Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 26 December 2022 doi:10.20944/preprints202212.0462.v1

Article

Structure of a Metacommunity of Urban Bees: Species Diversity and Spatio-temporal Modularity

Yoko L. Dupont [1], Henning Bang Madsen [2], Mette Balslev Greve [3] Claus Rasmussen [4] and Jens M. Olesen [1,5]

[1] Department of Ecoscience, Aarhus University, C.F. Møllers Allé, Building 1110, DK-8000 Aarhus C, Denmark
[2] Department of Biology, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark
[3] Department of Agroecology, Aarhus University, Blichers Allé 20, DK-8830 Tjele, Denmark
[4] Department of Agroecology, Aarhus University, Forsøgsvej 1, DK-4200 Slagelse, Denmark
[5] Department of Biology, Aarhus University, Ny Munkegade 116, DK-8000 Aarhus C, Denmark
* Correspondence: yoko.dupont@ecos.au.dk

Abstract: As the globe becomes more urban, the question how much natural biodiversity can subsist in cities becomes increasingly urgent to answer, and also how is urban diversity structured? To contribute to an answer, we studied the metacommunity of bees in a North European metropolitan area. The system consisted of 13 sites in the city of Aarhus, Denmark, censused from April to September during one year. Bees were sampled monthly in pan traps and a set of traits was related to their presence. In total, 40 species were collected–29 solitary species (40% of all sampled individuals), ten *Bombus* species (28%), and *Apis mellifera* (32%). Most sampled bees were soil-nesting, pollen generalists, and relatively common. Habitat diversity within a set of concentric circles with trap as centre and radius from 50 m to 1000 m was related to bee α diversity per site (total bee spp. with and without honeybee, solitary bees, and bumblebees). The relationship was only significant within the 1,000 m circle, and solitary bee diversity did not even correlate with habitat diversity at this large spatial scale level. The bee-site (space) and bee-month (time) networks were analyzed with respect to nestedness, modularity, and spatio-temporal β diversity. The two networks were weakly nested and strongly modular, being composed of five and six modules of tightly linked bees. Total β diversity, β_{TOTAL}, is the sum of species turnover, β_{TURN}, and species loss/gain or nestedness, β_{NEST}; and for both space and time, β_{TURN} was more important than β_{NEST}. Furthermore, β_{TOTAL} was higher than season β_{TOTAL}. Thus, the urban bee metacommunity was well-structured in both space and time and the high β_{TURN} indicated, that the network was strongly modular. We suggest the main reason is the high spatio-temporal patchiness of habitats, sustaining many unique species.

Keywords: *Apis*; beta diversity; city; nestedness; network; pollinator

1. Introduction

Growth of urban areas is certainly one of the most severe encroachments of nature and alongside, many species and their biotic interactions disappear (Seto *et al.* 2012). Loss and change in species composition due to urbanization, in general, are now fairly well understood. However, the questions go deeper, because urban areas are highly heterogenous. Recent reviews even suggest that urban areas can become novel ecosystems and should be considered as specific habitats for animal and plant life and not just degraded versions of former natural habitats (Hall *et al.* 2016). Urban areas represent a patchy mosaic of habitats, spanning from concrete deserts to green spaces of high biodiversity. The complex spatio-temporal dynamics of species and the metacommunities inhabiting these mosaics must certainly be significant components and drivers of urban diversity (Leibold *et al.* 2004). If true, green spaces of high biodiversity cannot be separated from their more "hostile" surrounding neighbourhoods. Thus, like any fragmented landscape, the biota of urban green spaces has to be understood within their dynamic matrix context (Ahrne *et* *al.* 2009), *i.e.* an important quality of a green space becomes the surrounding landscape (Tew *et al.* 2022).

Here, we studied how bees (Hymenoptera, Apoidea) as an ecological guild respond to urban patchiness. The quality of a habitat patch for bees obviously must depend on its flower richness and suitability for nesting, but food and nesting sites might often be located in different patches. The estimated influence of these two drivers (flowers, nesting sites) of bee diversity varies in different studies and has made further generalizations difficult (Steffan-Dewenter *et al.* 2002, Kleijn & van Langevelde 2006).

Bees are a key element in natural habitats, but also in urban areas (Baldock *et al.* 2015). They constitute a heterogeneous group, being not just rich in species, but also in ecology (Gathmann & Tscarntke 2002, Westphal *et al.* 2006, Greenleaf *et al.* 2007, Zurbuchen 2010ab, Baldock *et al.* 2015). At our study sites in a North European metropolitan region, bees make up a diverse community, from tiny, short-range, solitary species, to large, far-flying bumblebees and the ubiquitous honeybee, in addition to the cleptoparasites. These functional groups, but also their individual species members, are all expected to respond to urban patchiness according to their own specific ecology.

Here, we describe species diversity and estimate spatio-temporal modularity of bees in a North European cityscape. We focus upon the dynamics in species richness in a set of sites during an entire season and relate this to ecology of the species. By spatial and temporal modularity, we mean non-random, spatial association between bee groups and sites and temporal association between bee groups and months, respectively (Hagen *et al.* 2012). Finally, based on an analysis of the β diversity of our study system, we briefly discuss strategies for bee diversity conservation.

2. Material and methods

2.1. Study sites

The bee fauna was sampled at 13 sites along a NE-SW line crossing the city of Aarhus, Denmark, including suburban and satellite areas (Figure 1). The entire municipality covered a 468 km^2 urban area with *c.* 331.000 inhabitants in the study year of 2016 (Aarhus i tal 2022). The sites encompassed a diverse cityscape of parks, residential areas, private gardens etc.

