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Wild bees and hoverflies respond differently to urbanisation, human population density and urban form

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ABSTRACT

While urbanisation contributes to global biodiversity declines, flower-rich urban habitats may provide beneficial pollinator habitats. We investigated the potential of urban residential areas to contribute to pollinator diversity by analysing wild bee and hoverfly species richness and composition of species assemblages of summer-active species, sampled in 53 gardens across urban and rural landscapes of Malmö, the regional capital of Sweden's southernmost county. Species richness differed between urban and rural gardens, and between four urban residential types (ranging from low human density and high vegetation cover, to high human density and low vegetation cover), and taxonomic groups responded differently. Solitary bee species richness was higher in urban than rural gardens, driven by a higher richness in low-density urban gardens compared to both high-density urban gardens and rural gardens. In contrast, bumblebee species richness was higher in rural than urban gardens, whereas differences among the urban types were less clear. Hoverfly species richness was consistently higher in rural gardens than any urban garden type. Species richness of all groups was negatively related to human population density at the landscape scale (radius 500 m), but unrelated to vegetation cover. This indicates that population density affects pollinator habitat quality through associated green space management and design. Rural and urban wild bee species assemblages consisted of different species (significant species turnover), whereas urban hoverfly assemblages were a subset of rural ones (significant nestedness). Species nestedness of hoverflies, but not bees, increased with human population density. We show that urban areas can complement the regional wild bee species pool, mainly caused by large variation in tenure and management at small spatial scales, while urbanisation drives a systematic loss of hoverfly species. We suggest alternatives to improve dense residential areas for pollinators.

1. Introduction

Global urbanisation rates are accelerating. The proportion of people living in urban areas is projected to increase from 55% in 2018 to 68% by 2050 (UN, 2019), with urban land cover expansion occurring even faster (CBD, 2012). Because urbanisation causes habitat destruction and fragmentation, it is one of the major drivers of biodiversity loss (TNC, 2018). The development of compact cities and towns, which reduces the need for transport and energy (Hassan and Lee, 2015), is therefore also advocated as a way to reduce exploitation of surrounding landscapes (Bren d'Amour et al., 2017). However, this development is partly in conflict with increasing demands for both residential and public green space to promote public health (WHO, 2016), mitigate and adapt to climate change (Demuzere et al., 2014), and conserve urban biodiversity and ecosystem services (CBD, 2012).

Wild bees and hoverflies are important pollinators of wild plants (Ollerton, Winfree, & Tarrant, 2011) and crops (Klein et al., 2007), and contain many declining species of conservation concern (Potts et al., 2016). Pollinator declines are mainly caused by increased land use intensity and concomitant loss of semi-natural habitats, reduced quality of remaining natural and semi-natural habitats, and increased use of pesticides (e.g. Goulson, Nicholls, Botias, & Rotheray, 2015). While flower-rich habitats are rare in contemporary agro-ecosystems, cities and towns contain flowers in parks, residential and allotment gardens, semi-natural grassland fragments and brownfields (Aronson et al., 2017; Baldock et al., 2019). Urban areas may therefore provide beneficial habitats, including refuges for rare and declining species (Hall et al., 2017). However, urban landscapes differ from rural ones in multiple ways. They are, for example, fine-grained, with contrasting land-cover types and management regimes occurring within small spatial scales (Aronson et al., 2017; Gaston, Ávila-Jiménez, & Edmondson, 2013), and often contain high proportions of exotic plants. In addition, buildings and roads constitute barriers that fragment the foraging landscapes of pollinators (Buchholz, Gathof, Grossmann, Kowarik, & Fischer, 2020; Johansson, Koffman, Hedblom, Deboni, & Andersson, 2018). The high proportion of buildings and paved surfaces also lead to the urban heat island effect, making urban landscapes warmer than the surrounding (Mimet et al., 2009). Thus, while urban habitats are unlikely to act as replacements of lost rural semi-natural habitats, they may still contribute to pollinator conservation (Baldock

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et al., 2019).

