Plant–bee interactions and resource utilisation in an urban landscape

Muzafar Hussain Sirohi[1,2], Janet Jackson[1], Jeff Ollerton[1,3]

1. Faculty of Arts, Science and Technology, University of Northampton, Waterside Campus, Northampton, UK
2. Centre for Biodiversity and Conservation, Shah Abdul Latif University, Khairpur, Pakistan
3. Kunming Institute of Botany, Kunming, China

Corresponding author: Muzafar Hussain Sirohi

Email: muzafar.sirohi@salu.edu.pk , ORCID: 0000-0002-4717-0889

Abstract

Biodiversity is declining through human activities and urbanisation is often seen as a particular concern. Urban settings, however, provide diverse microclimatic conditions for plants and pollinating insects, and therefore may be significant habitats for the conservation of solitary and primitively eusocial bees, a major group of pollinators. This study analysed the interactions between these bees and the plants on which they forage, using a network approach. We compared urban habitats (gardens, roadsides, and open vegetation) in a large British town with nearby nature reserves. One native plant *Taraxacum officinale* (dandelion) was a core generalist species visited in all habitat types. Other core plant species restricted to particular habitats include species of *Geranium*, *Bellis*, *Crepis,* and *Ranunculus*. Two generalist bee species, *Anthophora plumipes* and *Osmia bicornis* were the core visitor species within the networks. The networks were comparatively more nested in urban habitat types than nature areas, suggesting more frequent interactions between generalist and specialist species in urban areas. Network connectance, network level specialisation (H_2' index), and plant generality (network level) were not significantly different in urban and nature areas. However, visitor generality was found to be significantly higher in urban gardens than in nature areas. Careful management of common urban vegetation would be beneficial for supporting urban wild pollinators.

Keywords Plant-visitor interactions, Pollinator, Solitary bee, Primitively eusocial bees, Urbanisation, Networks

Please cite as:

Sirohi MH, Jackson J, Ollerton J (2022) Plant–bee interactions and resource utilisation in an urban landscape. Urban Ecosystems. https://doi.org/10.1007/s11252-022-01290-z

Introduction

Urban gardens, parks and municipal land often contain an assortment of native and non-native plant taxa and a high diversity of pollinating insects (Pickett et al. 2011; Baldock et al. 2015; Sirohi et al. 2015; Hall et al. 2017; Prendergast and Ollerton 2021). Non-native species may attract more visitors, affecting local plant-flower visitor networks and resulting in reduced visits and reproductive success in native species (Morales and Traveset 2009; Williams et al. 2011). The exotic garden flowers may also affect the pollinator community composition (Wray et al. 2014). Moreover, non-native solitary bees can be more common in urban areas (Matteson et al. 2008) and compete for resources with native species (Roulston and Malfi 2012). Pollinators that include non-native plants in their diet thrive in disturbed environments, while others (i.e. specialist species requiring preferred plant taxa) may not find their place in urban habitats (Matteson et al. 2008). These findings suggest that urban plant-visitor interactions are potentially dissimilar and more diverse than those in areas containing predominantly native plants. Therefore, different types of urban and natural habitats need to be investigated separately and compared to understand plant and flower visitor communities in urban areas. Greater understanding of urban plant-pollinator networks could benefit both wild plant communities and urban food growers as it can inform management that will help to shape the plant communities within urban areas (Ollerton 2021).

Most studies conducted in urban areas have focused on all pollinators. Although such networks yield valuable information on the ecosystem services and interdependence of species, those results cannot be generalised for all pollinator guilds, particularly solitary and primitively eusocial bees (see Prendergast and Ollerton 2021). Resource utilisation of solitary and primitively eusocial bees have been recorded as different in relation to other pollinator species and resource availability (Jordano 1987; Ebeling et al. 2011). It is reported that honey bees tend to use the most abundant plants while solitary and primitively eusocial bees switch to less abundant plant species in the presence of other pollinators (Ebeling et al. 2011). Moreover, many solitary and primitively eusocial bees are specific in their dietary needs, such as monolectic and oligolectic species. Therefore, this needs a separate analysis of solitary and primitively eusocial bees, particularly if we are considering the conservation of these species.

In this study, we compared the interactions of solitary and primitively eusocial bees with plants (referred to as plant-flower visitor interactions hereafter) using a network approach. Plant-visitor bipartite networks hold valuable information about ecosystem functioning, ecological roles of pollinators, and pollination services (Pocock et al. 2016; Landi et al. 2018). However, relatively few network studies of urban areas have been published (but see Jędrzejewska-Szmek and Zych 2013; Zotarelli et al. 2014; Baldock et al. 2015; Udy et al. 2020; Prendergast and Ollerton 2021).

We focus specifically on solitary and primitively eusocial bees for two reasons. First of all, their ecologies are poorly known relative to social bees such as *Bombus* and *Apis*. Secondly, these larger social bees tend to have much greater foraging ranges than the other bees and therefore we cannot be certain that individuals that we find within the town are really part of the urban fauna, or whether they are treating the urban setting as part of a much wider landscape that includes both urban and rural habitats. During the surveys that we describe below we regularly saw social bees, as well as hoverflies, Lepidoptera and other flower visitors, in both urban settings and in the nature reserves, although they were not quantified as that was not the aim of the project. In this respect, the results that we present must be viewed as not being complete networks but rather partial networks in which the focus is on a specific taxon: solitary and primitively eusocial bees.

The following questions have been addressed: (1) How does the structure of the flower-insect webs compare in urban settings versus nature reserves? (2) How similar is the level of resource specialisation of the bee species in urban versus nature areas? (3) Which plants are predominantly used by the bees, and does this vary for generalist and specialist species across the urban and natural areas?

Methods

The plant-flower visitor interactions were recorded in the urban core of Northampton, England (see Sirohi et al. 2015 for further details). Five urban sites for each of three habitat types (gardens, open vegetation, and roadside verges) were selected within a 500 metre radius of the centre of town (Figure 1). Those urban habitats were compared with each other and with five nearby sites of nature conservation value located between 1,600-5,000 metres from the centre of the town.

