. & Knerer, G. (1986). An analysis of variation in the nest architecture of *Halictus ligatus* in Ontario. *Insectes Sociaux*. 33, 190-205.

Pardee, G.L. & Philpott, S.M. (2014). Native plants are the bee’s knees: local and landscape predictors of bee species richness and abundance in backyard gardens. *Urban Ecosystems*. 17, 641-659. https://doi.org/10.1007/s11252-014-0349-0

Pauw, A. (2007). Collapse of a pollination web in small conservation areas. *Ecology*. 88(7), 1759-1769. https://doi.org/10.1890/06-1383.1

Pearson, D.L. (1994). Indicator taxa for quantitative assessment of biodiversity. *Philosophical Transactions: Biological Sciences*. 345(1311), 75-79.

Petanidou, T. & Vokou, D. (1990). Pollination and pollen energetics in Mediterranean ecosystems. *American Journal of Botany*. 77(8), 986-992.

Potts, S.G. & Willmer, P. (1997). Abiotic and biotic factors influencing nest-site selection by Halictus rubicundus, a ground-nesting halictine bee. *Ecological Entomology*. 22(3), 319-328.

Potts, S.G., Vulliamy, B., Roberts, S., O’Toole, C., Dafni, A., Ne’eman, G. & Willmer, P. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*. 30(1), 78-85. https://doi.org/10.1111/j.0307-6946.2005.00662.x

Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Scheweige, O. & Kunin, W.E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*. 25, 345-353. https://doi.org/10.1016/j.tree.2010.01.007

Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.A., Garibaldi, L.A., Hill, R., Settele, J. & Vanbergen, A.J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*. 540(7632), 220-229. https://doi.org/10.1038/nature20588

Quistberg, R.D., Bichier, P. & Philpott, S.M. (2016). Landscape and local correlates of bee abundance and species richness in urban gardens. *Environmental Entomology*. 45(3), 592-601. https://doi.org/10.1093/ee/nvw025

Rader, R., Edwards, W., Westcott, D., Cunningham, S. & Howlett, B. (2011). Pollen transport differs among bees and flies in a human-modified landscape. *Diversity and Distributions*. 17, 519-529. DOI: 10.1111/j.1472-4642.2011.00757.x.

Ramos-Jiliberto, R., Espanés, P.M. & Vázquez, D.P. (2020). Pollinator declines and the stability of plant-pollinator networks. *Ecosphere*. 11(4), 1-11. https://doi.org/10.1002/ecs2.3069

Reinhardt, K., Köhler, G., Maas, S., Detzel, P. & Spence, J.R. (2005). Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the orthoptera of Germany. *Ecogeography*. 28, 593-602.

Rhodes, C.J. (2018). Pollinator decline – an ecological calamity in the making? *Science Progress*. 101(2), 121-160. https://doi.org/10.3184/003685018X15202512854527

Rosenzweig, M.L. (1996). Species diversity in space and time. *Journal of Wildlife Management*. 60(4), 971. DOI:10.2307/3802400

Rozen, J.G. (2001). A taxonomic key to mature larvae of cleptoparasitic bees (Hymenoptera: Apoidea). *American Museum Novitates*. 3309, 1-28.

Roubik, D.W. & Michener, C.D. (1980). The seasonal cycle and nests of Epicharis zonata, a bee whose cells are below the wet-season water table (Hymenoptera, Anthophoridae). *Biotropica*. 12(1), 56-60.

Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019). Worldwide decline of the entomofauna: A review of its drivers. *Biological Conservation*. 232, 8-27. https://doi.org/10.1016/j.biocon.2019.01.020

Sardiñas, H.S. & Kremen, C. (2014). Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic and Applied Ecology*. 15, 161-168. https://doi.org/10.1016/j.baae.2014.02.004

Schaetzl, R.J. (2013). *Treatise on Geomorphology. Weathering and Soils Geomorphology*. San Diego: Academic Press. ISBN 978-0-08-088522-3.

Seto, K.C., Güneralp, B. & Hutyra, L.R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*. 109(40), 16083-16088.

Severns, P. (2004). Creating bare ground increases presence of native pollinators in Kincaid's lupine seeding plots. *Ecological Restoration*. 22, 234-235.

Sheffield, C.S., Kevan, P.G., Pindar, A. & Packer, L. (2013a). Bee (Hymenoptera: Apoidea) diversity within apple orchards and old fields habitats in the Annapolis Valley, Nova Scotia, Canada. *The Canadian Entomologist*. 145, 94-114.

Sheffield, C.S., Pindar, A., Packer, L. & Kevan, P.G. (2013b). The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. *Apidologie*. 44, 501-510.