Since maximum flight range of most solitary bees is < 1 km (Gathmann & Tscharntke 2002, Darvill *et al.* 2004, Zurbuchen *et al.* 2010ab) and in order to reduce most effects of spatial autocorrelation, sites were separated by at least 2 km. However, many small species fly considerably shorter distances, when provisioning for their nests (Greenleaf *et al.* 2007).

2.2. Traps

At each site, bees were sampled using pan traps. Each trap consisted of three semi-spherical bowls, a white-coloured, a blue, and a yellow one (radius 6.5 cm). This tricoloured palette is well known to attract a wide range of bees (Leong & Thorp 1999, Campbell & Hanula 2007). Each bowl contained 250 ml of a 1:10 aqueous solution of Rodalon©. The latter was added in order to conserve trapped insects and to break water surface tension in order to reduce the ability of bees to escape traps. Bowls were placed on a metal plate mounted on a wooden stake with a height at level with surrounding vegetation. At each site, traps were positioned near to the most abundant type of vegetation, preferably plants in flower. However, owners of private gardens decided the exact location of the trap. In public areas, traps were placed at the edge of lawns or in open space.

The study was carried out in 2016 and traps were installed for a 5-day continuous period once a month: *viz.* 16-21 April, 15-20 May, 17-22 June, 16-21 July, 16-21 August, and 14-18 September; deviations were due to extended periods of rain. Samples from traps were stored in 70% ethanol. First, we discarded non-bee insects and subsequently all bees (Hymenoptera, Apiformes, Apoidea) were identified to species. However, as *Bombus cryptarum, B. lucorum, B. magnus,* and *B. terrestris* are difficult to distinguish, they were lumped into a '*Bombus terrestris* species complex' (Williams *et al.* 2012). *Bombus magnus* and probably also *B. cryptarum* might be ignored as options, because they were not known to the region.

2.3. Traits

For each species, a set of ecological traits was compiled from literature and our data: 1, soil nesting *vs.* cavity nesting *vs.* parasitic (Madsen & Dupont 2013); 2, oligolecty *vs.* polylecty, *i.e.* a few or many sources of pollen, respectively (Amiet *et al.* 1999, 2001, 2004, 2007, 2010); 3, active most of the season (April to September) *vs.* only in early season (June or earlier) *vs.* only in late season (May and onwards) (data from Rasmussen *et al.* 2016); and finally 4, univoltine *vs.* bivoltine, *i.e.* one or two annual generations, respectively (Amiet *et al.* 1999, 2001, 2004, 2007, 2010; data from Rasmussen *et al.* 2016); social species were regarded as univoltine (Dupont & Madsen 2010).

2.4. Habitat diversity and bee species diversity

At each site, we estimated habitat type diversity within a set of concentric circles with trap as centre and radii of 50 m, 100 m, 200 m, 500 m, and 1000 m, *i.e.* the 'landscape dimension'. This was done in *ArcGIS Pro 2.5.1*. Habitat type classification followed *Basemap02* (Levin *et al.* 2017): 1 urban/residential area, 2 forest/park, 3 industrial area, 4 roads, 5 railway, 6 recreational area, 7 farmland, 8 natural vegetation, 9 water bodies, and 10 others. Area of each type was calculated for each circle and site. Input data were from May-September 2016, except farmland area data (type 7), which were from 2011.

Using the Shannon-Wiener diversity function H (Good 1953), we analyzed, if habitat type diversity and bee species diversity per site, *i.e.* α diversity, were correlated. H was used both as a habitat type and bee α diversity index: $H = -\Sigma p_i \ln p_i$, where p_i was either the proportion of the area of each habitat type i at a site and concentric circle or the abundance of each bee species i in the sample at a site. In general, H ranges from 1.5 to 3.5.

2.5. Networks and spatio-temporal modularity (β diversity)

Firstly, we constructed bee-space and bee-time networks as presence-absence matrices, where columns represented bee species and rows represented sites or months, respectively. A link was present, if a bee species was found at a site or during a month or absent if not.

Secondly, we estimated how distinct the two link patterns, nestedness and modularity, were, using *R > maxnodf*, *R > Igraph > Generalized Louvain* (Figure 2; Olesen 2022), and *R > bipartite*, respectively.

Thirdly, we calculated the regional and seasonal species diversities of the bee metacommunity, *i.e.* the β diversity for bees across all 13 study sites and across all six months. As measure, we used total β diversity $\beta_{\mathrm{TOTAL}} = (b + c)/(2a + b + c)$, where a is number of shared species between two sites or months, b is number of unique species at one site or month, and c is number of unique species at another site or month.

β_{TOTAL} is further composed of two components with strong implications for management and planning of urban biodiversity (Figure 2) (Baselga & Orme 2012, Carstensen *et al.* 2014): (1) spatial or temporal turnover of species β_{TURN} between one site or month and another site or month, and (2) spatial or temporal nestedness β_{NEST}, *i.e.* species loss and gain at a site or month compared to the other sites or months. β_{NEST} measures the extent to which poorer species assemblages are subsets of richer ones. Thus, $\beta_{\mathrm{TOTAL}} = \beta_{\mathrm{TURN}} + \beta_{\mathrm{NEST}}$. We obtained estimates of all three indices, using *R > betapart > beta.multi*, (Baselga & Orme 2012).

Notice, that in Baselga & Orme (2012), β_{TOTAL}, β_{TURN}, and β_{NEST} are called β_{SOR}, β_{SIM}, and β_{SNE}, respectively.

