

Diversity and abundance of solitary and primitively eusocial bees in an urban centre: a case study from Northampton (England)

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Abstract

The apparent reduction of solitary and primitively eusocial bees populations has remained a huge concern over the past few decades and urbanisation is considered as one of the factors affecting bees at different scales depending on bee guild. As urbanisation is increasing globally it necessitates more research to understand the complex community dynamics of solitary and primitively eusocial bees in urban settings. We investigated the urban core of a British town for diversity and abundance of solitary bees using standardized methods, and compared the results with nearby meadows and nature reserves. The study recorded 48 species within the town, about 22 % of the total species and 58 % of the genera of solitary bees in the United Kingdom. Furthermore we found the urban core to be more diverse and abundant in solitary and primitively eusocial bees compared to the meadows and nature re-serves. Of particular note was an urban record of the nationally rare Red Data Book species *Coelioxys quadridentata* and its host *Anthophora quadrimaculata*. This research demonstrates that urban settings can contribute significantly to the conservation of solitary and primitively eusocial bees in Britain.

Keywords Biodiversity _ Solitary bees _ Pollinator decline _ Species richness _ Urbanisation _ Northampton

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Introduction

Biodiversity is one of the essential prerequisites that sustain human society; however, it is nevertheless declining through our activities (Butchart et al. 2010). These are resulting in a 1–10 % loss of biodiversity per decade (Wilson 1999). The recent report by the Natural Capital Committee (NCC) expressed concern over ongoing loss of biodiversity in Britain (Defra 2013) which results in the degradation of ecosystems. A significant example of this conflict between requirement and loss is biotic pollination. An estimated 87.5 % of wild flowering plant species use animals as pollinators (Ollerton et al. 2011) and fruit or seed set of three quarters of the world's main food crop types are increased by animal pollination (Klein et al. 2007). Wild bees (Hymenoptera) are one of the major pollinators of angiosperms (Moldenke 1976; Simpson 1977; Klein et al. 2007) but their diversity and abundance is generally reduced in many regions (Frankie et al. 2009; Grixti et al. 2009; Potts et al. 2010; Leonhardt et al. 2013; Ollerton et al. 2014). There are many potential drivers which may affect wild pollinator abundance in particular. Among the most important ones are land use changes and fragmentation (Goulson et al. 2008; Winfree et al. 2009), environmental pollution and pesticides (Kevan et al. 1997; Rortais et al. 2005), alien species including both, plants and pollinators (Thomson 2006; Stout and Morales 2009), climate change (Dormann et al. 2008), and decreased resource diversity (Biesmeijer et al. 2006). This, however, applies more to the specialist species which require a particular habitat and depend on a selected range of flowers for diet and pollen. The species having a wide range of floral choice and nesting requirements generally do well by switching to alternative resources.

An estimated 272 species of bees live in a variety of landscapes in the United Kingdom (BWARS 2013a). The majority of these are non-social, "solitary" species, or primitively eusocial with no morphological differences between castes. However it is the social genera *Bombus* and *Apis*, which make up <10 % of British bee diversity, upon which research has been most focused (Goulson et al. 2008; EFSA 2014). Data from the other bees are fragmentary because of the lack of coordinated programmes (Potts et al. 2010). Analysing records of native bee species from before and after 1980, Biesmeijer et al. (2006) re-reported a 52 % decline of solitary bees in United Kingdom, whilst data going back to the mid Nineteenth Century demonstrates that 11 species of solitary bee have become extinct in Britain, though at least one had recolonised in recent times (Ollerton et al. 2014). Evidence such as this has resulted in 11 solitary bees belonging to the genera *Osmia*, *Nomada*, *Colletes*, *Andrena*, *Lasioglossum*, *Eucera* and *Anthophora* being listed as targets for conservation action (Natural England 2013).

Our understanding of urban bee ecology is limited. In a review, Hernandez et al. (2009) found only 59 research publications worldwide on urban bee ecology and concluded that we are only beginning to

document urban bee communities and their dynamics. The interest in urban bee ecology has surged in recent years (Everaars et al. 2011; Winfree et al. 2011; Hennig and Ghazoul 2012; Banaszak-Cibicka and Zmihorski 2012; Hinnens et al. 2012; Matteson et al. 2013; Verboven et al. 2014; Lowenstein et al. 2014; Baldock et al. 2015). However urbanisation is predicted to increase dramatically, with the number of people living in urban areas reaching 5 billion by 2030 (UN 2011). The expansion of the physical extent and increased density of the urban setting is occurring more rapidly than the increase in urban populations (Elmqvist et al. 2013), therefore more land will be used and reused to accommodate urban growth. Urbanisation can affect bee species in different ways, depending on the guilds to which they belong (Liow et al. 2001; Fetridge et al. 2008) and may increase or decrease bee species richness depending on variables such as taxon, spatial scale of analysis, and intensity of urbanisation. However in their reviews, Hernandez et al. (2009) and Winfree et al. (2011) suggested that overall urbanisation has a negative impact on bee species richness

Urbanisation can eliminate resources (Czech et al. 2000) and replace previous native habitats with a mosaic of buildings, parks, pavements, gardens and small spontaneous vegetation patches (French et al. 2005; Johnson and Klemens 2005). However, gardens and small weedy patches are also considered to have biodiversity value in urban habitat studies (Matteson et al. 2008; Sarah and Jeremy 2012; Larson et al. 2014; MacIvor et al. 2014), providing refuge, food and apposite habitats to various species (Gilbert 1989). These habitats may be diverse in nectar and pollen producing flowers and hence support a variety of pollinating insects (Harrison and Davies 2002; MacIvor et al. 2014; Larson et al. 2014) and also provide nesting resources for bees (Cane et al. 2006).

Although research has shown that urbanisation may have overall negative effects on the abundance and diversity of bees (Fetridge et al. 2008; Hernandez et al. 2009; Winfree et al. 2011; though see Baldock et al. 2015), every urban area has a unique developmental history, and more research is needed to discover whether these findings are more widely applicable. In this study we report the diversity and abundance of solitary and primitively eusocial bees in churchyards, gardens, roadsides and spontaneous vegetation patches within a 500 m radius of the centre of a large English town, compared with the nearby meadows and orchards located on the fringes of the town.

The study was conducted in the urban core of Northampton town (52°14'53"N, 0° 53'49"W) situated in the county of Northamptonshire, England (Fig. 1). We selected a 500 m radius from the geographical centre of the town which comprises an area of largely solid surface and limited areas of vegetation. A further eighteen sites were selected within the 500 m radius on the basis of accessibility (Table 1). As a comparison to the urban study six reference sites were selected within Northampton and its fringes which comprised local nature reserves, meadows and orchards (Table 1), which are close enough

(1600–5000 m from the centre) to share a similar local climate. The reason for selecting a comparatively higher number of urban sites was to include a wide range of habitats that represent urban vegetation such as churchyards, gardens, traffic roundabouts, road verges and spontaneous vegetation patches.

Bee surveys were conducted during 2012 from the first appearance of solitary and primitively eusocial bees in March and continued until October. All surveys took place between 10 a.m. and 5 p.m., on warm and sunny days (Cane et al. 2000). Two methods, hand netting (30 min/ site/survey) and pan traps (3 pan traps for 7 h/site/survey), were used in bee surveys to avoid any biases in catching specific species (Toler et al. 2005; Roulston et al. 2007; Grundel et al. 2011). The sites were divided into two sampling groups, each containing 9 urban and 3 reference sites, and surveyed every week with one or the other method. The order of site visits was randomised to ensure that all sites would receive roughly equal morning and afternoon sampling. High frequency surveys throughout the season are particularly important to record rare species and species that are active over a short period (Magurran and McGill 2011; Banaszak et al. 2014). The 15 days of observation (hand net plus pan traps) was combined to make a single sampling unit for analysis. The species that could not be identified in the field were collected in glass tubes and brought to the laboratory for identification. The individuals were killed with ethyl acetate and preserved for future reference. Bee species were identified using test keys from George Else and further confirmed/corrected by Mike Edwards.