Shelford, V.E. (1911). Physiological animal geography. Journal of Morphology. 22(3), 551-618.

Simberloff, D. (1976). Experimental zoogeography of islands: Effects of island size. *Ecology*. 57, 629-648.

Soroye, P., Newbold, T. & Kerr, J. (2020). Climate change contributes to widespread declines among bumble bees across continents. *Science.* 367(6478), 685-688. DOI: 10.1126/science.aax8591

Stephen, W.P. & Evans, D.D. (1960). Studies in the alkali bee (*Nomia melanderi* Ckll.). *Agricultural Experiment Station*. 52, 1-39.

Stephen, W.P. (1965). Effects of soil moisture on survival of prepupae of the alkali bee. *Journal of Economic Entomology*. 58, 472-474.

Stevenson, P., Bidartondo, M., Blackhall-Miles, R., Cavagnaro, T., Cooper, A., Geslin, B., Koch, H., Lee, M., Moat, J., Hanlon, R., Sjöman, H., Sofo, A., Stara, K. & Suz, L. (2020). The State of the World's Urban Ecosystems: what can we learn from trees, fungi and bees? *Plants People Planet.* 2(5), 482-498. https://doi.org/10.1002/ppp3.10143

Stone, G.N. (1994). Activity patterns of females of the solitary bee *Anthophora plumipes* in relation to temperature, nectar supplies and body size. *Ecological Entomology*. 19, 177-189.

Säumel, I., Weber, F. & Kowarik, I. (2016). Toward liveable and healthy urban streets: Roadside vegetation provides ecosystem services where people live and move. *Environmental Science & Policy*. 62, 24-33. https://doi.org/10.1016/j.envsci.2015.11.012

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D. (2001). Forecasting agriculturally driven global environmental change. *Science.* 292(5515), 281-284. DOI: 10.1126/science.1057544

Theodorou, P., Albig, K., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T. & Paxton, R. (2017). The structure of flower-visitor networks in relation to pollination across an agricultural to urban gradient. *Functional Ecology*. 31(4), 838-847. https://doi.org/10.1111/1365-2435.12803

Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T.E. & Paxton, R. J. (2020). Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nature Communications*. 11, 576. https://doi.org/10.1038/s41467-020-14496-6

Threlfall, C.G., Walker, K., Williams, N.S.G., Hahs, A.K., Mata, L., Stork, N. & Livesly, S.J. (2015). The conservation value of urban green space habitats for Australian native bee communities. *Biological Conservation.* 187, 240-248. https://doi.org/10.1016/j.biocon.2015.05.003

Tsiolis, K. (2018). Do bare soil landscapes encourage ground nesting bees? Master thesis. Canterbury Christ Church University, School of Human and Life Sciences. https://repository.canterbury.ac.uk/item/89176/do-bare-soil-landscapes-encourage-ground-nesting-bees

Tonietto, R.K. & Larkin, D.J. (2018). Habitat restoration benefits wild bees: A meta-analysis. *Journal of Applied Ecology.* 55, 582-590.

Twerd, L., Banaszak-Cibicka, W. & Sandurska, E. (2019). What features of sand quarries affect their attractiveness for bees? *Acta Oecologica.* 96, 56-64. https://doi.org/10.1016/j.actao.2019.03.005

Twerd, L. & Banaszak-Cibicka, W. (2019). Wastelands: their attractiveness and importance for preserving the diversity of wild bees in urban areas. *Journal of Insect Conservation*. 23, 573-588. https://doi.org/10.1007/s10841-019-00148-8

Vanbergen, A.J. (2013). Threats to an ecosystem service: pressures on pollinators. *Frontiers in Ecology and the Environment.* 11(5), 251-259. https://doi.org/10.1890/120126

Wardhaugh, C.W. (2015). How many species of arthropods visit flowers? *Arthropod-Plant Interactions*. 9(6), 547-565. https://doi.org/10.1007/s11829-015-9398-4

Wcislo, W.T. & Cane, J.H. (1996). Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology.* 41, 257-286.

Weber, F., Kowarik, I. & Säumel, I. (2014). Herbaceous plants as filters: Immobilization of particulates along urban street corridors. *Environmental Pollution*. 186, 234-240. https://doi.org/10.1016/j.envpol.2013.12.011

Wentworth, C.K. (1922). A scale of grade and class terms for clastic sediments. *The Journal of Geology*. 30(5), 377-392.