3. Results

3.1. Metacommunity of the urban bees in space and time

A total of 313 individuals of bees belonging to 40 species were collected, *viz.* 124 solitary bees belonging to 29 species, 89 bumblebees (*Bombus* spp.) belonging to ten species, and 100 honeybees (*Apis mellifera*) (Supplemental Material 1). Thus, 40% of all sampled bee individuals were solitary bees, 28% were bumblebees, and 32% were honeybees.

Frequency distributions of number of bee species *S* and individuals *B* per site were right skewed. *B* ranged from only three at site L (dominated by gardens, Table 1) to 57 at site H (the main university campus with its green spaces and lakes), and *S* ranged from three species at site L to 17 species at site M (a university college-campus park with nearby industry and railway). *B* and *S* were significantly correlated (Figure 3). Bee diversity *H* at a site, *i.e.* α diversity, ranged from 1.10 at site L to 2.42 at site B (Table 1). Site H, however, was an outlier, because of relatively high abundances of *Apis mellifera* and *Andrena haemorrhoa*.

Table 1. Total bee species abundance per site *B*, bee species richness per site *S*, and local or a diversity *H* of bee species per site. Sites are sorted according to decreasing *H*.

Site	Main habitat types within a radius of 50 m from trap	*B*	*S*	*H*
B	industry, roads	36	14	2.42
M	campus, industry, railway	47	17	2.24
J	gardens, railway, roads	37	12	2.05
H	campus, roads, lakes	57	11	1.88
G	gardens, park, roads	13	8	1.84
A	gardens, roads	16	8	1.84
C	recreational, roads, lake	19	7	1.77
K	roads, industry, railway	31	11	1.70
I	park, roads	12	6	1.58
D	gardens, roads, lakes	12	6	1.56
E	gardens, park, railway	13	6	1.41
F	gardens, roads, park	17	6	1.38
L	gardens, roads	3	3	1.10

During the study period of six months, traps at all 13 sites were sampled monthly, *i.e.* adding up to a total of 78 trap samples. Mean numbers of bee individuals and species per trap sample and their standard deviation were 4.01 ± 4.83 individuals (range 0-21, median 2) and 2.19 ± 2.08 species (range 0-10, median 2). Twenty-three percent (18 traps) of all 78 trap samples were empty.

The total bee metacommunity included 12 genera, the three most species-rich genera being *Andrena* (11 spp.), *Bombus* (10 spp.), and *Lasioglossum* (7 spp.). Remaining genera were represented by only one or two species each (Supplementary Material 1).

Pooling data from all sites, monthly number of sampled bee species (honeybee included) varied from two in September to 23 in July (Figure 4A, Supplemental Material 2), and monthly number of sampled bee individuals, all sites pooled, varied from 13 in September to 97 in July (Figure 4B). This seasonal variation is partly driven by specific phenology differences. Average temporal species persistence *T*, *i.e.* average number of active months per species, was only 2.1 months. *Andrena* species peaked in April-May with a *T* = 1.2. *Lasioglossum* peaked in June-July with a *T* = 2.4 months, and bumblebees being almost omnipresent with *T* = 2.9 months.

3.2. Ecological traits of the urban bees

Data on ecological traits of the collected species are found in (Table 2A) and Supplemental Material 3.

Table 2. A. Distribution of ecological traits. *N*, no. species (Supplemental Material 3).

1 Nesting site	***N***	**Pct.**
1 soil-nesting	29	82.9
2 cavity-nesting	6	17.1
3 clepto-parasitism	5	
	40	100
2 Pollen diet	*N*	Pct.
1 oligolecty	5	14.3
2 polylecty	30	85.7
3 clepto-parasitism	5	
	40	100
3 Acticity period	*N*	Pct.
1 early season	13	32.5
2 late season	18	45.0
3 most of season	9	22.5
	40	100
4 Generations	*N*	Pct.
1 univoltine	37	92.5
2 bivoltine	3	7.5
	40	100

1–Almost all species were nest-builders, although the fauna included three social, parasitic *Bombus* spp. (*B. bohemicus, B. norvegicus,* and *B. vestalis*) and two clepto-parasitic species (*Sphecodes geoffrellus* and *S. miniatus*). Among solitary nest builders, 29 species were soil nesters and six were cavity nesters, *e.g. Anthidium manicatum, Chelostoma rapunculi,* and *H. hyalinatus*.

2–Almost all (30) species of the nest-builders were polylectic, only five were oligolectic: *Andrena praecox* on *Salix*, *Chelostoma rapunculi* on *Campanula*, *Colletes daviesanus* and *Dasypoda hirtipes* on Asteraceae, and *Megachile lapponica* on *Epilobium*.

3–Most species were either active in early (13 species) or mid-late season (18 species).

4–Almost all (37) species were univoltine, except *Andrena bicolor, A. flavipes*, and *A. minutula*. Social species were regarded as univoltine.

Most traits were not significantly associated, except (*a*) nesting site–activity period, (*b*) number of study sites (proxy of regional species distribution)–activity period, (*c*) number of study sites–number of generations (Table 2B).

Table 2. B. Associations among ecological traits (excluding Red List status) based on Cramer's *V* (association test of categorical variables). Upper-right matrix triangle: Cramer's *V* (positively associated, if sienna-coloured; negatively, if blue); lower-left matrix triangle: *P*-values. If $P > 0.05$ in a cell, the two corresponding variables were not significantly associated (grey). If $P \leq 0.05$, the cell is red. For variables, see text. Cramer's *V* is a measure of the strength of an association between two nominal variables; '0', no association between variables, and '1'.