For analysis of emergence and flight time of species, each month was divided into four quarters (Table 2). Each quarter consisted of 7 or 8 days, referred as "a week". The pan traps and hand netting observations were pooled in each relevant week as per dates of observations. The bee collection was started at the beginning of March. In the first week of March 2012 pan traps were installed but no bee individual was caught therefore we assumed that solitary and primitively eusocial bees were not in flight in that week or prior to it.

A Mantel test was performed to observe the spatial autocorrelation in data using the geographical distance and similarity matrix (Morisita Horn index) among the 18 urban sites. The Mantel test was carried out utilizing Xlstat software (Addinsoft 2014) and did not reveal autocorrelation (Mantel test, $r = 0.07$, $p = 0.18$, number of permutations = 1000). Rarefaction curves were calculated (Colwell et al. 2004, 2012) to estimate true species richness in urban and reference sites using the statistical software EstimateS 9.1 (Colwell 2013), with the data extrapolated up to 1000 samples to check the total expected number of species that had not been recorded. The species diversity among the sites was quantified by Simpson's diversity index (D) (Magurran 2004) which uses the following formula:

$$D = \frac{\sum n_i(n_i - 1)}{N(N - 1)}$$

Where n_i = the total number of organisms of each individual species

N = the total number of organisms of all species

Data were further analysed using SPSS 20 for Windows. Data were shown to be non-normally distributed using the Kolmogorov–Smirnov and Shapiro–Wilk test; therefore non-parametric tests were used for data comparison. Our data had a 3:1 ratio of urban to reference site surveys so to avoid any bias from unequal sampling we randomly selected samples using a random selection option in SPSS, to give a sample of urban sites equal to reference sites before comparing these sites. The Mann-Whitney U test (Fowler et al. 1998) was used to compare bee abundance, species richness and species diversity (Simpson's index) in urban and reference sites. The Kruskal–Wallis test (Fowler et al. 1998) was used to look for differences between sampling areas within urban and reference sites.

Results

A total of 3836 solitary and primitively eusocial bee individuals were found during the period of sampling, 3294 in the urban sites and 542 in the reference sites. Only 3.4 % of observed bees could not be identified, because of their condition following pan trapping. The remaining 96.6 % were identified to at least genus level, with 93.8 % of the total number of individuals identified to species level. Bees of 48 species belonging to 14 genera in 5 families were identified (Table 3). The family Andrenidae (12 spp., 38.8 % of total individuals) was present in all urban and reference sites and found to be the most abundant family, followed by Megachilidae (10 spp., 19.6 %), Halictidae (10 spp., 18.6 %), Apidae (12 spp., 16.4 %), and Colletidae (4 spp., 6.5 %).

All documented species were recorded at least in one urban site, and 37.5 % of the species were observed in ≥ 50 % of urban sites. Although 19 % of total recorded species in urban sites were not found at any reference sites, 48 % of the total species inventory (and 59 % of those recorded in reference sites) were found at 3 or more reference sites. Only 19 % of the species were represented by <10 individuals, of which 5 species were only recorded in at least one of the urban sites which includes the singletons of *Coelioxys quadridentata*, *Andrena chrysosceles* and *Nomada ruficornis*. The species inventory was dominated by ground nesting species and their cleptoparasites in urban (75 % spp., 26 soil nesting species and 10 cleptoparasites, of 48 species in total) and reference sites (76.9 % spp., 24 soil nesting species and 6 cleptoparasites, of 39 species in total). In contrast, only 25 % (12

spp. of 48 in total) and 23 % (9 spp. of 39 in total) of cavity nesting species were recorded in urban and reference sites, respectively. The proportion of solitary and primitively eusocial species was more or less equivalent in urban (52.1 % solitary, 27.1 % eusocial) and reference sites (53.8 % solitary and 30.8 % eusocial).

The bees started flying in the second week of March. Ten species of families Andrenidae, Apidae and Halictidae appeared at various sites during this first week of emergence. The number of species in flight continued to increase until mid May. The period of late spring and early summer was the richest in bee diversity where 30–39 species were observed in flight (Fig. 2). A little more than half (53 %) of the total observed species emerged in the first month (Fig. 2). The new species continued emerging until July, with no new species spotted in the months of August, September and October. Overall, a relatively higher number of species were observed in urban areas as compared to reference sites (Fig. 3). Many bee species were seen 1 or 2 weeks earlier in urban sites compared to reference sites. In the first week of emergence, no bees were observed at the reference sites compared with 10 species in urban sites. Later, in second week of emergence, five species were observed in flight at the reference sites compared with 13 species in urban sites.

The highest bee abundance was observed in the spring (March–May) and was dominated by the genus *Andrena*. The highest number of species (39 spp.) was active in this season but many of these species were also recorded in summer with a total of 38 species in flight. *Andrena bicolor*, was present in all urban and reference sites and was the most widespread. The most abundant species was *Osmia bicornis* which was observed in all urban and most (67 %) of the reference sites. *Megachile centuncularis*, *Hylaeus communis*, *Andrena flavipes*, *Lasioglossum villosulum*, and *Nomada fabriciana* were less abundant (each species represented by <1 % of total individuals) but present in a high percentage (40–60 %) of urban sites. Individuals from the family Colletidae were also predominantly found in urban sites (15 sites) whereas this family was represented by only 8 individuals at two reference sites. At one reference site, Abington Meadow (AM), a small meadow within an urban setting, 7 individuals of Colletidae were recorded and one individual was recorded in Wilson's Orchard (WO) which bordered the urban setting. *Colletes daviesanus* is a species often associated with manmade walls which it uses as a substitute for cliffs as a nest site. Hence the association with urban sites is not surprising.

Substantially more species were listed in urban sites, including a few parasitic species due to their association with their hosts. For example, *Melecta albifrons* was recorded in 76 % of urban sites due to the presence of its host *Anthophora plumipes* (BWARS 2013b). Over 90 % of observations of *A. plumipes* were recorded in 89 % of urban sites. This study also recorded the sporadic appearance of

Nomada species in urban sites, a genus that parasitises the *Andrena* group (BWARS 2013c). The species found only in urban sites are presented in Fig. 4. The comparison of species richness and abundance between urban and reference sites revealed the family Andrenidae and Apidae were widely distributed across both types of site, whereas the families Colletidae, Halictidae and Megachilidae were found to be significantly different in urban and reference sites (Table 4).

Rarefaction analysis showed we sampled effectively, with the accumulation curve beginning to plateau for urban sites and reference sites (Fig. 5). The curve rises rapidly in the beginning due to the appearance of a high number of species in the spring when we started sampling. We extrapolated results up to 1000 samples in urban and reference sites to check for potential species which had not been recorded. This showed a slight continuous increase in the curve for urban sites and an estimated 55 expected species (5.7 SD, in 1000 samples) against 48 observed. In contrast, for the reference sites the extrapolated curve plateaued after 1340 individuals estimating 41.2 expected species (with 2.4 SD, in 252 samples) against 39 observed.

The survey results revealed that the mean bee diversity and abundance were higher in urban sites (Table 5). The Mann-Whitney U test showed that the wild bee abundance ($U=3442$, $df=181$, $p<0.05$) and diversity (Simpson's Index, $U=3075$, $df=181$, $p<0.01$) were significantly different between urban and reference sites. In contrast, average species richness did not differ significantly between urban and reference sites ($U=3543$, $df=181$, $p=0.08$). Following the Kruskal-Wallis test for differences among urban and reference sites, solitary bee abundance ($\chi^2=48.6$, $df=17$, $p<0.01$), species richness ($\chi^2=46.7$, $df=17$, $p<0.01$) and species diversity (Simpson's Index) ($\chi^2=30.9$, $df=17$, $p<0.05$) were shown to vary among the urban sites. In contrast, reference sites were not found to be significantly different from each other in bee abundance ($\chi^2=7.6$, $df=5$, $p=0.17$), species richness ($\chi^2=8.8$, $df=5$, $p=0.11$) and diversity ($\chi^2=5.6$, $df=5$, $p=0.34$). This tells us that there is more local assemblage diversity amongst urban than reference sites.