Plant-flower visitor interaction data were collected in all 20 sites from March until October 2012, from 10 am to 5 pm on sunny and warm days (following Cane et al. 2000). Each site was surveyed twice a month for 30 minutes per survey by slowly walking around the site. Due to variations in the size, shape and layout of the sites, transect lengths could not be standardised. However the species accumulation curves that were construced showed that we effectively sampled the diversity of bees across the sites (see Sirohi et al. 2015). All interactions between solitary and primitively eusocial bees (called visitor species hereafter) and flowers were recorded within one metre of the walked transect and species that could not be accurately identified in the field were collected with a hand net for later identification in the laboratory. The bee species were identified based on test keys from George Else and verified by Mike Edwards from the Bees, Wasps and Ants Recording Society (BWARS). The timing of site surveys was randomised to reduce biases caused by differences in bee activity times. All sites receive roughly equal morning and afternoon sampling. It was challenging to standardize floral resources of plants due to the variety of floral forms and shapes. Regardless of its taxonomic terminology, the floral units of plants were seen as a unit attracting pollinators, such as the solitary flower of *Rosa* or *Papaver*, or the complete floral shoot/head of *Hebe*, *Taraxacum*, and *Bellis*. Whenever possible, floral units were counted directly; alternatively, square quadrats were used to count floral units and multiplied with the area of floral distribution to estimate the total number of floral units on site (Szigeti et al. 2016; Berthon et al. 2021).

Hanski (1982) used the term ‘core species’ for a locally common and abundant species in the context of the ecological distribution of species. The same term is used for the most common species interacting with a high number of species in plant-flower visitor network (Alarcon et al. 2008; Winfree et al. 2015) though “core generalist” is also used (Ollerton 2021). We selected the core taxa on two criteria: (a) taxa with a high (top 25%) frequency of interactions; and (b) highly connected taxa which interacted with at least 25% of other taxa in the networks.

The *d'* index is a measure of the species-level specialisation, which ranges from zero for no specialisation to one for a completely specialist bee species that interacts with just one plant (Blüthgen et al. 2006). We calculated species level specialisation (*d'* index) for all visitor species and analysed the distribution of generalist and specialist species across the landscape. For this, we pooled all interactions of bees with plants in all habitats including nature areas. This matrix of interactions was analysed to calculate d' value (species level specialisation) for each bee species with the *bipartite* package in R statistical software (Dormann et al. 2009; R Core Team 2014). Five bee species (*Andrena carantonica, Coelioxys quadridentata, Halictus rubicundus, Nomada marshamella, Nomada panzeri*) with single observations in the matrix were not assigned a d' value and therefore dropped from the analysis. Further, the presence of specialist bee species (based on d' index) was compared in urban habitats and nature sites.

The plant-flower visitor networks in all habitat types were analysed for plant and visitor generality, H2' index (network level specialisation), connectance, and nestedness. The H2' index, which ranges from zero to one, indicates the level of specialization of networks, with zero indicating total generalization and one meaning complete specialization, i.e. each flower visitor interacts with only one plant. Connectance refers to the proportion of possible interactions that are actually observed among plant and bee species. In general, low connectivity means little generalization at the community level. Nestedness is a metric of plant-visitor interaction networks that refers to the relationship between the most generalised and the increasingly more specialised species. When specialised pollinator species visit plant species that are subsets of those visited by more generalist pollinators, the networks are said to be nested (see Dormann et al. 2009; Watts et al. 2016 for more details). The network indices were again calculated using the *bipartite* package in R. The data were tested for normality prior to analysis. One-way ANOVA was used to confirm the difference in network properties among the urban habitats and nature sites, followed by post hoc analysis (Tukey test) for differences between specific habitat types and nature sites. Spearman's correlation was used to check the relationship of plant and visitor generality with bee species richness and plant species richness on site. One-way ANOVA and Spearman's correlation analysis were carried out in SPSS for Windows (IBM Corp. 2011). Means are presented ± SD. The indices, i.e. degree of specialisation at species and network level, are calculated with the interaction matrix of bee species and plant species or morphotypes where species could not be identified. However, species tend to specialise at plant genus level therefore plant genera (instead of species) were used for core taxa and the figures of bipartite interactions.

Results

Resource utilisation by species

A total of 145 plant genera from 58 plant families were recorded from urban sites. However, bees were recorded visiting only 41.3% (60 genera) among the available flowering plants with a total of 696 visits in all urban sites (Figure 2). At each urban site, bees only interacted with 14% to 42% of the available taxa (mean = 26.6 ± 2.1 % per site). In contrast, bees were recorded visiting 13 plant genera of 8 families in nature sites with a total of 61 interactions (Figure 2). About 80% of those interactions were made to only 20 common plant taxa, which included (ordered by highest visits) *Taraxacum* (Asteraceae), *Achillea* (Asteraceae), *Lamium* (Lamiaceae), *Geranium* (Geraniaceae), *Reseda* (Resedaceae), *Aubrietia* (Brassicaceae), *Erysimum*

(Brassicaceae), *Lavandula* (Lamiaceae), *Primula* (Primulaceae), *Pentaglottis* (Boraginaceae), *Bellis* (Asteraceae), *Cirsium* (Asteraceae), *Trifolium* (Fabaceae), *Cymbalaria* (Scrophulariaceae), *Deutzia* (Hydrangeaceae), *Anthriscus* (Apiaceae), *Elaeagnus* (Elaeagnaceae), *Crepis* (Asteraceae), *Hebe* (Plantaginaceae) and *Vinca* (Apocynaceae) (each plant taxon was visited at least 10 or more times by bees). The remaining 40 plant taxa in the plant-visitor network received 20% of the total bee visits. The correlation between the number of plant taxa available and the taxa visited by bee species was strong (Pearson correlation, $r = 0.75$, $p>0.001$).

Nestedness and core taxa in networks

Interactions in all urban habitat types were highly nested (weighted nestedness, gardens = 0.59, open vegetation = 0.6, and roadside verges = 0.6) compared to nature sites (weighted nestedness = 0.14). Each urban habitat type and nature site contained two core plant taxa, with *Taraxacum* the shared core taxon in all habitats (Table 1). *Taraxacum* was visited by 55.6% of the total bee species recorded in the interactions, with 19.6% of the total visits from bee species. The second core taxa were *Geranium*, *Bellis*, *Crepis*, and *Ranunculus* in gardens, open vegetation, roadside verges, and nature sites, respectively (Table 1). These plants are quite common in gardens, roadside strips, and wastelands and attract bees with longer bloom season (Figure 3). Of the bee species, *Osmia bicornis* and *Anthophora plumipes* were the core species in all urban and nature areas (Table 1). Both species visited at least half of the plant species in the networks of both urban and nature sites.

Plant generality (network level)

The mean plant generality was 2.7 ± 1.5 for all urban sites, with plant species being visited by more than two bee species in 53% of the urban sites. In contrast, only two nature sites had mean plant generality greater than two. There was no significant difference in plant generality between urban habitats and nature sites (Figure 4a). Moreover, there was no significant correlation between the number of plant species per site and plant generality (Spearman's correlation, $r = -0.15$, $p>0.05$). However, the plant generality was significantly correlated with the number of bee species in habitats (Spearman's correlation, $r = 0.45$, $p<0.05$).