Nesting site	Pollen diet	Activity period	No. generations	No. study sites	
	0.25	0.42	0.17	0.42	Nesting site
0.41		0.34	0.26	0.40	Pollen diet
0.04	0.13		0.30	0.61	Activity period
0.62	0.31	0.19		0.60	No. generations
0.53	0.60	0.03	0.03		No. study sites

3.3. Habitat diversity and bee species α diversity

All sites and their surroundings were a complicated mosaic of habitat types (Supplemental Material 4). We analysed, if habitat type diversity at each of the 13 sites and circle sizes was correlated with bee α diversity at sites (Supplemental Figure 1). Wild bee (*Apis mellifera* excluded), total bee, and *Bombus* α diversities *H* were all positively correlated with habitat type diversity within the largest radius of 1000 m, but never within any smaller circle. Solitary bee *H* was not correlated with habitat diversity at all. These findings are summarized in Figure 5, where the *F*-statistics of the correlation analyses are plotted against landscape dimension. Only at the largest landscape circle did we see an effect of habitat diversity on bee α diversity.

3.4. Spatio-temporal network structure

From a network analytical point of view, bees and sites/months represent two sets of interacting nodes, and links represent bee presence at sites or in months. The linkage pattern of these two-mode networks (Figure 6). The 40 urban bees (*S*), their 13 sites, six months activity period, and 115 links (*I*) gave the networks a connectance $c_{\text{site}} = 115 \cdot 100/(40 \cdot 13) = 22\%$ and $c_{\text{month}} = 115 \cdot 100/(40 \cdot 6) = 35\%$, *i.e.* the percent observed bee species presences out of the total potential presences, if present at all sites and in all months.

In general, ecological networks are both nested (Bascompte *et al.* 2003, Dupont *et al.* 2003, Almeida-Neto *et al.* 2008) and modular (Olesen *et al.* 2007, Olesen 2022) (see Figure 2 above for a textbook example), but to a varying extent, depending on history and present ecological settings. In our two-mode bee-site network, *NODF* = 0.35^{ns} (*R* > *bipartite*) and modularity level = 0.32* (*R* > *Generalized Louvain*; five modules; Figure 6) and in the bee-month network, *NODF* = 0.48^{*} and *M* = 0.31* (six modules; Figure 6).

One of the bee-site modules covered five sites in the North-western part of the city, all being gardens; the other bee-site modules included two sites each. Each site module included 1-3 bumblebees and 1-3 *Andrena* spp. and all site modules had representatives from 5-6 of the month modules, *i.e.* each site module consisted of a temporal sequence of species.

Each month had its own module in the bee-month network. *Andrena* spp. were only present in the April and May modules (except the later *A. fulvida*), and all *Lasioglossum* spp. were only found in the May and June modules. Thus, space and time not only strongly structured the bee metacommunity, but they also did it in different ways. However, any site module x month module combination included only 0-3 species (Supplemental Material 5).

3.5. Regional and seasonal bee β diversity

Regional or among sites, total β diversity $\beta_{\text{TOTAL}} = \beta_{\text{TURN}} + \beta_{\text{NEST}} \Leftrightarrow 0.85 = 0.77 + 0.08$, *i.e.* species turnover (β_{TURN}) contributed much more to the β diversity than species loss/gain (β_{NEST}) ($\beta_{\text{TURN}} : \beta_{\text{NEST}} = 9.6$; Figure 7). Species turnover (β_{TURN}) favours modularity, whereas species loss/gain favours nestedness (β_{NEST}). Turnover was high, because more than half of all species were unique to their site (Supplemental Material 1). Although weak, nestedness–and thus spatio-temporal autocorrelation–was partly driven by the three link-rich hubs (*Apis mellifera, Bombus terrestris* species complex, and site M).

Seasonal total β diversity $\beta_{\text{TOTAL}} = \beta_{\text{TURN}} + \beta_{\text{NEST}} \Leftrightarrow 0.74 = 0.58 + 0.16$, *i.e.* species turnover (β_{TURN}) contributed again more to β diversity than species loss/gain (β_{NEST}) ($\beta_{\text{TURN}} : \beta_{\text{NEST}} = 3.2$). Hence, total β diversity of the urban bee metacommunity in Aarhus was characterized by a high turnover of species among both sites and months.

4. Discussion

Many studies of the influence of urbanization on bee diversity show a negative effect, *e.g.* Hernandez *et al.* (2009), Bates *et al.* (2011), Banaszak-Cibicka (2012), and Deguines *et al.* (2012). However, this obviously depends on what the comparison is: agricultural, buildings, or natural areas (Theodorou *et al.* 2017). We did not test this here, because all study sites were within a metropolitan area. In stead we focused upon the structure of an urban bee metacommunity in space and time.

In our study, the urban bee fauna included 40 species in 12 genera. Seventy percent of the species belonged to *Andrena*, *Bombus*, and *Lasioglossum*. Slightly more than 1/3 (40%) of all sampled bee individuals were solitary species, slightly less than 1/3 (28%) were bumblebees, and ~1/3 (32%) were honey bees. The relative abundances of these major bee groups differ from a study of bees in large British cities, the figures were here 14%, 62%, and 24%, respectively (Baldock *et al.* 2019),

About 40% of the area in our study was residential areas and private gardens, a somewhat comparable figure for the study in Britain, where the area of gardens was 24-36% (Baldock *et al.* 2019). Thus, in Aarhus the diversity of solitary bees was 3-4 times higher than in the British studies. This difference cannot be explained by national differences, because the bee fauna in the two country is somewhat similar in size (296 for Denmark and ~270 for Britain). However, the pan trap method used in the current study, has been reported to have a better coverage and generally detects higher species richness of bees, compared to transect walks (*e.g.* Westphal *et al.* 2008), which was the sampling method of the British study. Another study of the bee-plant networks of a large British town and nearby nature reserves (Sirohi *et al.* 2022) observed 29 non-parasitic solitary bees compared to 26 here. The two studies had 13 species in common. This study suggests that the explanation of the high diversity of solitary bees might be the many native plant species, sustaining oligolectic species.