Discussion

The limited studies published present a blurred image of the status and activities of solitary and primitively eusocial bees in urban settings in Britain because of differences in goals, methods and study sites for research. For example, some studies focused on gardens only (Smith et al. 2006; Owen 2010). Owen (2010) recorded biodiversity of a garden for about 30 years; the study produced comprehensive inventories but included only a single garden so it is impossible to know if it is representative of urban habitats. Michael (2009) assessed observations of solitary bees and wasps recorded from the 1970s onwards in woodlands, gardens and derelict sites of urban Sheffield. The use

of Malaise traps to census bees in those studies was a commonly used method (and also used in Owen 2010) but every recording method has its flaws and Malaise traps are less effective in recording some taxa of wild bees, such as Halictidae and Apidae (Joshua et al. 2007). Therefore a combination of methods is recommended to produce a comprehensive inventory of solitary bees (Grundel et al. 2011). More recently Baldock et al. (2015) compared pollinator assemblages using flower visitation networks in urban, farmland and nature reserve landscapes across 12 British towns and cities. Although they found no overall differences in species richness and individual abundance of pollinators between these landscapes, as far as solitary bees are concerned the study was limited in that surveys did not begin until late May, missing the emergence of many early species. Comparison of these studies with our findings is therefore difficult, though it is clear that urban settings can host significant diversity and abundance of solitary and primitively eusocial bees and other pollinating insects. Considering the previous literature and goals of this study, to produce a comprehensive inventory of an urban setting, we studied a highly urbanised area and surveyed using combined methods in all months when bees were active. In this study, we did not group sites into categories or habitats such as gardens or road verges, because (a) our aim was to assess the diversity of solitary and primitively eusocial bees in the town centre, therefore we tried to include all possible habitat types which attract bees; and (b) the study area is highly built-up therefore was also not possible to have many replicates of similar habitat types in some cases.

Recording species richness is crucial for effective conservation of biodiversity. This study recorded about 22 % of the total species and 58 % of the total genera of solitary and primitively eusocial bees of the UK within a 500 m radius of a highly urbanised central town area, demonstrating the potential of urban settings for conservation of bees. Despite differences in methods and size of study sites, our species richness results are comparable with other studies of urban areas (Table 6). The noteworthy higher number of species listed by Michael (2009) in Sheffield reflected the wider range of sites where bees were recorded *Lasioglossum smeathmanellum* in urban sites, because of their nesting habit in the soft mortar of building walls. As noted above, similar reasoning explains the association of *Colletes daviesanus* with urban sites.

However, every urban setting has a unique developmental history that has influenced building heritage, microenvironments and survival of remnant habitats. Therefore, the history and geography of a town or city will consequently have an impact on the possible assemblages of solitary and primitively eusocial bees. Many bee species are confined to a particular geographical range. For example, *Lasioglossum fratellum*, the most common species recorded in the urban study in Sheffield by Michael (2009), was not observed in our study in Northampton. This may be primarily because *L.*

fratellum is mainly found in northern areas, though also associated with acidic sites in southern England. In contrast, *Lasioglossum morio* was found to be common in this study but was not present in the species list of Michael's (2009) study in Sheffield, perhaps because it is much more rare in northern England.

The species of family Colletidae were found associated mainly with urban sites, with few individuals found in reference sites. The latter were located at urban fringes bordering the residential areas or in some cases (Bradlaugh Fields and Abington Meadow) surrounded by houses. This produced a mosaic of urban features with natural sites at a broader scale, allowing pollinating insects to commute to the surrounding landscape in search of resources. Goddard et al. (2010) suggested that various floral patches including gardens and parks could be considered as contiguous resources by insects. Therefore, it is likely that those species living in the urban gardens benefit from the neighbouring meadows and nature reserves.

We recorded relatively higher numbers (36.7 % of total records) of individuals of Andrenidae in urban areas. This family largely consists of ground nesting species that are seen foraging in spring. A high abundance of this family was also recorded in the city of Poznan, Poland (Banaszak-Cibicka and Zmihorski 2012). In contrast, a few studies (e.g. Matteson et al. 2008; Owen 2010) reported a low diversity of Andrenidae in urban settings. Scarceness of these species probably reflects the insufficient food resources in spring (Matteson et al. 2008). Moreover, these studies were limited to urban gardens, whereas our study found that 60 % of Andrenidae records (from 6 of 18 of urban sites) were from wild patches or road sides with abundant wild flowers, particularly dandelion (*Taraxacum officinale* agg.). From the recorded flower-bee interactions, we observed 66 % of Andrenidae foraging on dandelion flowers, while the rest (33 %) were found on 15 different plant genera in urban sites. This confirms Perkins's (1919) observations of an association between *Andrena* and habitats containing abundant dandelion flowers in Britain. However, these early spring species often forage at garden fruit trees (Perkins 1919). Our garden sites had a few fruit trees but our search for bees was limited to accessible parts of gardens such as lawn (where present), flower beds, and shrubs. Foragers on trees out of our visual range would have not been recorded unless caught in pan traps installed every week on the ground.

Our study recorded *Coelioxys quadridentata*, a rare cleptoparasitic species in the United Kingdom (Falk 1991). However, *C. quadridentata*, is flexible in host selection having many known hosts such as *Anthophora furcata* (Rowson and Pavett 2008; Mike Edwards unpublished data), *Anthophora bimaculata* (Jørgensen 1921), *Anthophora quadrimaculata* and *Megachile circumcincta* (Rowson and Pavett 2008). Our study only recorded *Anthophora quadrimaculata* as a possible host, and both host

and parasite were found at the same site and time. Therefore we conclude that *C. quadridentata* was a cleptoparasite of *A. quadrimaculata*. A similar association of both species was also observed by D.B. Baker (pers. comm.) in Surrey, England. Although the habitat preferences of *C. quadridentata* are not known, flexibility in host selection of this species (Rowson and Pavett 2008) further increases the potential for its conservation in varied habitats, including urban settings.

A high abundance of bees in spring was anticipated as most bee species become active in this season (Wolda and Roubik 1986). About 75 % of the flowering species in the United Kingdom produce flowers from March till June (Fitter and Peat 1994). Therefore more flower-visiting insects are to be expected in this season, which is confirmed by this study; about 50 % of the species we recorded emerged in the first month of the season. Species records were dominated by the genera *Andrena*, *Osmia* and *Anthophora*, all of which are predominantly spring foraging taxa. Similar seasonal predictability was also observed by Tommasi et al. (2004) in urban gardens and parks of Vancouver, Canada. Though the members of various bee families were present in more than one season, these families exhibited a notable dominance in particular seasons. For example, species of Andrenidae, Apidae and Megachilidae were highly dominant in the spring season. In such taxa adults mature in summer or autumn and remain in cells during the unfavourable seasons (Michener 2007). They emerge from the cells in spring or summer and construct new nests. Conversely in other families such as Halictidae, pupation occurs in summer (Michener 2007). The resulting adults emerge next summer and visit summer and autumn flowers; therefore most of the Halictidae species were seen in the summer season.

The urban landscape is a result of direct human activities which are reflected in the physical environment of the area. In this manmade landscape, people add maintained patches and alter the range of plants, some of which are potential bee resources. In addition, every urban area has a different economic, historical and geographical scenario, and therefore we expect a varied response of species to urbanisation (McKinney 2008). A heterogeneous urban environment will have a complex matrix of habitat and available resources and it was suggested that urban heterogeneity has a close relationship with insect diversity and abundance (Frankie and Ehler 1978; Smith et al. 2006). Moreover, floral diversity (Gaston et al. 2005; Wojcik 2011) and green areas (Hennig and Ghazoul 2012) within urban landscapes have proven to have a positive impact on bee diversity. In our study, the extent of resources available for bees varied across the urban sites. Churchyards and gardens had a different diversity of plant species depending on the gardener's choice. On the other hand the floral composition of weedy leftover patches and roadside vegetation was not only entirely different to those in churchyards and gardens, but also vegetation was mowed frequently leaving no flowers for a

short period of time. This could have affected the bee assemblage and abundance across the urban site and will be assessed in future analyses.