Visitor generality (network level)

The visitor generality varied among the sites, with a mean 2.6 ± 1.09 for all urban sites. Bee species in urban areas visited more plant species on average, with mean visitor between 2.0 and 4.6 in about 66% of urban habitats. In contrast, visitor generality remained less than two in all nature sites. In particular, the species in urban garden habitats interacted with a significantly higher number of plants than in nature areas (Figure 4b). There was a significant correlation between visitor generality and the number of plant species on sites (Spearman's correlation, $r = 0.607$, $p<0.01$). This confirms that the urban areas, particularly gardens, provide relatively more floral options for the visitor, and consequently visitor generality increases.

Connectance and network specialisation (H_2' index)

Network connectance varied among the sites from about 0.2 to 0.6 (mean = 0.23 ± 0.1). The mean connectance was lower in urban sites (gardens = 0.19 ± 0.06; open vegetation = 0.21 ± 0.08; roadside verges =0.30 ± 0.14) than in nature areas (0.37 ± 0.18). However, there was no statistically significant effect of landscape types on mean connectance (Figure 4c). The mean network specialisation index was relatively higher in nature sites (0.81 ± 0.14) than in urban habitat types: gardens = 0.71 ± 0.21; open vegetation = 0.51 ± 0.19; roadside verges = 0.59 ± 0.14; however, this was not significantly different (Figure 4d).

Bee species specialisation and distribution across the landscape

The bee species specialisation (d' index) varied from 0.1 to 0.8 for all species in urban and nature areas (Table 2). All habitats were dominated by relatively generalist species in terms of species abundance and number of species visited. Looking at the more generalised species with d' index 0.5 or less, although the abundance of species varied, the number of species was not different among urban habitats and from nature sites (Figure 5). Almost all generalist species (total 19 species with d' value 5 or less) were found in all urban habitat types and nature sites, except *Melecta albifrons* (d'=0.3), which was not recorded in nature sites and *Lasioglossum leucozonium* which was very low in abundance and not recorded in the open vegetation category of urban habitats (Table 2). On the other hand, all specialist species having d'= 0.6 or more (12 in total) were present in gardens and open vegetation. About 50% of such species were not found in roadside verges and 33% were absent from nature sites. The most specialist species *Anthophora quadrimaculata* (with d'=0.8) were found in all urban habitat types but not found at any nature site. This indicates that urban areas, particularly gardens and open vegetation sites, provide resources to more specialist bees.

Discussion

Resource utilisation by species

Because the success or failure of local bee populations is intimately dependent on the plants on which they feed, knowledge of the available floral resources is vital for their conservation. We surveyed flowers and their bee visitors in all possible habitat types in the urban core of the town of Northampton, such as urban gardens, roadside verges and areas of open vegetation. Those urban habitat types differed in their plant communities and, at a town landscape scale, provide a wide range of floral resources. The analysis of plant-visitor networks at larger scales, including all possible habitats in urban areas, provides information on all possible food options for bee species and identifies flower preferences. Many studies have reported lists of plant taxa visited by bees in urban areas (e.g. Matteson and Langellotto 2011; da Silva Mouga et al. 2015; Mach and Potter 2018; Rollings and Goulson 2019; Prendergast and Ollerton 2021), although few report the proportion of the available plant species that was used by bees. Although a large diversity of flowering plants was available to bees at these urban sites, they were recorded visiting only about 26% of the plant taxa on average during the surveys. In a study conducted in nature areas and restored habitats within 50 km of Northampton, Tarrant (2009) found 50% of the plant species interacting with pollinators. However, that study recorded all groups of pollinators, not just bees.

The sixty genera of flowering plants visited by bees recorded in the plant-visitor network included both garden and wild flowers. A large number of bees favoured wild plant taxa; however, a few garden plants such as *Aubretia*, *Erysimum*, *Hebe*, *Deutzia*, and *Lavandula* also attracted a diversity of bee species (Figure 2). Urban gardens often comprise a large variety of exotic and alien plants in the United Kingdom (Smith et al. 2006; Rollings and Goulson 2019) and each garden provides relatively different resources. These resources may enhance the diversity of bees and support a wide array of species (da Silva Mouga et al. 2015; Lowenstein et al. 2019).

The plant-visitor network revealed that wildflowers were the core taxa of the network (see Figure 2 and Table 1). A similar pattern of bees preferring wildflowers has also been recorded in other urban areas (Tommasi et al. 2004; Jędrzejewska-Szmek and Zych 2013; Lowenstein et al. 2019). *Taraxacum* (dandelion) was visited by the highest diversity of bees (22 species) and received approximately one in five visits in the plant-visitor network in the urban core (Figure 2). This is similar to Tommasi *et al.* (2004) who found the highest diversity of bees visiting dandelions in wild urban areas while the planted flower beds in gardens received little attention from bees. The interactions of bees with dandelion were recorded in 15 (out of 18) urban sites including gardens in this study. The high number of bee species and a relatively higher number of bee visits recorded on dandelions was possibly because the species is widespread in all habitats and has a long flowering period. Dandelion is one of the most common weeds in urban areas of England (Ollerton 2021). Whilst the species does produce a lot of nectar which is used by bees, the pollen from dandelion flowers is considered low in nutrition and bees have difficulty rearing brood on pure dandelion pollen (Herbert et al. 1987; Loper and Cohen 1987). Although dandelion was the second most abundant urban plant, it was much less abundant in the nature areas, but still an important component of the network. So abundance is not the only factor determining the value of dandelion to the bees.

Plant-flower visitor interactions are often asymmetric, where specialist bee species visit generalist flowers which may increase the stability of the networks (Vázquez and Aizen 2004). The measure of nestedness was relatively higher in urban networks compared to nature sites (Figure 2) which suggests higher stability in urban networks (Allesina and Tang 2012). The nestedness values measured in nature sites were comparable to the weighted nestedness (0.1) in the plant–flower visitor interactions in a heathland at Dorset, United Kingdom (Ballantyne et al. 2015). The strength of interactions and the number of species also affects nestedness, with complex interaction networks with a high number of species tending to be highly nested (Bascompte et al. 2003). We found relatively high numbers of plant and bee species, and more interactions, in urban areas, possibly explaining higher nestedness in urban areas.

Many wild plant species were used by solitary and primitively eusocial bees as food resources, with *Taraxacum* (dandelion) being particularly notable, supporting both specialist and generalist pollinators. Apart from the 22 bee species recorded in this study, large numbers of other solitary and primitively eusocial bees feed on dandelion including many nationally rare and scarce bee species, for example, *Andrena labiata*, *Andrena lathyri*, *Andrena varians*, *Anthophora retusa*, *Colletes cunicularius*, *Lasioglossum pauxillum*, *Lasioglossum xanthopus*, *Nomada signata*, and *Osmia aurulenta* (Shirt 1987; Falk 1991; BWARS 2015; Falk and Lewington 2015). Moreover, this study recorded one nationally rare species, *Coelioxys quadridentata*, feeding on a wild plant species, *Senecio jacobea*. Hence the maintenance of such wild plant patches may not only support the common pollinating species but also the rare and scarce species in urban areas.