In our study, most urban bees were soil-nesting, polylectic (food generalized), univoltine, and relatively common species, being active in either early or mid-late season. Baldock *et al.* (2015, 2019) also observed a preponderance of generalist species. However, other studies find, that specialist bees also thrive in cities, *e.g.* Casanelles-Abella *et al.* (2021) and da Rocha-Filho *et al.* (2021). Some studies find more cavity-nesting bees, which they suggest is caused by the high tarmacked surface cover, being an obstacle to soil-nesting species (Cane 2006, Hernandez *et al.* 2009).

The diversity of urban bees is influenced by a long list of external factors, *e.g.* urban temperature (the urban heat island effect; Oke 1973, McCune *et al.* 2019), habitat heterogeneity (the mosaic), green space, “impervious” surface area (Geslin *et al.* 2016), food plant-nesting site distance (Walther-Hellwig & Frankl 2000, Chapman 2003, Wolf & Moritz 2008, Zurbuchen 2010ab, Hofmann *et al.* 2020), flowering season length for social bees (Bengtson & Bredesen 2014), pesticide pressure (differential response from insecticide and herbicide; Muratet & Fontaine 2015), heavy metal pollution (Sivakoff 2019), light pollution (Gaston 2013, Isaksson 2015), high honey bee hive density (Ropar *et al.* 2019), and the proportions of exotic and natural flora (Sirohi *et al.* 2022, Tew 2022), but also internal factors such as phenotypic plasticity (diet switching) of the bees matters (Saure 1996, Gaston 2010).

The relationship between local bee or α diversity and habitat diversity was analysed at five spatial scales (from 50 m to 1,000 m radius). At the largest scale, *i.e.* within a circle of a radius of 1,000 m and with the trap as centre, we found a positive relationship between habitat type diversity and both total bee and bumblebee α diversity. Solitary bee α diversity, however, did not correlate with habitat diversity at any of the five spatial scale levels. Some species of *Andrena* and *Bombus*, two of the largest genera in our study and in Denmark, are known to forage over distances larger than 1000 m from their nest (Wolf & Moritz 2008, Zurbuchen *et al.* 2010ab), whereas other bees fly considerably shorter distances (Gathmann & Tscharntke 2002, Darvill *et al.* 2004). In a Swedish study of bumblebee diversity along an urban gradient, Ahrne *et al.* (2009) used three concentric circles 330, 500, and 1000 m to describe the cityscape and also found the strongest correlation between bumble bee diversity and proportion of suitable surface at a radius of 1000 m.

In a large British study, encompassing sites in cities, farmland and nature, communal allotments and gardens had the highest bee diversity (Baldock *et al.* 2015). Two of "our" gardens were devoid of honey bees, but it was unclear, how this affected wild bee diversity, because one had the lowest and the other the highest wild bee diversity of all gardens. However, the bee quality of a garden and its surroundings is intricate and complicated to estimate; *e.g.* nectar availability and pollen diversity are important (Tew *et al.* 2022) and differential responses to habitat quality by solitary and social bees.

The literature presents many studies of bee communities in urban areas, but no strong consensus is achieved about which generalizations to be expected (Hernandez *et al.* 2009). The reason is obvious–the world has many cities and bees and both vary. However, the analysis of bee β diversity among sites and months did show, that diversity in our study city was driven by spatio-temporal species replacement (the turnover component), especially of solitary bees, but only poorly by species gain or loss (the nestedness component). This high turnover in species diversity has also been observed by Tew *et al.* (2022). Thus, every green patch in a city seems to matter to diversity, and so does the quality of the entire season, because each patch and time of the year are expected to sustain at least some unique species. This is especially the case, if a green patch is embedded in a landscape of high habitat diversity. Hence, as our overall message to conservation managers, we conclude that our results suggest, that in terms of regional or β biodiversity, especially of the solitary bee fauna, a few large areas may not compensate for the loss of several small ones (however, see Stewart *et al.* 2018). Thus, establishment and protection of many small green patches with a long bee "friendly" season is recommended.

Author Contributions: Conceptualization, Y.L.D. and J.M.O; methodology, Y.L.D., H.B.M., M.B.G, C.R., J.M.O.; formal analysis, Y.L.D., J.M.O., M.B.G.; investigation, Y.L.D. and H.B.M.; resources, Y.L.D.; writing—original draft preparation, Y.L.D. and J.M.O.; writing— review and editing, Y.L.D., H.B.M., M.B.G, C.R., J.M.O. All authors have read and agreed to the published version of the manuscript.

Acknowledgments: Thomas Blindbæk is thanked for sharing his collection of bees from his MSc study (Blindbæk 2017).