Some studies have compared bee communities in urban and natural areas and documented a higher abundance and richness of bee species in natural habitats (Matteson et al. 2008; Fretwell et al. 2008). However, Kearns and Oliveras (2009) did not find species richness and abundance of bees in urban sites significantly different from those in remote areas of Boulder, Colorado. Winfree et al. (2007) found higher bee abundance in urban and suburban rather than natural forests in New Jersey (U.S.A.) and suggested a moderate level of anthropogenic disturbance can benefit many bee species. Our study found the urban landscape to have a more abundant and diverse solitary and primitively eusocial bee assemblage. However one possible reason for the high abundance of bees in urban landscapes is the presence of high floral diversity (Gaston et al. 2005; Lorm et al. 2007) and heterogeneity (Gilbert 1989) which supports a wide array of bee species.

Overall, our results indicate a very encouraging finding in relation to the conservation of bees in urban settings. Finding a high diversity and abundance in the urban core and a subset of that diversity in surrounding nature reserves and meadows of relatively much larger size, accentuates the ecological and conservation value of gardens and small weedy sites within British towns and cities (see also Baldock et al. 2015). Moreover, it gives a broader perspective that the urban landscape may also act as a refuge to these bees and serve as a base to disperse from into the connecting landscape. Apart from urban gardens which provide diverse resources, leftover wild patches and roadsides are equally important for conservation of solitary and primitively eusocial bees, and provide different resources to managed gardens. These findings add weight to the argument that anthropogenic habitats can support pollinator assemblages that are as diverse and abundant as sites of specific nature conservation value (Tarrant et al. 2013) and contribute to the landscape-level conservation of pollinators in Britain.

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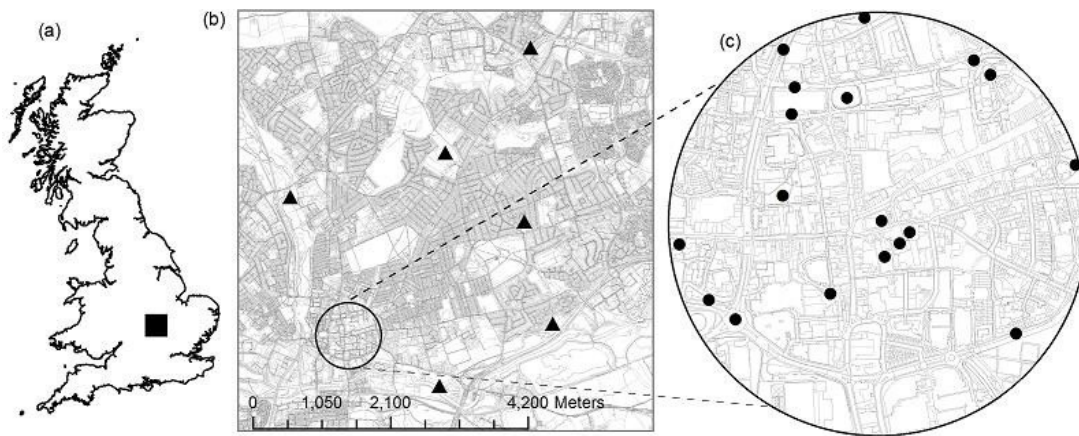


Fig. 1 Distribution of study sites: a location of Northampton in Great Britain b Northampton town, circle representing 500 m radius of town marked for urban sites and distribution of reference sites (triangles) in relation to town centre c distribution of urban sites within circle of 500 m radius. Data and map Crown Copyright/database right 2013. An Ordnance Survey/EDINA supplied service

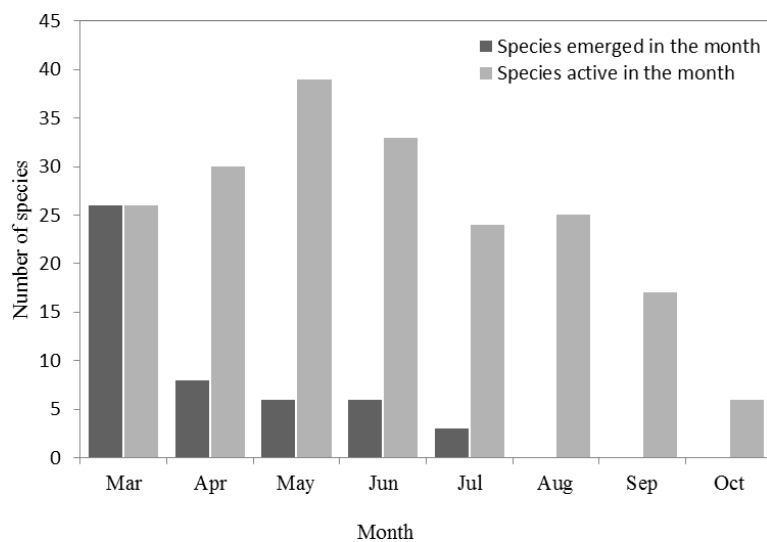


Fig. 2 Number of solitary and primitively eusocial bee species emerged and total species observed in flight during 2012. This includes the species detected in both urban and reference sites. Some species produce more than one generation in a year; for example *Andrena flavipes* was observed in the field from March to May and then from July to September; only the first emergence of such species is included in the figure

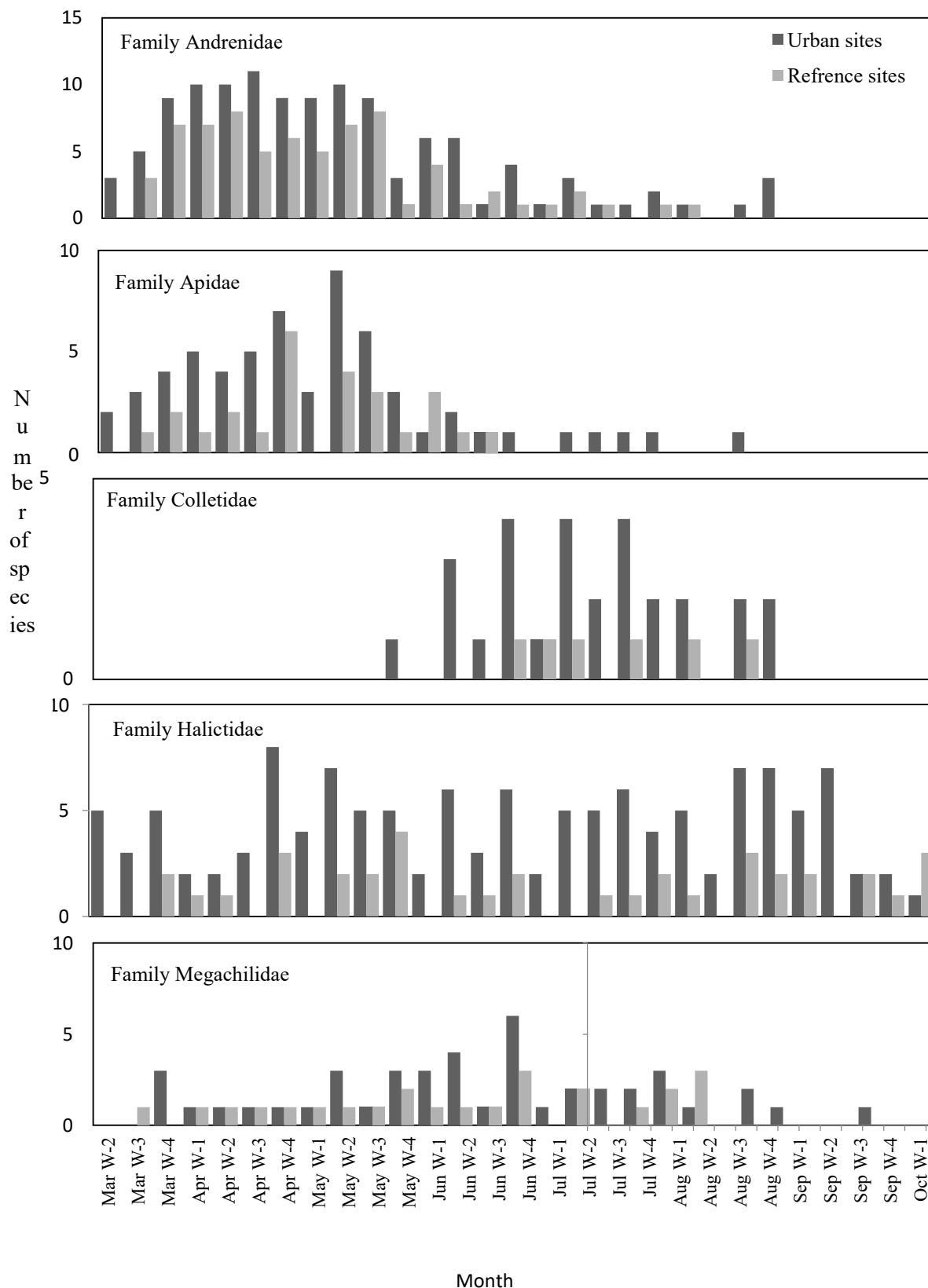


Fig. 3 Number of species observed of bee families in urban and reference sites in field season 2012. (Note y-axis varies). The figure only includes the species detected in the field. We surveyed from the beginning of March to late October. No solitary bee individual was detected in the first week of March or after second week of October.