Wenzel, A., Grass, I., Belavadi, V.V. & Tscharntke, T. (2020). How urbanization is driving pollinator diversity and pollination – A systematic review. *Biological Conservation.* 241, 108321. https://doi.org/10.1016/j.biocon.2019.108321

Weissel, N., Mitesser, O., Liebig, J., Poethke, H.J. & Strohm, E. (2006). The influence of soil temperature on the nesting cycle of the halictid bee *Lasioglossum malachurum*. *Insectes Sociaux*. 53, 390-398.

Wesserling, J. & Tscharntke, T. (1995). Habitat selection of bees and digger wasps - experimental management of plots. *Communications of the German Society for General and Applied Entomonology*. 9, 697-701.

Westerberg, L., Berglund, H.-L., Jonason, D. & Milberg, P. (2021). Color pan traps often catch less when there are more flowers around. *Ecology and Evolution.* 11, 3830-3840. DOI: 10.1002/ece3.7252

Westrich, P. (2018). *Die Wildbienen Deutschlands*. Verlag Eugen Ulmer, ISBN:978381860884.

Widenfalk, L.A., Sallmén, N., Hedin, Å. & Berggren, Å. (2018). Translocation of a sand-associated blister beetle due to urban development in Uppsala, Sweden. In: Global Reintroduction Perspectives: 2018: Case studies from around the globe, pages 1-6. Abu Dhabi: IUCN/SSC Reintroduction Specialist Group (RSG). ISBN 978-2-8317-1902-3.

Williams, C.B. (1964). *Patterns in the Balance of Nature*. Academic Press, London.

Williams, P.H. & Osborne, J.L. (2009). Bumblebee vulnerability and conservation world-wide. *Apidologie.* 40, 367-387. DOI: 10.1051/apido/2009025

Wuellner, C.T. (1999). Nest site preference and success in a gregarious, ground-nesting bee *Dieunomia triangulifera*. *Ecological Entomology.* 24(4), 471-479. https://doi.org/10.1046/j.1365-2311.1999.00215.x

Zattara, E.E. & Aizen, M.A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth.* 4(1), 114-123. https://doi.org/10.1016/j.oneear.2020.12.005

Zurbuchen, A. (2010). Distance matters: Impact of increasing foraging distances on population dynamics in native bees. Diss. ETH Zürich, Nr. 18852. https://doi.org/10.3929/ethz-a-006020778

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. & Dorn, S. (2010a). Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation.* 143, 669-676. https://doi.org/10.1016/j.biocon.2009.12.003

Zurbuchen, A., Cheesman, S., Klaiber, J., Müller. A., Hein, S. & Dorn, S. (2010b). Long foraging distances impose high costs on offspring production in solitary bees. *The Journal of Animal Ecology.* 79(3), 674-681. https://doi.org/10.1111/j.1365-2656.2010.01675.x

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Appendix A

Table A1. Descriptive summary of study sites with coordinates.

Site ID	**Site Name**	**Coordinates SWEREFF99 1800**	**Nature of the site**	**Artificial/Natural**	**Purpose of establishment**
N1	Sunnersta	131086.1, 6630977.3	Winter skiing slope	Artificial	na
N2	Sunnersta	131077.34, 6631147.41	Winter skiing slope in winter	Artificial	na
N3	Kronparken	130112.46, 6635880.74	public park with mix tree cover	Artificial	Conservational, specifically for *C. cunicularius* & *A.bimaculatus*, sand translocation (2016, August)
N4	Pollacksbacken	129897.29, 6636469.13	public park with mix tree cover and open field	Artificial	Conservational, specifically for *C. cunicularius* & *A.bimaculatus*, sand translocation (2016, August)
N5	Pollacksbacken	130044.03, 6636404.90	public park with mix tree cover and open field	Artificial	Conservational, specifically for *C. cunicularius* & *A.bimaculatus,* sand translocation (2016, August)
BP	Biparken, Rosendal	129465.5, 6635978.3	Open area with sandy soil translocated from Skjutvallen	Artificial	Conservational, specifically for sand nesting bees, sand translocated from nearby Skjutvallen (SV) sand pile (2018, December)
O1	Kungshamn Naturreservat	130757.5, 6630146.1	Slope in the mix forest by the river	Natural	na
O3	Sunnersta	130920.7, 6630791.7	Open area with sandy soil, human disturbance	Natural	na
O4	Linnestigen	131031.58, 6634792.70	Sandy slope area in the mix forest	Natural	na
SV	Skjutvallen, Rosendal	129322.2, 6636090.6	Old sand pile, historically used for military to train shooting	Artificial	na
R1	Gozzis, Lövstalöt	127102.7, 6650137.0	Sand and gravel quarry	Artificial	na
R2	Högstaåsen	126821.6, 6651071.5	Sand and gravel quarry	Artificial	na