This study confirms that a wide range of wild plants is visited by bees (Figure 2). It was impossible to establish from the visitation records whether the plants visited by a bee were pollen hosts, and pollen load analysis was not a part of this study. Therefore, the true number of bee species actually collecting pollen from these wild plant taxa is unknown. Bee species can visit a large number of plant taxa for nectar but often collect pollen from selected plant taxa. However, when desired plant taxa for pollen were absent, bees have been recorded collecting pollen from other plant taxa that were mainly visited for nectar only (Cane and Schiffhauer 2003). This indicates the significance of wild plant taxa that may provide resources to the species in an acute shortage of preferred pollen sources, reinforcing the importance of high plant diversity.

The specialist-generalist continuum

In order to calculate the specialisation and distribution of species across the landscape, this study assumed all sites comprised a single landscape and pooled all plant-visitor interactions in a single matrix. This interaction matrix was used to calculate the species specialisation index (d' index) which categorised the bees from more generalised to specialised. This was done to observe the distribution of specialist and generalist species across the landscape network. Based on the d' index, generalised bee species were present across the landscape whereas specialised species were more associated with gardens and open vegetation sites in urban areas (Figure 5). Numbers of plant species, and therefore plant-visitor interactions, were comparatively higher in gardens and open vegetation sites in urban areas. Often in the presence of higher number of plant species, visitors tend to specialise, favouring the most profitable resources, a trend that has been observed in solitary and primitively eusocial bees (Ebeling et al. 2011). However, these bees appear to visit less abundant flowers, perhaps to avoid competition with more generalised pollinators, such as honey bees which concentrate on more abundant flowers especially in urban areas (Prendergast and Ollerton 2021, in review).

Although the more abundant bee species were largely generalised in diet, urban areas also hold highly specialised species of solitary and primitively eusocial bees. Perhaps the occurrence of such species was driven by specialised resources. For example, *Hylaeus signatus*, recorded as notable B (scarce) by Falk (1991), visits a number of plant taxa for nectar but has been recorded as very selective in pollen gathering, collecting pollen only from *Reseda* spp. (BWARS 2015; Falk and Lewington 2015). This pollen host plant was only recorded from one roadside verge (LLV site) where individuals of *Hylaeus signatus* were recorded foraging exclusively on *Reseda*. However, the males of *Hylaeus signatus* were also recorded from five other urban sites visiting *Achillea*, *Hebe*, *Tanacetum*, *Cymbalaria*, and *Tagetes*. In the nature areas, the species was represented by two individuals from Wilson's Orchard and Abington Meadow, but we did not record any plant taxa from the Resedaceae in those habitats. *H. signatus* might therefore have collected its desired pollen from nearby urban areas. Similarly, *Anthophora quadrimaculata* was a highly specialist species in our urban networks. The species is recorded as polylectic with a preference for Lamiaceae flowers (BWARS 2015; Falk and Lewington 2015). This study also confirmed a higher interaction (about 70% visits) of species with *Lavandula* (Lamiaceae) in gardens. However, the species was also recorded visiting Asteraceae, Fabaceae, and

Papaveraceae in absence of Lamiaceae from the urban sites. Unlike generalised species, the specialised bees foraging on a selected taxon usually maintain constancy and become efficient consumers by taking away a huge quantity of pollen from a flower (Larsson 2005). This indicates a potentially higher amount of pollen transfer between conspecific plants, which may lead to higher pollination success. However, it very much depends on how pollen is packed into corbiculae and how frequently bees groom pollen from their bodies.

It is quite possible that specialised bee species interacted with other plant species which were not be recorded in this study. This may be with the flowers present in nearby areas and gardens which were not part of this study but close enough for bees to collect pollen. Patchy floral resources, such as small areas of wild vegetation, or wall flora, or plants on the balconies of apartments, are characteristics of urbanised areas. Based on these visitation records, we cannot be sure that these specialist species have not interacted with other plants than those recorded. Jędrzejewska-Szmek and Zych (2013) compared the generality of visitor species using both pollen analysis and visitation networks. The study confirmed that insect species had greater generality (more links) in the pollen network than the network calculated just from observing visits. Therefore, this needs more case studies to determine whether such species were actually specialist bees with specialist needs.

A previous study of urban habitats found a significantly higher plant generality in nature areas than urban sites and attributed this difference to the number of species available (Baldock et al. 2015). In contrast, mean plant generality in urban areas of Northampton was not significantly different from nature sites in this study. The difference compared to could be due to the inclusion of all pollinators in analysing plant-visitor interactions, including more generalist honey bees, bumblebees, and hoverflies in Baldock et al. (2015). Furthermore, we did not find any significant correlation of plant generality with number of floral options available on sites. The generality was increased with the number of bee species present at sites, indicating that many solitary and primitively eusocial species were generalised and flexible in their diet options.

The visitor generality was higher in urban areas, particularly in gardens where bees visited significantly higher numbers of plants on average than in nature areas (Figure 4). A similar trend of higher visitor generality in urban areas than in non-urban was also recorded in other cities of the United Kingdom (Baldock et al. 2015) and in Paris, France (Geslin et al. 2013). The latter study found that visitor generality varies across landscape types, though this is more profound in solitary and primitively eusocial bees than other functional groups of pollinators such as bumblebees, honey bees, and Lepidoptera (Geslin et al. 2013). The significant relationship between the number of floral options in habitats and visitor generality showed that species visited more plants when more options were available.

A higher visitor generality may have been influenced by some exotic species in gardens. Urban garden floras contain 70% of the alien species in the United Kingdom (Smith et al. 2006). Often, alien species with showy floral displays attract more pollinators and influence plant-pollinator network properties, though this depends on the traits of flowering species (Bartomeus et al. 2008; Tiedeken and Stout 2015). The plant–visitor network in garden sites of this study was larger than other habitat types, with 36 plant taxa visited by 26 bee species (see Figure 2). Nevertheless, a few garden flowers, for example, *Lavandula*, *Primula*, *Aubretia*, *Erysimum*, and *Deutzia* attracted bee visitors. About 61% of the plants in gardens were visited less frequently with fewer than 5 visits each. Wild plants growing in lawns were the core of the network, however lawns are frequently mowed leaving no resources for pollinators. In that case, pollinators may have visited alternate flowers available in flower beds which increases the number of links and subsequently overall visitor generality.