Residential gardens and backyards (hereafter gardens) can cover as much as 20–30% of urban areas (Goddard, Dougill, & Benton, 2010). Gardens are known to benefit bees in urban (Fetridge, Ascher, & Langellotto, 2008; Osborne et al., 2008), suburban (Martins, Gonzalez, & Lechowicz, 2017) and in intensively managed agricultural landscapes (Samnegård, Persson, & Smith, 2011). However, not all groups of pollinators may be able to find refuge in urban gardens because of different responses to urbanisation, for example, between bees and hoverflies (Bates et al., 2011; Verboven, Uyttenbroeck, Brys, & Hermy, 2014). For example, central-place foraging bees commute between foraging habitats and a fixed nest, whereas hoverflies lack a fixed nest and are less constrained by aggregated flower resources, but instead need habitat to lay their eggs in (e.g. plants, dead organic matter or aquatic environments). Such contrasting life-history strategies, in combination with variation in movement capacity, will affect susceptibility to resource fragmentation caused by urbanisation (Fortel et al., 2014; Hinners, Kearns, & Wessman, 2012) and, in turn, affect the composition of species assemblages (Luder, Knop, & Menz, 2018; Martins et al., 2017). Hence, while urban gardens are undoubtedly important for pollinators, their value will depend on the built form, vegetation cover, composition and management regime, as well as distribution of green spaces and human population density at the neighbourhood scale (Goddard, Dougill, & Benton, 2013; Lin et al., 2017; Soga, Yamaura, Koike, & Gaston, 2014).

In order to improve urbanised regions for a range of pollinators it is crucial to understand how urban and rural landscapes differ in species richness and composition of species assemblages of pollinators and how different taxonomic groups respond to urbanisation (Wenzel, Grass, Belavadi, & Tscharntke, 2019), both in the form of quantitative measures of urbanisation (land-use gradients) and qualitative measures (contrasting urban forms). For example, a relatively species-poor habitat along an urbanisation gradient may still contribute substantially to the species pool if it contains a high share of unique species, or if there is high species turnover between sites. Alternatively, an urbanisation gradient can result in a systematic loss of species, in which case species-poor habitats consist of a subset of species observed in species-rich habitats (Baselga, 2010). To study this, we sampled two important insect pollinator taxa – wild bees and hoverflies – in gardens of typical urban residential neighbourhoods distributed over gradients of vegetation cover and human population density, as well as in rural residential gardens embedded in agricultural landscapes.

We investigated (i) to what extent urban areas contribute to pollinator diversity in a region dominated by intensive agriculture, (ii) to what extent different residential neighbourhoods can support pollinator diversity, and (iii) how human density and vegetation cover at local and landscape scales affect pollinator communities. We expected urban gardens to be richer in bee species but poorer in hoverflies than rural gardens, because urban areas potentially provide ample bee nesting and foraging habitats but may lack hoverfly larval habitats. We also expected the composition of species assemblages to differ between urban and rural gardens for both bees and hoverflies, because the two areas largely offer different types of resources, and because species with restricted mobility may suffer from increased barriers in urban areas. Furthermore, we expected that urban gardens in less densely populated neighbourhoods would support higher richness of both bees and hoverflies, compared to densely populated areas, because they provide more habitat variation over small spatial scales and fewer barriers to movement. Finally, we expected a negative relationship between landscape-scale human population density and richness of all taxa, but a positive relationship with vegetation cover.