Appendix B

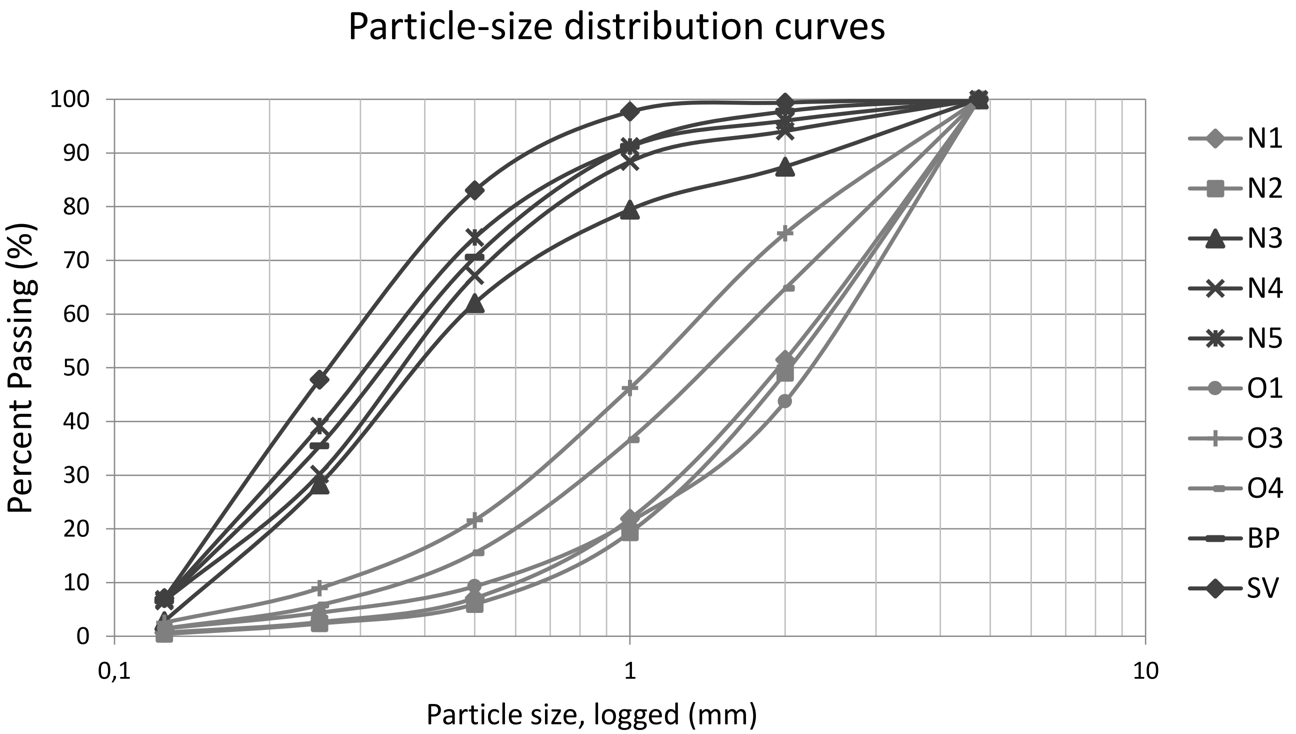

Figure B1. Graph represents particle-size distribution curves of soil samples at each study site (n = 10). The x-axis represents logarithmic scale (base 10) of sieve mesh sizes, and y-axis the percentage of particles passing through each sieve. Darker lines correspond to 'medium' and lighter lines to 'coarse' sand samples based on sand categorization scheme (Table 2.2).