Network specialisation and connectance

Mean connectance was not significantly different across habitat types, though the mean connectance of the plant-visitor network in garden and open vegetation habitats was relatively lower than roadside verges and nature areas (Figure 4). This may have been influenced by the size of the interactions in such habitats. Network connectivity tends to decrease with the increasing network size (Olesen and Jordano 2002). Despite the differences in pollinator guild, the mean connectance recorded in this study (mean 0.23 ± 0.1) was comparable to network connectance (mean 0.18 and 0.20) of social bees and plants in two urban areas of Brazil (Zotarelli et al. 2014) and the connectance (mean 0.17 to 0.40) of plants and all potential pollinators recorded in the nature areas near to Northampton town (Tarrant 2009). s

The network specialisation index (H_2') of various urban habitat types (gardens 0.71 ± 0.21, open vegetation 0.51 ± 0.19, roadside verges 0.59 ± 0.14) calculated in this study were higher than the same recorded for urban networks (0.47 ± 0.03) in other areas of the United Kingdom (Baldock et al. 2015), the 0.42 and 0.57 recorded for two urban networks including all pollinator species in Warsaw, Poland (Jędrzejewska-Szmek and Zych 2013), and the 0.39 and 0.45 for the network of social bees and plants in two urban areas of Brazil (Zotarelli et al. 2014). Also, the urban plant visitor network in this study was slightly specialised, yet not significantly different from nature areas. In contrast, Baldock et al., (2015) suggested relatively specialised networks in farmlands, compared to urban and nature reserves. The higher network specialisation in plant-visitor networks in this study may be due to the pollinator guilds under observation, as solitary and primitively eusocial bees are comparatively selective in resource utilisation compared with social bees, as discussed above. In contrast, Baldock et al., (2015) include all pollinator guilds and started surveying from late May, therefore may have missed a wider set of interactions of solitary and primitively eusocial bees in spring. This study found a high number of bees emerged and flying in spring than summer and autumn (see Sirohi et al. 2015).

Our findings suggest that urban areas have a huge potential for conservation of solitary and primitively eusocial bees. Diverse urban plant communities that contain native species of *Taraxacum*, *Geranium*, *Bellis*, *Achillea,* and *Trifolium*, can support a large diversity of bees. Many such wildflowers grow in gardens and attract a number of bees (Larson et al. 2014) but often they are considered as “weeds” and are heavily mowed or even sprayed with herbicides to make the habitat more “aesthetic”. These plants can occur in public parks, private gardens, wild leftover patches, and roadsides, and are thus a common feature of most urban settings. Therefore, the appropriate and low-intensity management of such area make a meaningful contribution to supporting wild pollinators in urban areas (Ollerton 2021).

Declarations:

Acknowledgments: We are indebted to all those who helped this research at any stage, particularly landowners Northampton Borough Council, The Wildlife Trust BCN, Northampton and County Club, South Court

Environmental, The Churches Conservation Trust, Church of the Holy Sepulchre, New Testament Church, St. Giles Church and All Saints Church, for providing access to their land and other necessary support. We are thankful to Mike Edwards for his generous help in identification of bee species.

Authors' contributions: All authors contributed to the conception and design. Data collection and analysis were performed by Muzafar H. Sirohi, Jeff Ollerton and Janet Jackson. The first draft of the manuscript was written by Muzafar H. Sirohi, and all authors commented on the previous version of manuscript. All authors read and approved the final manuscript.

Conflicts of interest/Competing interests: All authors certify that they have no affiliations with or involvement in any organization or entity with any financial interest or non-financial interest in the subject matter or materials discussed in this manuscript.

Funding: The research was funded by HEC Pakistan.

Ethics approval and consent to participate: The ethical approval was not applicable to the study. Moreover, the insects (bees) were studied according to the scientific guidelines and a prior permission was obtained to conduct the bee surveys on private land.

Consent for publication: I, on behalf of authors, give my consent for the publication of this manuscript in the journal Urban Ecosystem. I confirm that all authors have seen and been given opportunity to read the final draft of manuscript thoroughly.

Availability of data and materials: The data used in this study is available with authors and would be shared on request.

Software application: Statistical analyses were conducted in the free R statistical software, and code involved the free downloadable packages available for R.

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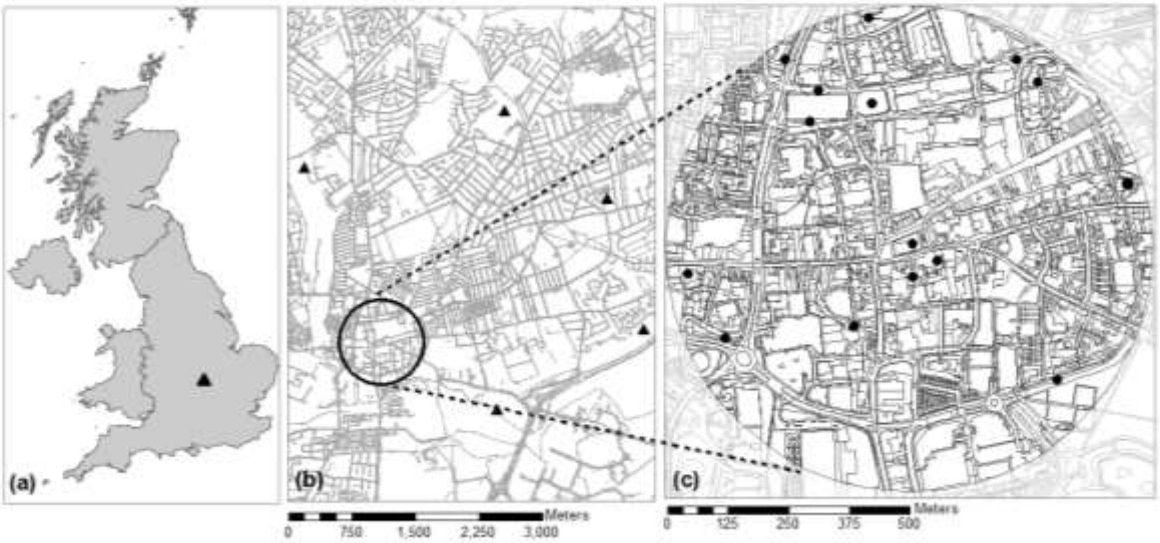

Fig. 1 Distribution of the study sites, (a) a triangle represents the location of Northampton in the United Kingdom. (b) Northampton town, fifteen urban sites were present within a circle of 500m in the centre of the town, a triangle showing the location of nature sites (c) location of urban sites within a circle of 500m in the centre of the town (Ordnance Survey boundary and OS MasterMap® 2013, using the Digimap Ordinance Survey Collection).