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Ahrne, K., Bengtsson, J. & Elmqvist, T. 2009. Bumble bees (Bombus spp.) along a gradient of increasing urbanization. PLoS ONE 4(5), e5574. doi.org/10.1371/journal.pone.0005574
2. Almeida-Neto, M., Guimaraes, P., Guimaraes, P. R., Loyola R. D. & Ulrich, W. 2008. A consistent metric for nestedness analysis in ecological systems: Reconciling concept and measurement. Oikos 117: 1227-1239. doi.org/10.1111/j.0030-1299.2008.16644.x
3. Amiet, F., Herrmann, M., Müller, A. & Neumeyer, R. 2001. *Fauna Helvetica 6. Apidae 2* (*Lasioglossum, Halictus*). Centre suisse de cartographie de lafaune (CSCF), Neuchâtel.
4. Amiet, F., Herrmann, M., Müller, A. & Neumeyer, R. 2004. *Fauna Helvetica 9. Apidae 4* (*Anthidium, Chelostoma, Coelioxys, Dioxys, Heriades, Lithurgus, Megachile, Osmia* & *Stelis*). Centre suisse de cartographie de la faune (CSCF), Neuchâtel.

5. Amiet, F., Herrmann, M., Müller, A. & Neumeyer, R. 2007. *Fauna Helvetica 20. Apidae 5* (*Ammobates, Ammobatoides, Anthophora, Biastes, Ceratina, Dasypoda, Epeoloides, Epeolus, Eucera, Macropis, Melecta, Melitta, Nomada, Pasites, Tetralonia, Thyreus, Xylocopa*). Centre suisse de cartographie de lafaune (CSCF), Neuchâtel.
6. Amiet, F., Herrmann, M., Müller A. & Neumeyer R. 2010. *Fauna Helvetica 26. Apidae 6* (*Andrena, Melitturga, Panurginus, Panurgus*). Centre suisse de cartographie de la faune (CSCF), Neuchâtel.
7. Amiet, F., Müller, A. & Neumeyer, R. 1999. *Fauna Helvetica 4. Apidae 2* (*Colletes, Dufourea, Hylaeus, Nomia, Nomioides, Rhophitoides, Rophites, Sphecodes, Systropha*). Centre suisse de cartographie de lafaune (CSCF), Neuchâtel.
8. Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Staniczenko, P. P. A., Stone, G. N., Vaughan, I. P. & Memmott, J. 2019. A systems approach reveals urban pollinator hotspots and conservation opportunities. Nature Ecology & Evolution 3: 363-373. doi.org/10.1038/s41559-018-0769-y 2019
9. Baldock, K. C. R., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Osgathorpe, L. M., Potts, S. G., Robertson, K. M., Scott, A. V., Stone, G. N., Vaughan, I. P. & Memmott, J. 2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. Proceedings of the Royal Society, B 282: 20142849. doi.org/10.1098/rspb.2014.2849
10. Banaszak-Cibicka, Z. 2012. Wild bees along an urban gradient: Winners and losers. Journal of Insect Conservation 16: 331-343. doi.org/10.1007/s10841-011-9419-2
11. Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. 2003. The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences, U.S. 100: 9383-9387. doi.org/10.1073/pnas.16335761
12. Baselga, A. & Orme, C. D. L. 2012. betapart: An R package for the study of beta diversity. Methods in Ecology and Evolution 3: 808-812. doi.org/10.1111/j.2041-210X.2012.00224.x
13. Bates, A. J., Sadler, J. P., Fairbrass, A. J., Falk, S. J., Hale, J. D. & Matthews, T. J. 2011. Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. PLoS ONE 6, e23459. doi.org/10.1371/journal.pone.0023459
14. Bengtson, R. & Bredesen, B. Ø. 2014. *Humler på hageplanter i Oslo sentrum.* Rapport til Bymiljøetaten i Oslo. Pp. 18.
15. Blindbæk, T. 2017. Competition between honeybees and wild Danish bees in an urban area. MSc. thesis, Aarhus University, Aarhus.
16. Campbell, J. W. & Hanula, J. L. 2007. Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. Journal of Insect Conservation 11: 399-408. doi.org/10.1007/s10841-006-9055-4
17. Cane, J. A. 2006. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. Ecological Applications 16: 632-644. doi.org/10.1890/1051-0761(2006)016[0632:crwadb]2.0.co;2
18. Carstensen, D. W., Sabatino, M., Trøjelsgaard, K. & Morellato, L. P. C. 2014. Beta diversity of plant-pollinator networks and the spatial turnover of pairwise interactions. PLoS ONE 8, e112903. doi.org/10.1371/journal.pone.0112903
19. Casanelles-Abella, J., Müller, S., Keller, A., Aleixo, C., Orti, M. A., Chiron, F., Deguines, N., Hallikma, T., Laanisto, L., Pinho, P., Samson, R., Tryjanowski, P., van Mensel, L. & Moretti, M. 2021. How wild bees find a way in European cities: Pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. Journal of Applied Ecology 59: 457-470. doi.org/10.1111/1365-2664.14063
20. Chapman, R. E., Wang, J. & Bourke, A. F. G. 2003. Genetic analysis of spatial foraging patterns and resource sharing in bumble bee pollinators. Molecular Ecology 12: 2801-2808. doi.org/10.1046/j.1365-294X.2003.01957.x
21. da Rocha-Filho, L., Montagnana, P. C., Araújo, T. N., Moure-Oliveira, D., Boscolo, D. & Gatófalo, C. A. 2021. Pollen analysis of cavity-nesting bees (Hymenoptera: Anthophila) and their food webs in a city. Ecological Entomology 37: 146-157. doi.org/10.1111/een.12097
22. Darvill, B., Knight, M. E. & Goulson, D. 2004. Use of genetic markers to quantify bumblebee foraging range and nest density. Oikos 107: 471-478. doi.org/10.1111/j.0030-1299.2004.13510.x
23. Deguines, N., Julliard, R., de Flores, M. & Fontaine, C. 2012 The whereabouts of flower visitors: Contrasting land-use preferences revealed by a country-wide survey based on citizen science. PLoS ONE 7, e45822. doi.org/10.1371/journal.pone.0045822
24. Dupont, Y. L., Hansen, D. M. & Olesen, J. M. 2003. Structure of a plant-pollinator network in the high altitude sub-alpine desert of Tenerife, Canary Islands. Ecography 26: 301-310. doi.org/10.1034/j.1600-0587.2003.03443.x
25. Dupont, Y. L., Hansen D. M., Valido, A. & Olesen, J. M. 2004. Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. Biological Conservation 118: 301-311. doi.org/10.1016/j.biocon.2003.09.010
26. Dupont, Y. L. & Madsen, H. B. 2010. Humlebier. *Natur & Museum* nr. 1, March.
27. Gaston, K. J. 2010. *Urban ecology*. Cambridge: Cambridge University Press.
28. Gaston, K. J., Bennie, J., Davies, T. W. & Hopkins, J. 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biological Reviews 88: 912-927. doi.org/10.1111/brv.12036
29. Gathmann, A. & Tscharntke, T. 2002. Foraging ranges of solitary bees. Journal of Animal Ecology 71: 757-764. doi.org/10.1046/j.1365-2656.2002.00641.x
30. Geslin, B., Le Féon, V., Folschweiller, M., Flacher, F., Carmignac, D., Motard, E., Perret, S. & Dajoz, I. 2016. The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. Ecology & Evolution 6: 6599-6615. doi.org/10.1002/ece3.2374
31. Good, I. J. 1953. The population frequencies of species and the estimation of population parameters. Biometrika 40: 237-264. doi.org/10.1093/biomet/40.3-4.237
32. Goulson, D. 2003 *Bumble bees - behaviour and ecology*. Oxford: Oxford University Press.