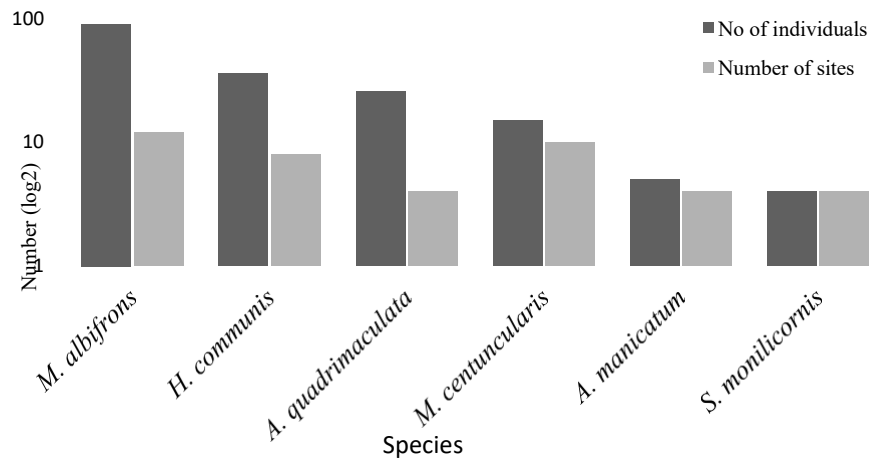


Fig. 4 Abundance and distribution of selected bee species found only in urban areas (Three species *Nomada ruficornis*, *Andrena chrysosceles* and *Coelioxys quadridentata* were only represented by one individual and are therefore not included)

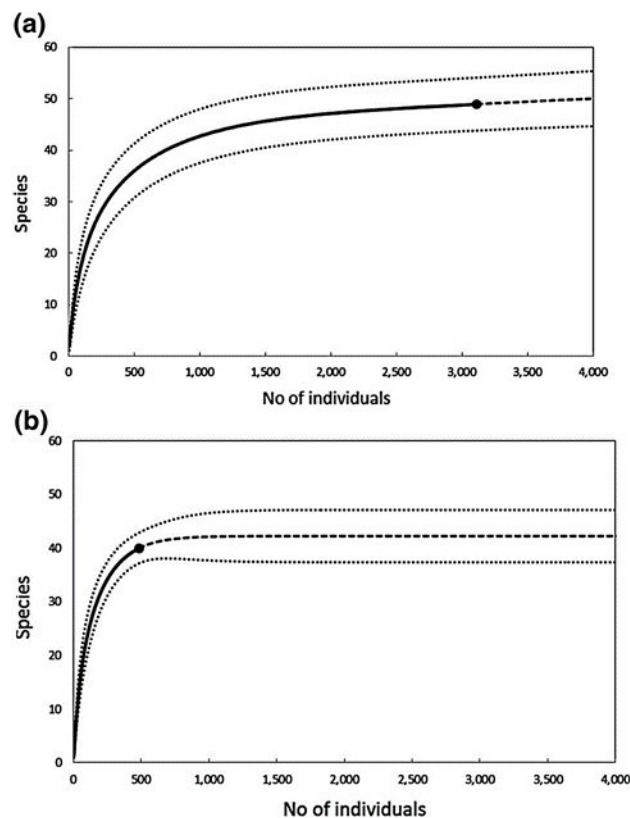


Fig. 5 Species accumulation curves using interpolation (solid curves) and extrapolation (dash curves) with 95 % confidence intervals calculated using EstimateS 9.0 (Colwell 2013), species richness and individuals observed during sampling period are indicated by solid circles a in urban sites and b in reference sites

Table 1 List of the sites surveyed for bees in and around Northampton, with their descriptions and size

Site name	Size (m ²)	Brief description of the site
All Saints Church (ASC)	1287	A churchyard with planted flowers at margin and a well maintained lawn which was mown frequently
St Giles Church (SGC)	7556	A churchyard with planted flowers at margin, the lawn was covered with a number of trees and was mown frequently
Church of the Holy Sepulchre (HSC)	8217	A churchyard with a few flowers planted at one side of the church. A number of trees were present at the sides and lawn was mown frequently
New Testament Church (NTC)	5383	A church yard with few wild flowers at the sides and walls, with number of trees and lawn was mown frequently
St Peter's Church (SPC)	1669	A churchyard with a few planted flowers at the front, lawn was mown frequently
County Club Garden (CCG)	330	A small garden with exotic flowers exposed to sunlight and had a very small lawn which was mown very frequently
County Hall Garden (CHG)	662	A small garden with exotic flowers surrounded by buildings and lawn was mown very frequently. The garden was shaded by the buildings
County Car Park (CCP)	6380	A car park where surface was not paved. It had a small vegetation patch of wild flowers which was not maintained at all
Island Bus Station (IBS)	2911	A round island surrounded by roads. It produced a wide range of wild flowers which were mown regularly every 4–6 weeks
Island Kingswell (IKW)	90	A small wild vegetation patch surrounded by the paved surfaces, buildings, roads and parking lots. Vegetation was cleared every year
Broad Street Verge (BSV)	517	A road verge with wild flowers, where vegetation was cleared every year except a few shrub species
Mayorhold South Verge (MSV)	964	A road verge with wild flowers, where vegetation was cleared every year except a few shrub species
Mayorhold North Verge (MNV)	754	A road verge with wild flowers, where vegetation was cleared every year except a few shrub species
Ladys Lane Verge (LLV)	314	A triangular wild vegetation patch, surrounded by roads on all sides. The vegetation was removed every year except a few shrub species
Mounts Open Vegetation (MOV)	1303	Open wide vegetation patch with wild flowers and few trees surrounded by houses and road. Site was mown every 4–6 weeks
Victoria Promenade Verge (VPV)	990	A road verge with few trees, shrubs and a mix of wild and planted flowers in spring and summer
St Peter's Way Verge (PWV)	400	A road verge with wild flowers exposed to sun and was mown frequently 4–6 week time
St Peter's Way Roundabout (PRI)	711	A traffic roundabout island with wild flowers and few trees. The ground was mown frequently in 4–6 weeks
Bradlaugh Fields (BF)*	82,124	A wild life park and local nature reserve
The Barnes Meadow (BM)*	41,856	A local nature reserve, managed by grazing
Kingsthorpe Meadow LNR (KM)*	96,591	Local nature reserve, managed by grazing
Wilson's Orchard (WO)*	20,220	An orchard with apple trees at the fringes of town
Abington Meadow (AM)*	21,043	A small meadow inside the Northampton with a few trees
Child First Orchard (CF)*	8827	A small orchard and garden inside a small forest patch at the fringes of town

* Non-urban reference sites are marked

Table 2 Week dates for bee sampling: each month was divided into four quarters and each quarter assumed to be "'a week'

Week one (W-1)	Day 1–7 of the month (7 days)
Week two (W-2)	Day 8–15 of the month (8 days)
Week three (W-3)	Day 16–23 of the month (8 days)
Week four (W-4)	Day 24–30/31 of the month (7/8 days)