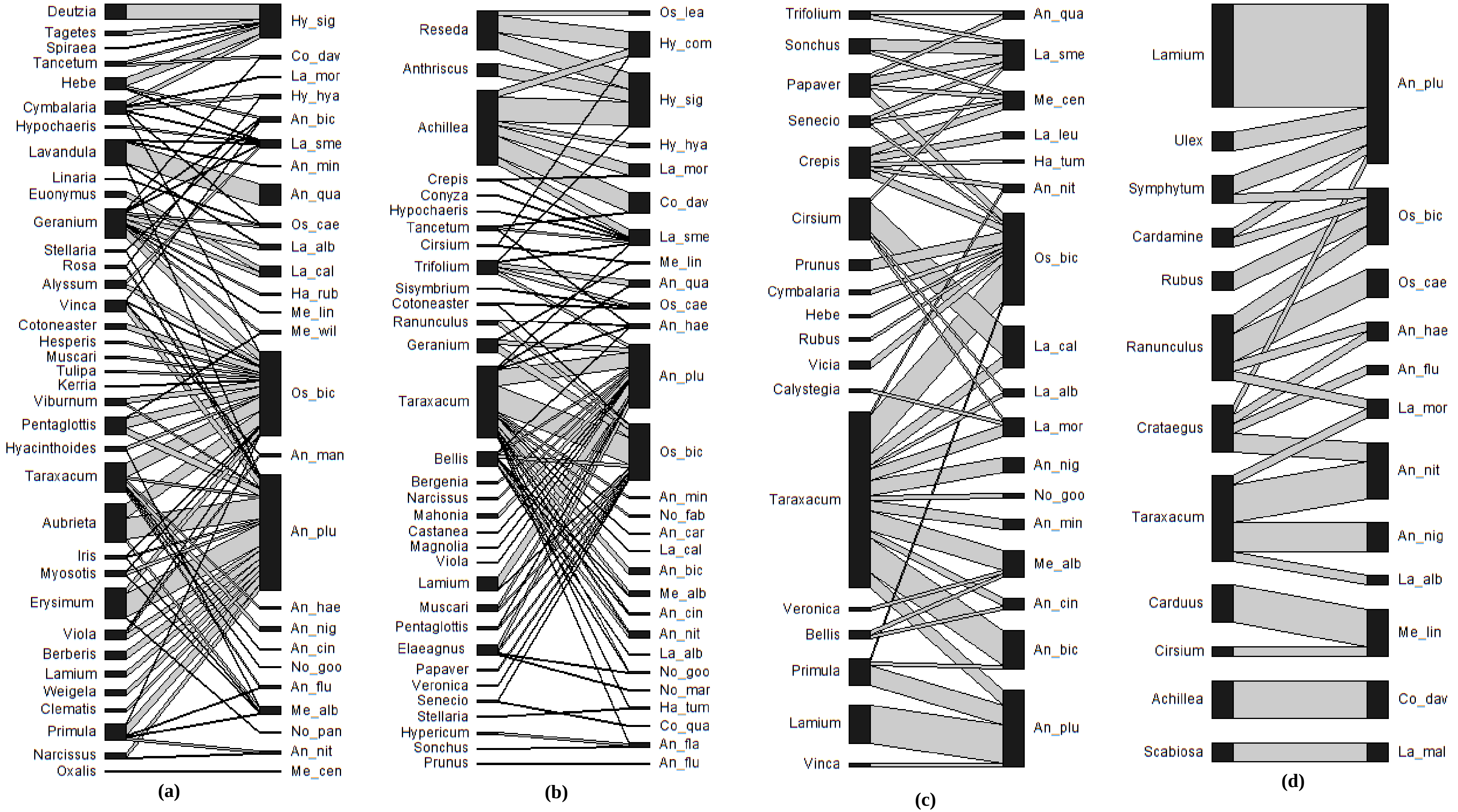

Fig. 2 Plant-visitor interaction networks in urban habitat types, arranged by CCA method, with lowest overlap possible, (a) gardens (b) open vegetation (c) Roadside verges (d) Nature sites. The left and right nodes correspond to the plant and visitor taxa respectively. The height of each node is proportional to the number of visits recorded per species. The lines between the nodes indicate the interactions of between plant and visitor taxa. The codes for bee species: An_bic = *Andrena bicolor*, An_car = *Andrena carantonica*, And_cin = *Andrena cineraria*, An_fla = *Andrena flavipes*, An_flu = *Andrena fluva*, An_hae = *Andrena haemorrhoa*, An_min = *Andrena minutula*, An_nig= *Andrena nigroaenea*, An_nit = *Andrena nitida*, An_man = *Anthidium manicatum*, An_plu, *Anthophora plumipes*, An_qua = *Anthophora quadrimaculata*, Ch_cam = *Chelostoma campanularum*, Co_qua = *Coelioxys quadridentata*, Co_dav = *Colletes daviesanus*, Ha_rub = *Halictus rubicundus*, Ha_tum = *Halictus tumulorum*, Hy_com = *Hylaeus communis*, Hy_hya = *Hylaeus hyalinatus*, Hy_sig = *Hylaeus signatus*, La_alb = *Lasioglossum albipes*, La_cal = *Lasioglossum calceatum*, La_leu = *Lasiglossum leucozonium*, La_mal = *Lasioglossum malachurum*, La_mor = *Lasioglossum morio*, La_sme = *Lasioglossum smeathmanellum*, Me_alb = *Melecta albifrons*, Me_cen = *Megachile centuncularis*, Me_lin = *Megachile ligniseca*, Me_wil= *Megachile willughbiella*, No_fab = *Nomada fabriciana*, No_goo = *Nomada goodeniana*, No_mar= *Nomada marshamella*, No_pan= *Nomada panzeri*, Os_cae= *Osmia caerulescens*, Os_lea = *Osmia leaiana*, Os_bic = *Osmia bicornis.*