33. Greenleaf, S. S., Williams, N. M., Winfree, R. & Kremen, C. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153: 589-596. doi.org/10.1007/s00442-007-0752-9
34. Gunnarsson, B. & Federsel, L. M. 2014. Bumblebees in the city: Abundance, species richness and diversity in two urban habitats. Journal of Insect Conservation 18: 1185-1191. doi.org/10.1007/s10841-014-9729-2
35. Hagen, M., Kissling, W. D., Rasmussen, C., Aguiar, M. A. M. de, Brown, L. E., Carstensen, D. W., Alves-Dos-Santos, I., Dupont, Y. L., Edwards, F. K., Genini, J., Guimaraes Jr., P. R., Jenkins, G. B., Jordano, P., Kaiser-Bunbury, C. N., Ledger, M. E., Maia, K. P., Marquitti, F. M. D., Mclaughlin, Ó., Morellato, L. P. C., O'Gorman, E. J., Trrøjelsgaard, K., Tylianakis, J. M., Vidal, M. M., Woodward, G. & Olesen, J. M. 2012. Biodiversity, species interactions and ecological networks in a fragmented world. Advances in Ecological Research 46: 89-210. doi.org/10.1016/B978-0-12-396992-7.00002-2
36. Hall, D. M., Camillo, G. R., Tonietto, R. K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J. S., Baldock, K. C. R., Fowler, R., Frankie, G., Goulson, D., Gunnarson, B., Hanley, M. E., Jackson, J. I., Langellotto, G., Lowenstein, D., Minor, E. S., Philpott, S. M., Potts, S. G., Sirohi, M. H., Spevak, E. M., Stone, G. N. & Threlfall, C. G. 2016. The city as a refuge for insect pollinators. Conservation Biology 31: 24-29. doi.org/10.1111/cobi.12840
37. Hernandez, J. L., Frankie, G. W. & Thorp, R. W. 2009. Ecology of urban bees: A review of current knowledge and directions for future study. Cities and the Environment 2, article 3. digitalcommons.lmu.edu/cate/vol2/iss1/3
38. Hofmann, M. M., Fleischmann, A. & Renner, S. S. 2020. Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. Journal of Hymenoptera Research 77: 105-117. doi.org/10.3897/jhr.77.51182
39. Isaksson, C. 2015. Urbanization, oxidative stress and inflammation: A question of evolving, acclimatizing or coping with urban environmental stress. Functional Ecology 29: 913-923. doi.org/10.1111/1365-2435.12477
40. Kleijn, D. & van Langevelde, F. 2006 Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic and Applied Ecology 7: 201-214. doi.org/10.1016/j.baae.2005.07.011
41. Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M. & Gonzalez, A. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7: 601-613. doi.org/10.1111/j.1461-0248.2004.00608.x
42. Leong J. M. & Thorp R. W. 1999. Colour-coded sampling: The pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. Ecological Entomology 24: 329-335. doi.org/10.1046/j.1365-2311.1999.00196.x
43. Levin, G., Iosub C.-I. & Jepsen M. R. 2017. *Basemap02. Technical documentation of a model for elaboration of a land-use and land-cover map for Denmark*. 64 pp. Technical Report No. 95, Danish Centre for Environment and Energy (DCE), Aarhus University. dce2.au.dk/pub/TR95.pdf.
44. Madsen, H. B. & Dupont, Y. L. 2013. Vilde bier. Natur og Museum 52 (1): 1-36.
45. McCune, F., Normandin, E., Mazerolle, M. J. & Fournier, V. 2019. Response of wild bee communities to beekeeping, urbanization, and flower availability. Urban Ecosystems 23(3). doi.org/10.1007/s11252-019-00909-y
46. Muratet, A. & Fontaine, B. 2015. Contrasting impacts of pesticides on butterflies and bumblebees in private gardens in France. Biological Conservation 182: 148-154. doi.org/10.1016/j.biocon.2014.11.045
47. Oke, T. R. 1973. City size and the urban heat island. Atmospheric Environment 7: 769-779. doi.org/10.1016/0004-6981(73)90140-6
48. Olesen, J. M. 2022. Ego network analysis of the trophic structure of an island land bird through 300 years of climate change and invaders. Ecology and Evolution 12, e8916. doi.org/10.1002/ece3.8916
49. Olesen, J. M., Bascompte, J., Dupont, Y. L. & Jordano, P. 2007. The modularity of pollination networks. Proceedings of the National Academy of Sciences, U.S. 104: 19891-19896. doi.org/10.1073/pnas.07063751
50. Rasmussen, C., Schmidt, H. T. & Madsen, H. B. 2016. Distribution, phenology and host plants of Danish bees (Hymenoptera, Apoidea). Zootaxa 4212: 1-100.
51. Ropars, L, Dajoz, I, Fontaine, C, Muratet, A. & Geslin B. Wild pollinator activity negatively related to honey bee colony densities in urban context. PLOS ONE. 2019;14(9): e0222316.
52. Saure, C. 1996. Urban habitats for bees: The example of the city of Berlin. In A. Matheson, S. L. Buchmann, C. O. Toole, P. Westrich & I. H. Williams, eds.). *The conservation of bees*. Pp. 47–53. Linnean Society Symposium Series No. 18. New York: Academic Press.
53. Seto, K. C., Guneralp, B. & Hutyra, L. R. 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. Proceedings of the National Academy of Sciences, USA 109: 16083-16088. doi.org/10.1073/pnas.1211658109
54. Sirohi, M. H., Jackson, J. & Ollerton, J. 2022. Plant-bee interactions and resource utilization in an urban landscape. Urban Ecosystems 17 Sept. doi.org/10.1007/s11252-022-01290-z
55. Sivakoff, F. S. & Prajzner, S. P. 2019. Urban heavy metal contamination limits bumblebee colony growth. Journal of Applied Ecology 57: 1561-1569. doi.org/ 10.1111/1365-2664.13651
56. Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. 2002. Scale-dependent effects of landscape context on three pollinator guilds. Ecology 83: 1421-1432. doi.org/10.1890/0012-9658(2002)083[1421:SDEOLC]2.0.CO;2
57. Stewart, A. B., Sritongchuay, T., Teartisup, P., Kaewsomboon, S. & Bumrungsri, S. 2018. Habitat and landscape factors influence pollinators in a tropical megacity, Bangkok, Thailand. *PeerJ* 6, e5335. doi.org/ 10.7717/peerj.5335
58. Tew, N. E., Baldock, K. C. R., Vaughan, I. P., Bird, S. & Memmott, J. 2022. Turnover in floral composition explains species diversity and temporal stability in the nectar supply of urban residential gardens. Journal of Applied Ecology 59: 801-811. doi.org/10.1111/1365-2664.14094