Table 3 Solitary and primitively eusocial bee species collected from 18 urban and 6 reference sites in Northampton, England in 2012

Species	% urban sites where present (n = 18)	% reference sites where present (n = 6)	Relative abundance (n = 3836) ^a	% abundance urban sites ^b	% abundance reference site ^b
<i>Andrena bicolor</i> Fabricius, 1775	100	100	9.7	88.2	11.8
<i>Andrena carantonica</i> Pe´rez, 1902	44	50	1.4	66.7	33.3
<i>Andrena chrysosceles</i> (Kirby, 1802)	5.6	Absent	0.03	100	Absent
<i>Andrena cineraria</i> (Linnaeus, 1758)	50	67	4.9	83	17
<i>Andrena dorsata</i> (Kirby, 1802)	72	83	4.7	83.8	16.2
<i>Andrena flavipes</i> Panzer, 1799	44	33	0.9	73.5	26.5
<i>Andrena fulva</i> (Mu¨ller, 1766)	56	67	1.4	73.1	26.9
<i>Andrena haemorrhoa</i> (Fabricius, 1781)	67	83	2.1	67.1	32.9
<i>Andrena minutula</i> (Kirby, 1802)	83	67	3.4	85.6	14.4
<i>Andrena nigroaenea</i> (Kirby, 1802)	78	67	2.2	72.6	27.4
<i>Andrena nitida</i> (Mu¨ller, 1776)	89	83	5.0	79.6	20.4
<i>Andrena</i> spp.	83	83	1.6	80.6	19.4
<i>Andrena tibialis</i> (Kirby, 1802)	33	50	0.5	50	50
<i>Anthidium manicatum</i> Linnaeus, 1758	22	Absent	0.1	100.0	Absent
<i>Anthophora plumipes</i> (Pallas, 1772)	89	100	8.6	90.9	9.1
<i>Anthophora quadrimaculata</i> (Panzer, 1798)	22	Absent	0.7	100	Absent
<i>Chelostoma campanularum</i> (Kirby, 1802)	5.6	17	0.1	50	50
<i>Coelioxys quadridentata</i> (Linnaeus, 1758)	5.6	Absent	0.03	100	Absent
<i>Coelioxys</i> spp.	11	Absent	0.1	100.0	Absent
<i>Colletes daviesanus</i> Smith, 1846	17	17	0.7	85.7	14.3
<i>Halictus rubicundus</i> (Christ, 1791)	28	50	0.4	71.4	28.6
<i>Halictus tumulorum</i> (Linnaeus, 1758)	28	67	0.4	58.8	41.2
<i>Hylaeus communis</i> Nylander, 1852	44	Absent	0.9	100	Absent
<i>Hylaeus hyalinatus</i> Smith, 1842	72	17	2.1	97.5	2.5
<i>Hylaeus signatus</i> (Panzer, 1798)	44	33	2.5	97.9	2.1
<i>Hylaeus</i> spp.	17	Absent	0.1	100	Absent
<i>Lasioglossum leucozonium</i> (Schränk, 1781)	28	33	0.4	78.6	21.4
<i>Lasioglossum pauxillum</i> (Schenck, 1853)	17	33	0.4	87.5	12.5
<i>Lasioglossum albipes</i> (Fabricius, 1781)	56	50	1.5	91.5	8.5
<i>Lasioglossum calceatum</i> (Scopoli, 1763)	67	50	1.8	95.7	4.3
<i>Lasioglossum lativentre</i> (Schenck, 1853)	33	17	0.3	91.7	8.3
<i>Lasioglossum malachurum</i> (Kirby, 1802)	33	50	0.8	38.7	61.3
<i>Lasioglossum morio</i> (Fabricius, 1793)	78	67	6.1	94.4	5.6
<i>Lasioglossum smeathmanellum</i> (Kirby, 1802)	67	17	4.2	98.8	1.2
<i>Lasioglossum</i> spp.	33	67	0.4	66.7	33.3
<i>Lasioglossum villosulum</i> (Kirby, 1802)	44	50	0.6	81.8	18.2
<i>Megachile centuncularis</i> (Linnaeus, 1758)	56	Absent	0.4	100	Absent
<i>Megachile ligniseca</i> (Kirby, 1802)	22	33	0.3	33.3	66.7
<i>Megachile</i> spp.	28	17	0.3	92.3	7.7
<i>Megachile willughbiella</i> (Kirby, 1802)	17	17	0.2	83.3	16.7
<i>Melecta albifrons</i> (Forster, 1771)	67	Absent	2.4	100	Absent
<i>Nomada fabriciana</i> (Linnaeus, 1767)	44	67	0.5	76.2	23.8
<i>Nomada flavoguttata</i> (Kirby, 1802)	17	33	0.1	60	40
<i>Nomada flava</i> Panzer, 1798	27	50	1.5	40	60
<i>Nomada goodeniana</i> (Kirby, 1802)	67	67	1.3	83.7	16.3
<i>Nomada marshalli</i> (Kirby, 1802)	39	33	0.4	71.4	28.6
<i>Nomada panzeri</i> Lepeletier, 1841	17	17	0.3	90	10

Table 3 continued

Species	% urban sites where present (n = 18)	% reference sites where present (n = 6)	Relative abundance (n = 3836) ^a	% abundance urban sites ^b	% abundance reference site ^b
<i>Nomada ruficornis</i> (Linnaeus, 1758)	5.6	Absent	0.03	100	Absent
<i>Nomada</i> spp.	33	33	0.4	57.1	42.9
<i>Osmia caerulea</i> (Linnaeus, 1758)	28	17	0.4	80.0	20.0
<i>Osmia leaiana</i> (Kirby, 1802)	28	17	0.3	90.9	9.1
<i>Osmia bicornis</i> (Linnaeus, 1758)	100	67	16.8	92.1	7.9
<i>Osmia spinulosa</i> (Kirby, 1802)	5.6	33	0.2	16.7	83.3
<i>Sphecodes monilicornis</i> (Kirby, 1802)	22	Absent	0.1	100	Absent

The bee individuals that could not be identified to species level are recorded with relevant genus name followed by spp.

- a Relative abundance of species observed in 18 urban and 6 reference sites
- b Percentage of the total number of the individuals of a species observed in 18 urban and 6 reference site

Table 4. Results of Mann-Whitney U test for the differences in average species richness and abundance of solitary bee families among urban and reference sites. The significant results are highlighted in bold.

Bee families	Bee abundance		Species richness	
	<i>U</i>	<i>p</i>	<i>U</i>	<i>p</i>
Andrenidae	4046	0.76	3804	0.25
Apidae	3737	0.17	3962	0.56
Colletidae	3246	<0.01	3270	<0.01
Halictidae	3337	<0.05	3435	<0.05
Megachilidae	3414	<0.05	3534	<0.05

Table 5 Descriptive statistics of bee abundance, species richness and diversity for the sites surveyed in 2012 (data pooled for 15 days includes 30 min hand netting and 7 h pan traps)

Sites	Descriptive statistics					Diversity and richness		
	N	Min	Max	Mean	SD	Simpson's diversity (D)	Species abundance	Species richness
ASC	16	0	48	13.2	17.2	0.18	206	18
BSV	16	0	199	5.0	4.8	0.17	72	18
CCG	16	0	54	20.4	14.7	0.14	310	27
CCP	16	0	34	10.6	8.5	0.12	146	22
CHG	16	0	11	3.4	3.2	0.14	50	14
HSC	16	0	50	11.3	16.4	0.08	175	21
IBS	16	0	133	26.6	41.7	0.13	410	30
IKW	15	0	62	18.4	16.0	0.1	264	22
LLV	16	0	40	12.3	11.5	0.08	187	29
MNV	16	0	6	1.1	1.7	0.18	17	07
MOV	15	0	66	14.7	20.7	0.16	207	24
MSV	15	0	34	12.0	9.7	0.09	170	25
NTC	15	0	26	9.5	7.8	0.13	131	20
PRI	16	0	54	10.7	17.3	0.14	163	20
PWV	16	0	41	8.1	12.4	0.11	123	18
SGC	16	0	57	14.9	16.8	0.1	220	29
SPC	15	0	31	8.6	9.9	0.09	123	18
VPV	16	0	77	8.9	20.2	0.29	139	13
AM*	15	0	28	7.8	7.7	0.08	102	29
BF*	16	0	33	7.9	9.1	0.06	116	26
BM*	15	0	36	6.2	11.5	0.1	91	18
CF*	15	0	13	3.7	5.2	0.34	49	09
KM*	15	0	18	4.7	1.6	0.11	58	13
WO*	15	0	29	5.3	8.6	0.12	68	19
Urban sites	283	0	133	11.64	8.27	0.077	3294	48
Reference sites	91	0	36	5.96	16.99	0.053	542	39

Diversity and richness excludes the individuals which could not be identified to species level. Sites are arranged in alphabetical order.