Appendix C

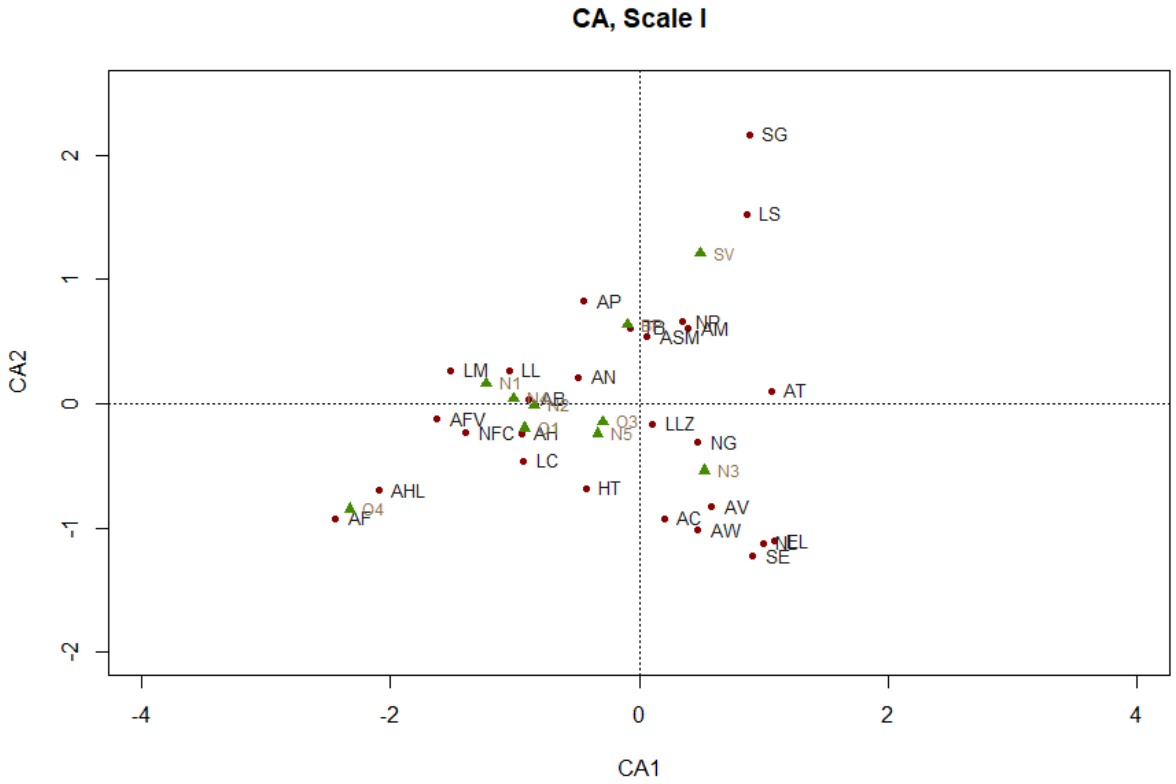

Figure C1. CA biplot of wild bee species composition plotted with sites-oriented scaling (I), showing axes 1 and 2; sites (n = 10) marked as green triangular shapes and species (n = 27) as red circles. Abbreviated IDs of both sites and species are located on the right side of the marks.