59. Theodorou, P., Albig, K., Radzevicˇiu¯tė, R., Settele, J., Schweiger, O., Murray, T. E. & Paxton, R. J. 2017. The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. Functional Ecology 31: 838-847. doi.org/10.1111/1365-2435.12803
60. Walther-Hellwig, K., Frankl, R. 2000. Foraging distances of *Bombus muscorum*, *Bombus lapidarius*, and *Bombus terrestris* (Hymenoptera, Apidae). Journal of Insect Behavior 13: 239-246. doi.org/10.1023/A:1007740315207
61. Westphal, C., Steffan-Dewenter, I. & Tscharntke, T. 2006. Bumblebees experience landscapes at different spatial scales: Possible implications for coexistence. *Oecologia* 149: 289-300. doi.org/10.1007/s00442-006-0448-6
62. Williams, P. H., Brown, M. J. F., Carolan, J. C., An, J., Goulson, D., Aytekin, A. M., Best, L. R., Byvaltsev, A. M., Cederberg, B., Dawson, R., Huang, J., Ito, M., Monfared, A., Raina, R. H., Schmid-Hempel, P., Sheffield, C. S., Sima, P. & Xie, Z. 2012. Unveiling cryptic species of the bumblebee subgenus *Bombus s. str.* worldwide with COI barcodes (Hymenoptera: Apidae). Systematics and Biodiversity 10: 21-56. doi.org/10.1080/14772000.2012.664574
63. Wolf, S. & Moritz, R. F. A. 2008. Foraging distance in *Bombus terrestris* L. (Hymenoptera: Apidae). Apidologie 39: 419-427. doi.org/10.1051/apido:2008020
64. Zurbuchen, A., Cheesman, S., Klaiber, J., Müller, A., Hein, S. & Dorn, S. 2010a. Long foraging distances impose high costs on offspring production in solitary bees. Journal of Animal Ecology 79: 674-681. doi.org/10.1111/j.1365-2656.2010.01675.x
65. Zurbuchen, A., Landert, L., Klaiber, J., Mu¨ller, A., Hein, S. & Dorn, S. 2010b. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. Biological Conservation 143: 669-676. doi.org/10.1016/j.biocon.2009.12.003
66. Aarhus i tal 2022. Ledelsesinformation.aarhuskommune.dk/aarhus-i-tal/default.aspx?doc=vfs://Global/AARHUS-I-TAL/BEFOLKNING_I_TAL.xview.