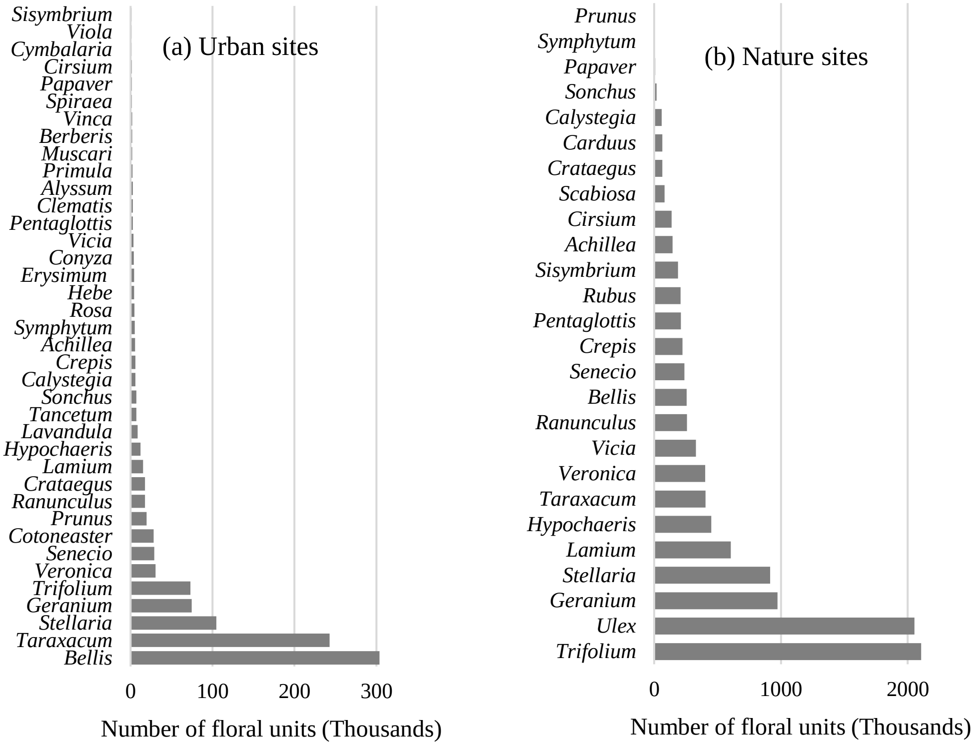

Figure 3. Abundance of floral resources at (a) urban and (b) natural sites. The number represents the sum of floral units assessed twice a month during surveys from March to October, and it represents the flowers discovered in interacting with bees.

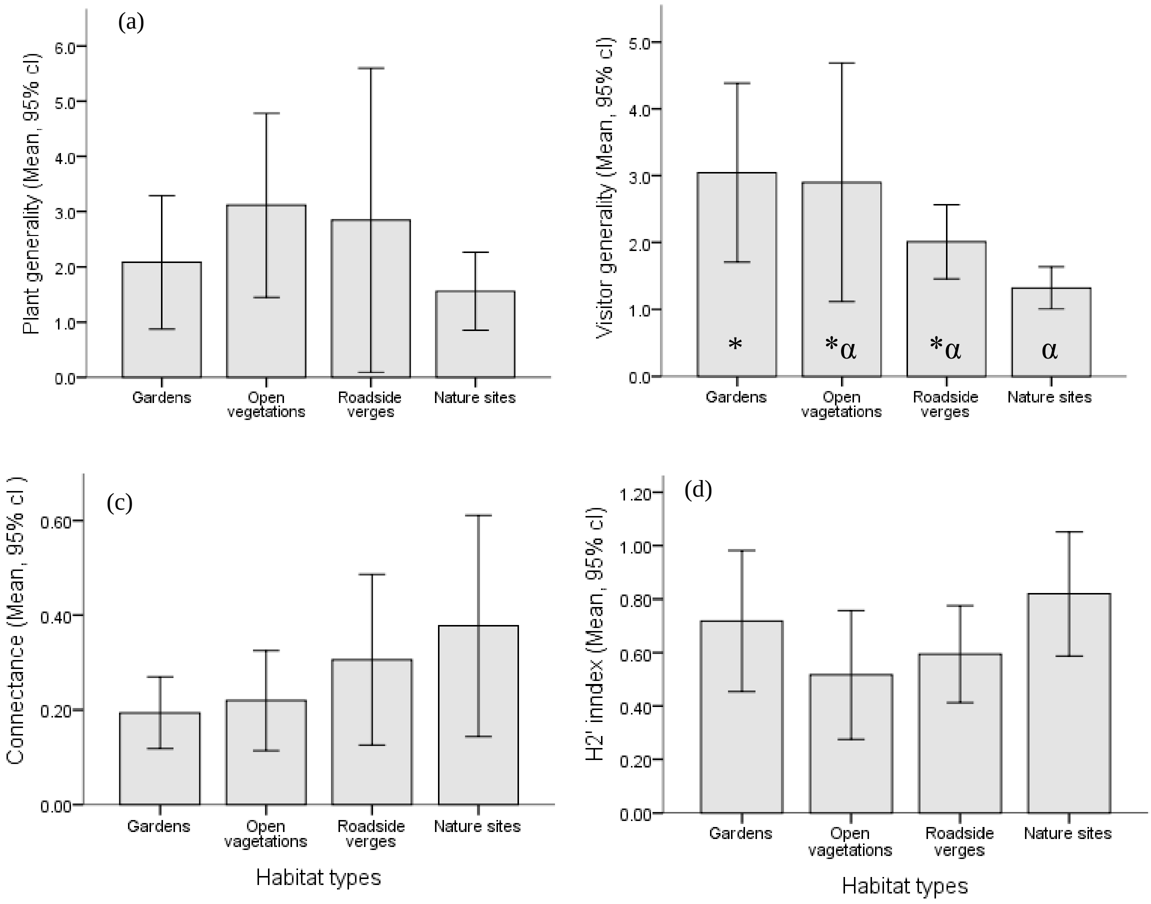

Fig. 4 Comparison of network level indices in urban habitats types and nature areas. (a) Plant generality (one way ANOVA, F=1.27, p=0.32), (b) Visitor generality (One way ANOVA, F=3.73, $p<0.05$, Post hoc Tukey's test showed a significant difference between Gardens and Nature sites T= 1.7, $p<0.05$) (c) network connectance (one way ANOVA, F=2.08, p=0.14, df=4) and, (d) H_2' index (network level specialisation, one way ANOVA, F = 2.52, p=0.097, df=3).