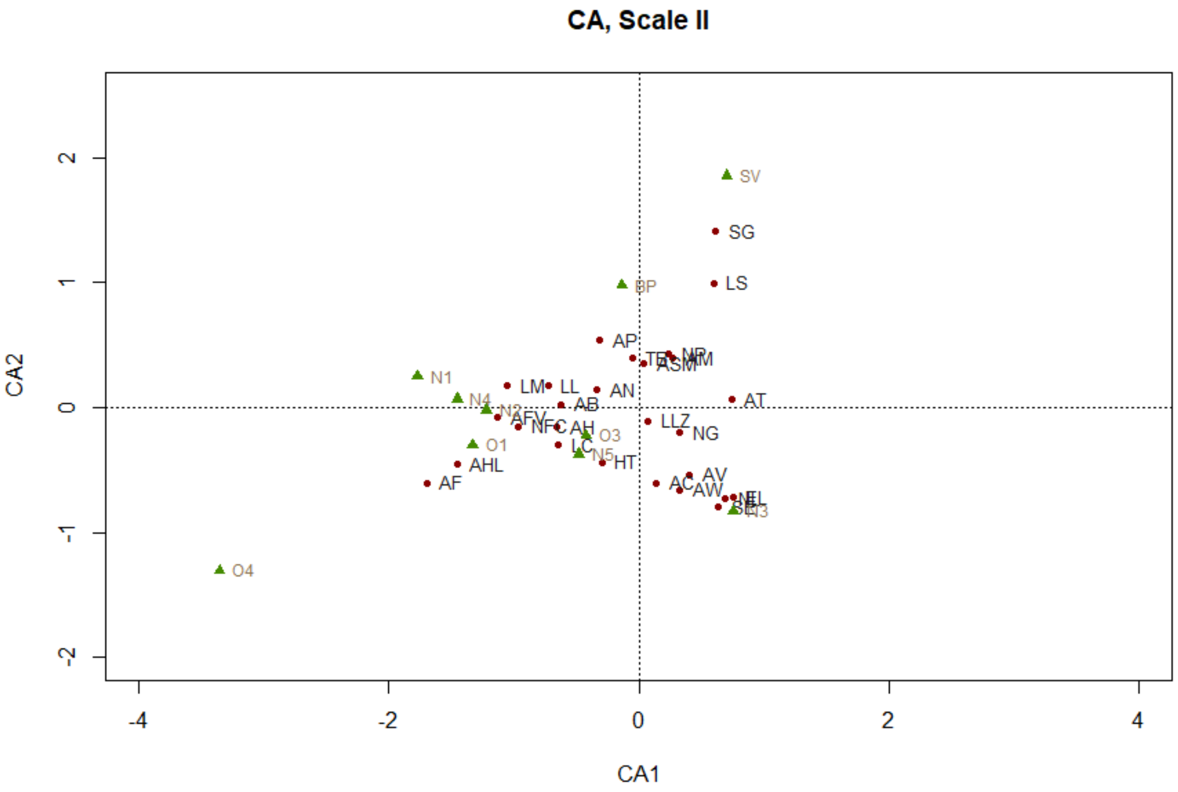

Figure C2. CA biplot of wild bee species composition plotted with species-oriented scaling (II), showing axes 1 and 2; sites (n = 10) marked as green triangular shapes and species (n = 27) as red circles. Abbreviated IDs of both sites and species are located on the right side of the marks.

Appendix D

Table D1. Full list of wild bee species with categorization based on their nesting and breeding ecology as well as the total number of individuals collected of each species.

Species name	**Sand specialist**	**Ground nesting (G) Cleptoparasite (C)**	**Number of individuals**
Andrena barbilabris	YES	G	4
Andrena bicolor	na	G	1
Andrena cineraria	na	G	2
Andrena fucata	na	G	7
Andrena fulvago	na	G	3
Andrena haemorrhoa	na	G	13
Andrena helvola	na	G	4
Andrena labiata	na	G	1
Andrena minutula	na	G	8
Andrena nigroaenea	na	G	8
Andrena praecox	YES	G	3
Andrena ruficrus	YES	G	1
Andrena scotica	na	G	1
Andrena semilaevis	na	G	6
Andrena subopaca	na	G	2
Andrena tibialis	na	G	3
Andrena vaga	YES	G	29
Andrena wilkella	na	G	8
Anthidium punctatum	na	na	6
Apis mellifera	na	na	44
Ceratina cyanea	na	na	2
Colletes daviesanus	na	G	1
Dasypoda hirtipes	YES	G	1
Eucera longicornis	na	G	25
Halictus rubicundus	na	G	1
Halictus tumulorum	na	G	20
Heriades truncorum	na	na	2
Hoplitis claviventris	na	na	10
Hoplitis leucomelana	na	na	3
Hylaeus communis	na	na	1

Species name	**Sand specialist**	**Ground nesting (G) Cleptoparasite (C)**	**Number of individuals**
Hylaeus confusus	na	Partly G	7
Hylaeus hyalinatus	na	Partly G	1
Lasioglossum albipes	na	G	1
Lasioglossum calceatum	na	G	8
Lasioglossum fulvicorne	na	G	1
Lasioglossum leucopus	na	G	37
Lasioglossum leucozonium	na	G	16
Lasioglossum morio	na	G	77
Lasioglossum rufitarse	na	G	2
Lasioglossum semilucens	na	G	48
Lasioglossum sexstrigatum	YES	G	1
Lasioglossum villosulum	na	G	2
Megachile versicolor	na	na	6
Megachile willughbiella	na	Partly G	1
Nomada flavoguttata	na	C	2
Nomada fulvicornis	na	C	2
Nomada goodeniana	na	C	8
Nomada lathburiana	na	C	39
Nomada leucophthalma	na	C	1
Nomada panzeri	na	C	6
Osmia bicolor	na	na	17
Osmia bicornis	na	na	3
Osmia caerulescens	na	na	1
Osmia leaina	na	na	2
Sphecodes crassus	na	C	2
Sphecodes ephippius	na	C	17
Sphecodes geoffrellus	na	C	23
Trachusa byssina	YES	G	7
Bombus spp.	na	na	107

Table D2. The summary of collected bees at all sand patches (including reference sites at the sand quarries).

Collected bees:	**Species no.:**	**Total no.:**
Ground-nesting bees	34	352
Cleptoparasitic bees	9	100
Domestic bees	1	44
Total wild bees identified to species level	57	514
Total wild bees incl. *Bombus* spp.	na	665

Table D3. The overall bee abundance (by family) collected at all sand patches (including reference sites at the sand quarries). Note: the table includes bumblebee data as well, since they belong to family Apidae.