N = number of sampling units. For abbreviations see Table 1

* Reference sites are marked

Table 6 Selected literature which recorded solitary and primitively eusocial bees from urban sites

Study reference	Solitary bee species	No of individuals caught	Study sites	Place	Duration
This study	48	3294	Garden, churchyard, road sites, roundabout, wild patches	Northampton, United Kingdom	1 year
Matteson et al. (2008)	48	944	Gardens	New York City, United States	4 years
Michael (2009)	69	590	Garden, derelict land, woodlands	Sheffield, United Kingdom	[20 years
Owen (2010)	45	6686	Single garden	Leicester, United Kingdom	[20 years
Hennig and Ghazoul (2012)	44	508	Garden, roadsides, parks	Zurich, Switzerland	1 year
Hinners et al. (2012)	84	6777	Grassland	Colorado, USA	2 years
Banaszak-Cibicka and Zmihorski (2012)	92	1809	Green areas, home Garden, botanical garden, meadow, Parks, cemeteries, neighbourhood blocks	Pozan, Poland	3 years
Matteson et al. (2013)	41	521		New York City, USA	2 years
Lowenstein et al. (2014)	32	368	Neighbourhood blocks	Chicago, USA	1 year

References:

- Addinsoft (2014) XLSTAT, Data analysis and statistics with MS Excel. Addinsoft, NY, USA.
- Baldock KCR, Goddard MA, Hicks DM, Kunin WE, Mitschunas N, Osgathorpe LM, Potts SG, Robertson KM, Scott AV, Stone GN, Vaughan IP, Memmott J. (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proc Roy Soc B* 282: <http://dx.doi.org/10.1098/rspb.2014.2849>
- Banaszak J, Banaszak-Cibicka W, Szefer P (2014) Guidelines on sampling intensity of bees (Hymenoptera: Apoidea: Apiformes). *J Insect Conserv* 18:651-656
- Banaszak-Cibicka W, Zmihorski M (2012) Wild bees along an urban gradient: winners and losers. *J Insect Conserv* 16:331-343
- Biesmeijer JC, Roberts SP, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect pollinated plants in Britain and the Netherlands. *Science* 313:351–354
- Butchart SH, Walpole M, Collen B, van Strien A, Scharlemann JP, Almond RE, Baillie JE, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Csirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD, Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TE, Pauly D, Quader S, Revenga C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R. (2010) Global biodiversity: indicators of decline. *Science* 328:1164-1168
- BWARS (2013a) List of British and Irish aculeate Hymenoptera (January 2012), Bees, Wasp and Ants Recording Society. <http://www.bwars.com/index.php?q=content/checklist-british-and-irish-aculeate-hymenoptera-0> Accessed 15 September 2013
- BWARS (2013b) *Melecta albifrons* (Forster, 1771), Bees, Wasp and Ants Recording Society. <http://www.bwars.com/index.php?q=bee/apidae/melecta-albifrons> Accessed 10 September 2013
- BWARS (2013c) *Nomada signata* (Jurine, 1807), Bees, Wasp and Ants Recording Society. <http://www.bwars.com/index.php?q=bee/apidae/nomada-signata> Accessed 10 September 2013
- Cane JH, Minckley R, Kervin L (2000) Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *Journal Kansas Entomol Soc* 73:225–231
- Cane JH, Minckley RL, Kervin LJ, Roulston TH, Williams NM (2006) Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecol Appl* 16:632–644
- Colwell RK (2013) EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's guide and application. <http://purl.oclc.org/estimates> Accessed 15 September 2013
- Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JL (2012) Models and estimators linking individual-based and sample-based rarefaction, extrapolation, and comparison of assemblages. *J Plant Ecol* 5:3-21
- Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating and comparing incidence-based species accumulation curves. *Ecology* 85:2717-2727

- Czech B, Krausman PR, Devers PK (2000) Economic associations among causes of species endangerment in the United States. *Bioscience* 50:593–601
- Defra (2013) The State of Natural Capital: Towards a framework for measurement and valuation. A report from the Natural Capital Committee. <http://www.defra.gov.uk/naturalcapitalcommittee/files/State-of-Natural-Capital-Report-2013.pdf>. Accessed 10 September 2013
- Dormann CF, Schweiger O, Arens P, Augenstein I, Aviron S, Bailey D, Baudry J, Billeter R., Bugter, R, Bukáček R, Burel F, Cerny M, Cock RD, De Blust G, DeFilippi R, Diekötter T, Dirksen J, Durka W, Edwards PJ, Frenzel M, Hamersky R, Hendrickx F, Herzog F, Klotz S, Koolstra B, Lausch A, Le Coeur D, Liira J, Maelfait JP, Opdam P, Roubalova M, Schermann-Legionnet A, Schermann N, Schmidt T, Smulders M J, Speelmans M, Simova P, Verboom J, van Wingerden W, Zobel M (2008) Prediction uncertainty of environmental change effects on temperate European biodiversity. *EcolLett* 11:235–244
- EFSA (2014) Towards an integrated environmental risk assessment of multiple stressors on bees: review of research projects in Europe, knowledge gaps and recommendations. *EFSA Journal* 12:3594 doi:10.2903/j.efsa.2014.3594
- Elmqvist J, Fragkias M, Goodness J, Güneralp B, Marcotullio PJ, McDonald RI, Parnell S, Schewenius M, Sendstad M, Seto KC, Wilkinson K (2013) *Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities*. Springer, New York
- Everaars J, Strohbach MW, Gruber B, Dormann CF (2011) Microsite conditions dominate habitat selection of the red mason bee (*Osmiabicornis*, Hymenoptera: Megachilidae) in an urban environment: A case study from Leipzig, Germany. *Landscape Urban Plan* 103:15–23
- Falk S (1991) A review of the scarce and threatened bees, wasps and ants of Great Britain. Research and Survey in Nature Conservation No. 35. Nature Conservancy Council for England, Peterborough
- Fetridge ED, Ascher JS, Langellotto GA (2008) The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea). *Ann Entomol Soc Am* 101:1067–1077
- Fitter AH, Peat HJ (1994) The ecological flora data base. *JEcol* 82:415–425
- Fowler L, Cohen L, Jarvis P (1998) *Practical Statistics for Field Biology*, 2nd edition. John Wiley and Sons Ltd, Chichester
- Frankie GW, Rizzardi M, Vinson SB, Griswold TL (2009) Decline in bee diversity and abundance from 1972–2004 on a flowering leguminous tree, *Andira inermis* in Costa Rica at the interface of disturbed dry forest and the urban environment. *J Kans Entomol Soc* 82:1–20
- Frankie GW, Ehler LE (1978) Ecology of insects in urban environments. *Ann Rev Entomol* 23:367–387
- French K, Major R, Hely K (2005) Use of native and exotic garden plants by suburban nectarivorous birds. *Biol Cons* 121:545–559
- Gaston K, Smith R, Thompson K, Warren P (2005) Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. *Biodivers Conserv* 14:395–413
- Gilbert OL (1989) *The Ecology of Urban Habitats*. Chapman and Hall, London
- Goddard MA, Dougill AJ, Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends Ecol Evol* 25:90–98