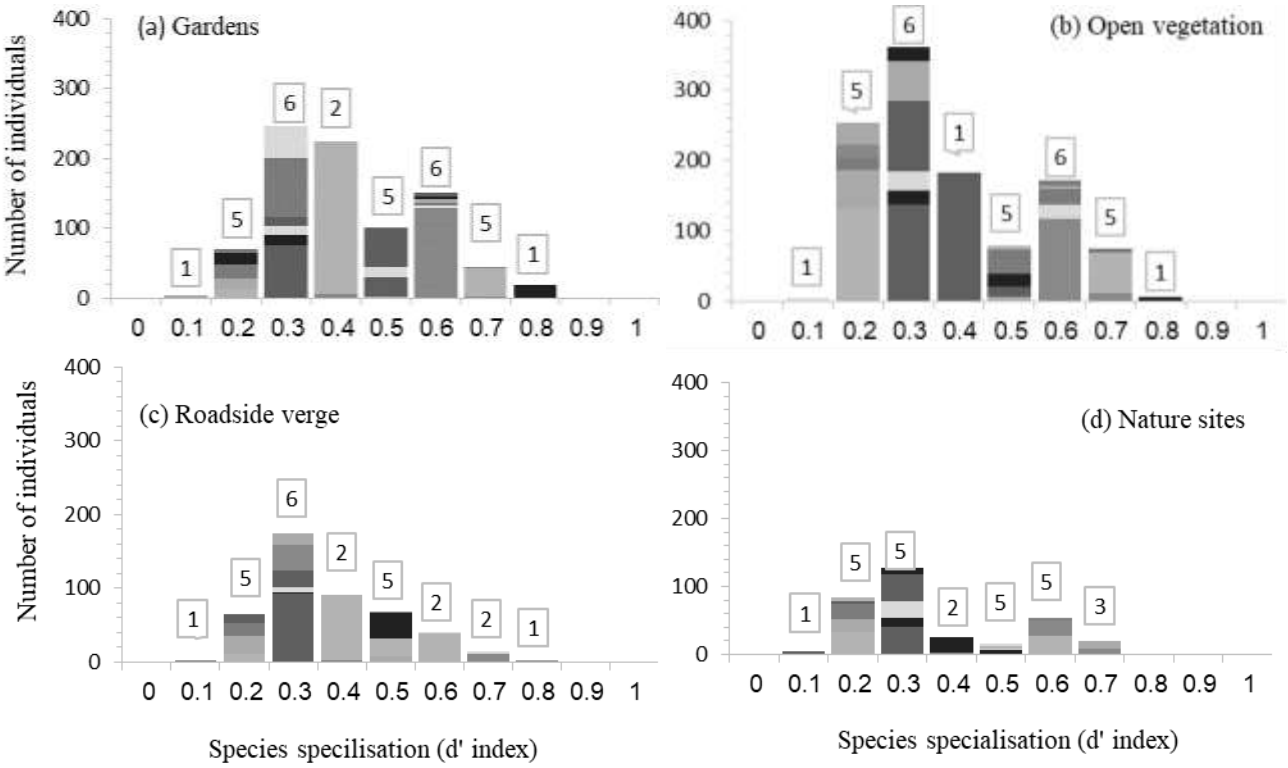

Fig. 5 Frequency distribution of visitor species based specialisation (*d'* index) in urban habitats and nature sites, (a) Garden sites (b) Open vegetation (c) Road verges, and (d) Nature sites. The bars represent the total number of individuals in each category. Bars are separated by colours for species, with the total number of species written on the top.

Table 1 List of the core plant and visitor taxa in different urban habitat types and nature sites. The value for percentage of interacting species and visits are highlighted in bold for core species in relevant habitat, while species relative importance in other habitats are placed in brackets. NR=No Record. Taxa are arranged by the number of interacting species.

		Garden		**Open vegetations**		**Roadside verges**		**Nature sites**		**All habitat types**	
	Core taxa	% of interacting species	% of visits	% of interacting species	% of visits	% of interacting species	% of visits	% of interacting species	% of visits	% of interacting species	% of visits
Plant taxa	*Taraxacum*	**26.9**	**8.5**	**57.1**	**22.1**	**70.6**	**41.8**	**33.3**	**17.3**	**55.6**	**19.6**
	Geranium	**38.5**	**8.5**	(10.7)	(4.1)	NR	NR	NR	NR	**30.6**	**4.8**
	Bellis	NR	NR	**28.6**	**4.8**	(11.8)	(1.8)	NR	NR	(22.2)	(2.2)
	Crepis	NR	NR	(7.1)	(0.7)	**29.4**	**7.3**	NR	NR	(19.4)	(1.4)
	Ranunculus	NR	NR	(7.1)	(1.7)	NR	NR	**33.3**	**13.6**	(11.1)	(1.7)
Bee	*Osmia bicornis*	**52.7**	**25**	**37.5**	**17.6**	**55.5**	**21.8**	**33.3**	**11.5**	**50**	**20.6**
	Anthophora plumipes	**50**	**33.8**	**43.7**	**19.7**	**22.2**	**18.2**	**41.7**	**32.7**	**46.9**	**25.7**

Table 2 Species specialisation index (*d’* value) and their presence in urban habitat types and nature sites. Species arranges by the ascending *d’* value.

Family	Species	*d'* index	Garden sites	Open vegetation	Roadside verges	Nature sites
Apidae	*Nomada fabriciana*	0.1	Y	Y	Y	Y
Andrenidae	*Andrena minutula*	0.2	Y	Y	Y	Y
Andrenidae	*Andrena nigroaenea*	0.2	Y	Y	Y	Y
Halictidae	*Lasioglossum albipes*	0.2	Y	Y	Y	Y
Andrenidae	*Andrena cineraria*	0.2	Y	Y	Y	Y
Apidae	*Nomada goodeniana*	0.2	Y	Y	Y	Y
Andrenidae	*Andrena bicolor*	0.3	Y	Y	Y	Y
Halictidae	*Lasioglossum morio*	0.3	Y	Y	Y	Y
Andrenidae	*Andrena nitida*	0.3	Y	Y	Y	Y
Andrenidae	*Andrena fulva*	0.3	Y	Y	Y	Y
Andrenidae	*Andrena haemorrhoa*	0.3	Y	Y	Y	Y
Apidae	*Melecta albifrons*	0.3	Y	Y	Y	**N**
Halictidae	*Lasioglossum leucozonium*	0.4	Y	**N**	Y	Y
Megachilidae	*Osmia bicornis*	0.4	Y	Y	Y	Y
Halictidae	*Halictus tumulorum*	0.5	Y	Y	Y	Y
Colletidae	*Hylaeus hyalinatus*	0.5	Y	Y	Y	Y
Halictidae	*Lasioglossum calceatum*	0.5	Y	Y	Y	Y
Halictidae	*Lasioglossum smeathmanellum*	0.5	Y	Y	Y	Y
Megachilidae	*Osmia leaiana*	0.5	Y	Y	Y	Y
Apidae	*Anthophora plumipes*	0.6	Y	Y	Y	Y
Halictidae	*Lasioglossum malachurum*	0.6	Y	Y	**N**	Y
Colletidae	*Colletes daviesanus*	0.6	Y	Y	**N**	Y
Megachilidae	*Osmia caerulescens*	0.6	Y	Y	**N**	Y
Megachilidae	*Megachile willughbiella*	0.6	Y	Y	**N**	Y
Colletidae	*Hylaeus communis*	0.6	Y	Y	Y	**N**
Andrenidae	*Andrena flavipes*	0.7	Y	Y	Y	Y
Megachilidae	*Anthidium manicatum*	0.7	Y	Y	**N**	**N**
Megachilidae	*Megachile centuncularis*	0.7	Y	Y	Y	**N**
Megachilidae	*Megachile ligniseca*	0.7	Y	Y	**N**	Y
Colletidae	*Hylaeus signatus*	0.7	Y	Y	**N**	Y
Apidae	*Anthophora quadrimaculata*	0.8	Y	Y	Y	N