Family	**No. of individuals**	**Percentage**
Andrenidae	104	15.6
Apidae	236	35.5
Colletidae	10	1.5
Halictidae	256	38.5
Megachilidae	58	8.7
Melittidae	1	0.2
Total no. of individuals	665	100

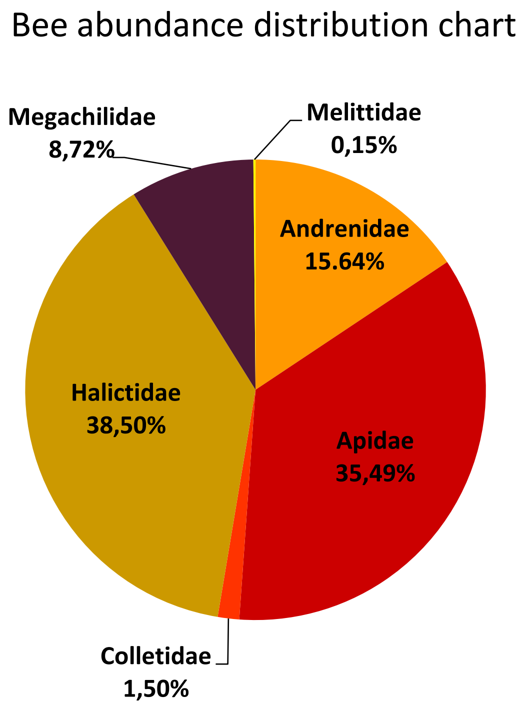

Figure D1. The chart above depicts the overall bee abundance (by family) collected at all sand patches (including reference sites at the sand quarries). Note: the chart includes bumblebee data as well, since they belong to family Apidae.

The highest proportion of collected bees was represented by families Halictidae (38.5%) and Apidae (35.49%), followed by Andrenidae (18.64%), Megachilidae (8.72%), and a very small proportion of Colletidae (1.5%) and Melittidae (0.15%) (Fig. D1).

Appendix E

Detailed GLM result tables are presented below.

Table E1. Environmental variables fitted in a stepwise manner by forward selection in GLM with species richness as a response variable. Results of estimated regression parameters, standard errors, t-values and p-values.

	Estimate	**Std. error**	**t-value**	***p*-value**
Intercept	7.000	2.207	3.172	0.013*
Sand type (medium)	9.800	3.121	3.140	0.014*

Table E2. Environmental variables fitted in a stepwise manner by forward selection in GLM with Shannon ENS as a response variable. Results of estimated regression parameters, standard errors, t-values and p-values.

	Estimate	**Std. error**	***t*-value**	***p*-value**
Intercept	26.776	3.204	8.358	<.001***
Size of the patch	-3.086	1.009	-3.057	.022*
Litter cover	-0.462	0.142	-3.263	.017*
Bare ground	-0.104	0.058	-1.801	.122

Table E3. Environmental variables fitted in a stepwise manner by forward selection in GLM with Simpson ENS as a response variable. Results of estimated regression parameters, standard errors, t-values and p-values.

	Estimate	**Std. error**	***t*-value**	***p*-value**
Intercept	23.928	3.247	7.369	<.001***
Size of the patch	-2.946	0.731	-4.033	.009**
Litter cover	-0.445	0.107	-4.146	.008**
Bare ground	-0.088	0.040	-2.192	.079
Sand type (medium)	-1.326	0.958	-1.383	.225

Table E4. Environmental variables fitted in a stepwise manner by backward elimination in GLM with species richness as a response variable. Results of estimated regression parameters, standard errors, t-values and p-values. Data with excluded cleptoparasitic bees.

	Estimate	**Std. error**	**t-value**	**p-value**
Intercept	-9.229	16.336	-0.565	.589
Size of the patch	-5.889	1.551	-3.796	.007**
Soil temperature	2.053	1.049	1.958	.091

*Table E5***.** *Environmental variables fitted in a stepwise manner by forward selection in GLM with Shannon ENS as a response variable. Results of estimated regression parameters, standard errors, t-values and p-values. Data with excluded cleptoparasitic bees.*

	Estimate	**Std. error**	**t-value**	***p*-value**
Intercept	19.38	1.76	10.99	< .001***
Size of the patch	-3.87	0.55	-7.06	< .001***
Litter cover	-0.41	0.12	-3.41	.011*

Table E6. Environmental variables fitted in a stepwise manner by forward selection in GLM with Simpson ENS as a response variable. Results of estimated regression parameters, standard errors, t-values and p-values. Data with excluded cleptoparasitic bees.