- Goulson D, Lye GC, Darvill B (2008) Decline and conservation of bumble bees. *AnnRevEntomol* 53:191–208
- Grixti CJ, Wong LT, Cameron SA, Favret C (2009) Decline of bumble bees (*Bombus*) in the North American Midwest. *Biol Cons* 142:75-84
- Grundel R, Fronhnapple KJ, Jean RP, Pavlovic NB (2011) Effectiveness of bowl trapping and netting for inventory of a bee community. *Environ Entomol* 40:274-380
- Harrison C, Davies G (2002) Conserving biodiversity that matters: practitioners' perspectives on brownfield development and urban nature conservation in London. *J Environ Manage* 65:95–108
- Hennig EI, Ghazoul J (2012) Pollinating animals in the urban environment. *Urban Ecosyst* 15:149-166.
- Hernandez JL, Frankie GW, Thorp RW (2009) Ecology of urban bees: A review of current knowledge and directions for future study. *Cities Environ* 2:article 3 <http://escholarship.bc.edu/cate/vol2/iss1/3>
- Hinners SJ, Kearns CA, Wessman CA (2012) Role of scale, matrix and native habitat in supporting a diverse suburban pollinator assemblage. *EcolAppl* 22:923-1935
- Johnson EA, Klemens MW (2005) *Nature in fragments: the legacy of sprawl*. Columbia University Press, New York
- Jørgensen, P (1921) *Bier.Danmarks Fauna* 25. G.E.C.Gads, København.
- Joshua W, Campbell J, Hanula L (2007) Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. *J Insect Conserv* 11:399-408
- Kearns CA, Oliveras DM (2009) Environmental factors affecting bee diversity in urban and remote grassland plots in Boulder, Colorado. *J Insect Conserv* 13:655–665
- Kevan PG, Greco CF, Belaoussoff S (1997) Log-normality of biodiversity and abundance in diagnosis and measuring of ecosystemic health: pesticide stress on pollinators on blueberry heaths. *JApplEcol* 34:1122–1136
- Klein AM, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham S, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. *Proc Roy Soc B* 274:303–313
- Larson JL, Kesheimer AJ, Potter DA (2014) Pollinator assemblage on dandelion and white clover in urban and suburban lawns. *J Insect Conserv* 18:863-873
- Leonhardt SD, Gallai N, Garibaldi LA, Kuhlmann M, Klein A (2013) Economic gain, stability of pollination and bee diversity decrease from southern to northern Europe. *Basic ApplEcol* 14:461-471
- Liow LH, Sodhi NS, Elmquist T (2001) Bee diversity along a disturbance gradient in tropical lowland forests of south-east Asia. *J Appl Ecol* 38:180-192
- Loram A, Tratalos J, Warren P, Gaston K (2007) Urban domestic gardens (X): the extent and structure of the resource in five major cities. *Landsc Ecol* 22:601–615
- Lowenstein DM, Matteson KC, Xiao I, Silva AM, Minor ES (2014) Humans, bees, and pollination services in the city: the case of Chicago, IL (USA). *Biodivers Conserv* 23:2857–2874.
- MacIvor JS, Ruttan A., Salehi B (2014) Exotic on exotics: pollen analysis of urban bees visiting Sedum on a green roof. *Urban Ecosyst*. doi: 10.1007/s11252-014-0408-6
- Magurran AE (2004) *Measuring biological diversity*. Blackwell, Malden

- Magurran AE, McGill BJ (2011) Biological diversity, frontiers in measurement and assessment. Oxford University Press, Oxford
- Matteson KC, Ascher JS, Langellotto GA (2008) Bee richness and abundance in New York City urban gardens. *Ann Entomol Soc Am* 101:140-150
- Matteson KC, Grace JB, Minor ES (2013) Direct and indirect effect of land use on floral resources and flower-visiting insects across an urban landscape. *Oikos* 122:682-69
- McKinney ML (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosyst* 11:161–176
- Michael A (2009) The solitary wasps and bees (Hymenoptera: Aculeata) of the 'GREEN SPACES' of urban Sheffield. *Entomol Mon Mag* 145:11-25
- Michener CD (2007) Bees of the world. 2nd edit. Maryland. The Johns Hopkins University Press
- Moldenke AR (1976) California pollination ecology and vegetation types. *Phytologia* 34:305-361
- Natural England (2013) Habitats and species of principal importance in England, Natural England. <http://www.naturalengland.org.uk/ourwork/conservation/biodiversity/protectandmanage/habsandspeciesimportance.aspx>. Accessed 12 September 2013
- Ollerton J, Tarrant S, Winfree R (2011) How many flowering plants are pollinated by animals? *Oikos* 120: 321–326
- Ollerton J, Erenler H, Edwards M, Crockett, R (2014) Extinctions of aculeate pollinators in Britain and the role of large-scale agricultural changes. *Science* 346:1360-1362
- Owen J (2010) Wildlife of a garden: a thirty-year study. Royal Horticultural Society, Peterborough
- Perkins RCL (1919) The British species of *Andrena* and *Nomada*. *TransEntomolSoc London* 1919: 218-319
- Potts SG, Biesmeijer JC, Kremen C, Neumann P, Schweiger O (2010) Global pollinator declines: trends, impacts and drivers. *Trends EcolEvol* 25:345–353
- Rortais A, Arnold G, Halm M, Touffet-Briens F (2005) Modes of honeybees exposure to systemic insecticides: estimated amounts of contaminated pollen and nectar consumed by different categories of bees. *Apidologie* 36:71–83
- Roulston TH, Smith SA, Brewster AL (2007) Comparison of pan trap and intensive net sampling techniques for documenting a bee (Hymenoptera: Apiformes) fauna. *JKansEntomolSoc* 80:179–181
- Rowson R, Pavett M (2008) A visual guide for the identification of British *Coelioxys* bees. Privately published, Cardiff, UK
- Sarah L, Jeremy T (2012) Ecosystem services provided by urban spontaneous vegetation. *Urban Ecosyst* 15:545-557
- Simpson BB (1977) Breeding systems of a dominant perennial plants of two disjunct warm desert ecosystems. *Oecologia* 27:203-226
- Smith RM, Gaston KJ, Warren PH, Thompson K (2006) Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. *BiodiversConserv* 15:2515-2545

- Stout J, Morales CL (2009) Ecological impacts of invasive alien species on bees. *Apidologie* 40: 388–409
- Tarrant S, Ollerton J, Rahman L Md, Griffin J, McCollin D (2013) Grassland restoration on landfill sites in the East Midlands, UK: an evaluation of floral resources and pollinating insects. *Restoration Ecol* 21:560–568
- Thomson DM (2006) Detecting the effects of introduced species: a case study of competition between *Apis* and *Bombus*. *Oikos* 114:407–418
- Toler TR, Evans EW, Tepedino VJ (2005) Pan-trapping for bees (Hymenoptera: Apiformes) in Utah's West Desert: the importance of colour diversity. *Pan-PacEntomol* 81:103–113
- Tommasi D, Miro A, Higo HA, Winston ML (2004) Bee diversity and abundance in an urban setting. *CanEntomol* 136:851–869
- UN (2011) World urbanization prospectus, the 2011 revision. Department of Economic and Social Affairs (Population division) United Nations report. United Nations, New York
- Verboven HAF, Uyttenbroeck R, Brys R, Hermy M (2014) Different responses of bees and hoverflies to land use in an urban–rural gradient show the importance of the nature of the rural land use. *Landscape Urban Plan* 126:31–41
- Wilson EO (1999) *The Diversity of Life*. W.W. Norton and Company Inc., New York
- Winfree R, Aguilar R, Vázquez, DP, LeBuhn G, Aizen MA (2009) A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology* 90:2068–2076
- Winfree R, Bartomeus I, Cariveau DP (2011) Native pollinators in anthropogenic habitats. *Ann Rev Ecol Evol Syst* 42:1–22
- Winfree R, Griswold T, Kremen C (2007) Effect of human disturbance on bee communities in a forested ecosystem. *Conserv Biol* 21:213–223
- Wojcik V (2011) Resource abundance and distribution drive bee visitation within developing tropical urban landscapes. *J PollEcol* 4:48–56
- Wolda H, Roubik DW (1986) Nocturnal bee abundance and seasonal bee activity in a Panamanian forest. *Ecology* 62:426–433