	Estimate	**Std. error**	***t*-value**	***p*-value**
Intercept	8.06	7.67	1.05	.341
Size of the patch	-4.37	0.76	-5.78	.002**
Litter cover	-0.31	0.13	-2.33	.067
Sand type (medium)	-2.12	1.03	-2.06	.095
Soil temperature	0.69	0.48	1.44	.209

Appendix F

Table F1. A number of individuals of each species (ground-nesting and cleptoparasitic bees) collected at each study site. Rows represent sites, columns bee species. Full names of abbreviated species are provided bellow the table.

Site	**AB**	**ABC**	**AC**	**AF**	**AFV**	**AH**	**AHL**	**AL**	**AM**	**AN**	**AP**	**AR**	**AS**	**ASM**	**ASB**	**AT**	**AV**	**AW**	**CD**	**DH**	**EL**	**HR**	**HT**
N1	1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
N2	0	0	0	0	0	3	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	3
N3	1	0	1	1	0	2	1	0	3	1	0	0	1	2	0	2	18	6	0	0	23	0	9
N4	0	0	0	2	2	3	1	0	0	1	0	0	0	1	0	0	0	1	0	0	0	0	0
N5	0	0	1	0	1	4	0	0	0	1	0	0	0	0	0	0	6	1	1	0	0	0	3
BP	1	0	0	0	0	1	0	0	2	0	0	0	0	0	0	0	1	0	0	0	0	1	0
O1	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
O3	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	0	0	0	0	1
O4	0	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SV	0	0	0	0	0	0	0	0	2	1	1	0	0	2	0	1	1	0	0	0	1	0	0
R1	0	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	2	0	0	0	1	0	0
R1	0	0	0	1	0	0	0	0	0	2	0	0	0	0	2	0	0	0	0	1	0	0	0

Site	LA	LC	LF	LL	LLZ	LM	LR	LS	LSX	LV	NF	NFC	NG	NL	NLC	NP	SC	SE	SG	TB	***Total:***
N1	0	0	0	7	0	18	0	0	0	0	0	0	1	0	0	0	0	0	0	1	31
N2	0	4	1	4	0	4	1	0	0	0	0	0	0	0	0	0	0	0	0	0	24
N3	0	2	0	4	5	4	0	12	0	0	0	0	4	35	0	1	0	16	3	2	159
N4	0	0	0	5	2	5	0	0	0	0	0	1	0	0	0	0	0	0	1	1	26
N5	1	1	0	3	2	3	0	1	0	0	0	1	0	1	0	2	0	0	0	0	33
BP	0	0	0	2	0	2	0	5	0	1	0	0	0	0	0	0	0	0	0	0	16
O1	0	1	0	5	0	2	0	0	0	0	0	0	0	0	0	0	0	1	0	0	15
O3	0	0	0	3	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	9
O4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
SV	0	0	0	5	2	3	0	27	1	0	2	0	1	1	1	2	1	0	18	2	75
R1	0	0	0	0	2	34	0	2	0	0	0	0	2	1	0	1	1	0	1	1	51
R1	0	0	0	0	2	5	1	1	0	1	0	0	0	0	0	0	0	0	0	0	16

AB	*Andrena barbilabris*	AR	*Andrena ruficrus*	HT	*Halictus tumulorum*	NF	*Nomada flavoguttata*
ABC	*Andrena bicolor*	AS	*Andrena scotica*	LA	*Lasioglossum albipes*	NFC	*Nomada fulvicornis*
AC	*Andrena cineraria*	ASM	*Andrena semilaevis*	LC	*Lasioglossum calceatum*	NG	*Nomada goodeniana*
AF	*Andrena fucata*	ASB	*Andrena subopaca*	LF	*Lasioglossum fulvicorne*	NL	*Nomada lathburiana*
AFV	*Andrena fulvago*	AT	*Andrena tibialis*	LL	*Lasioglossum leucopus*	NLC	*Nomada leucophthalma*
AH	*Andrena haemorrhoa*	AV	*Andrena vaga*	LLZ	*Lasioglossum leucozonium*	NP	*Nomada panzeri*
AHL	*Andrena helvola*	AW	*Andrena wilkella*	LM	*Lasioglossum morio*	SC	*Sphecodes crassus*
AL	*Andrena labiata*	CD	*Colletes daviesanus*	LR	*Lasioglossum rufitarse*	SE	*Sphecodes ephippius*
AM	*Andrena minutula*	DH	*Dasypoda hirtipes*	LS	*Lasioglossum semilucens*	SG	*Sphecodes geoffrellus*
AN	*Andrena nigroaenea*	EL	*Eucera longicornis*	LSX	*Lasioglossum sexstrigatum*	TB	*Trachusa byssina*
AP	*Andrena praecox*	HR	*Halictus rubicundus*	LV	*Lasioglossum villosulum*		