2. Methods

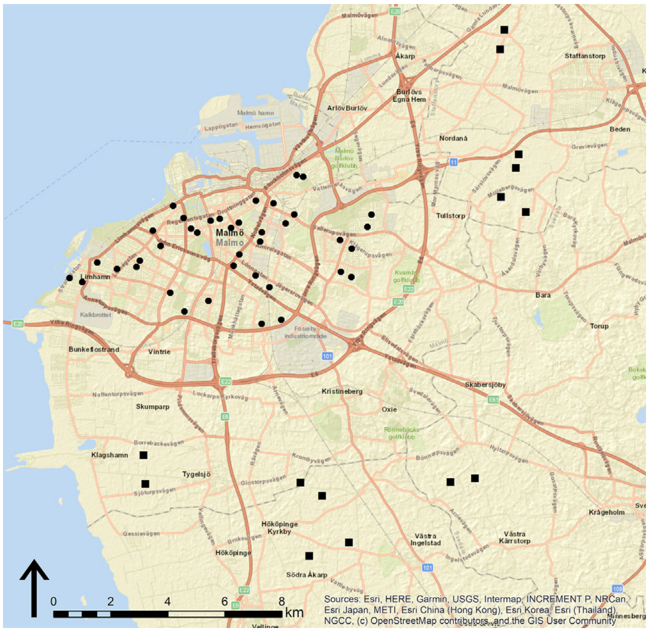
We studied pollinators in and surrounding the town of Malmö, southern Sweden, a region characterised by intensive agriculture with annual crop production. Malmö has a population of approximately 312,000 people (in 2017), covers 77 km^2 (SCB, 2019), and thus has a mean population density just over 4000 inhabitants/km^2. Residential neighbourhoods cover 35% of the urban part of Malmö municipality, while industrial, railway and commercial land make up 31%. Formal and informal green spaces cover 15% and roads and associated land 10% (data compiled from Urban Atlas; Copernicus, 2019).

2.1. Study design and sites selection

We surveyed pollinators in residential gardens of neighbourhoods that differed qualitatively in morphological type relevant to urban planning, as well as quantitatively in vegetation cover and human population density at spatial scales relevant for pollinators. To select sites, we analysed existing spatially explicit data on human population density and vegetation cover, provided by Malmö City council (Streets and Parks department): number of inhabitants in 100 × 100 m grid cells, and vegetation cover (grass, shrubs and trees combined) as a vector shape-file. We transformed the latter into an aligned 100 × 100 m raster using R v3.2.3 (R Core Team, 2015) and packages sp, rgdal, rgeos and raster (Bivand, Keitt, & Rowlingson, 2016; Bivand & Rundel, 2016; Bivand, Pebesma, & Gomez-Rubio, 2013; Hijmans, 2016). In order to better capture aspects of the typology of the urban area, rather than the number of people per hectare of land, we re-calculated human population density as: population/(1.05 – prop. vegetation cover), using 1.05 to avoid division by zero (Hahs & McDonnell, 2006), that is, inhabitants per non-vegetated and thus mainly built land. Using these raster layers, we performed moving window analyses to calculate the mean vegetation cover and population density per 1 × 1 km window (10 × 10 pixels). The output was visually inspected and data points outside the 0.1 and 0.9 percentiles on each axis removed to avoid selecting sites where the two gradients were highly correlated (Pasher et al., 2013). We divided the remaining data points into four categories of combinations of either low (15–35%) or high (35–55%) vegetation cover and low (5–75 people/ha) or high (75–145 people/ha) human population density. The categories were exported as tiff-files to draw maps in ArcGIS (Esri).

We then used social media to reach garden owners or tenants and urge them to sign up on a free online survey form (Google forms). We received around 200 applications. Using ArcGIS, we combined the applicants' positions with maps of the four categories (described above) to identify 40 suitable gardens situated in contrasting urban types and dispersed over the urban gradients (Figs. 1 and 2). We aimed for an equal representation, but were limited by the location of applicants and garden types. Therefore, the category with low vegetation cover and low population density was underrepresented, while the category with low vegetation and high population was overrepresented and included ten sites with population density above the 0.9 percentile (approx. 150 to 225 people/ha) (Fig. 2). The selected gardens were characteristic of their neighbourhoods and composed of four distinct types: (i) gardens of detached houses with continuous vegetation surrounding the house (N = 15), (ii) semi-detached houses connected in rows with distinct front- and/or backyards (N = 6), (iii) multifamily houses with open yards between building blocks (N = 11), and (iv) multifamily houses with courtyards surrounded by buildings (N = 8) (Fig. 2, Table 1). We hereafter refer to these categories as garden types. The mean (± std) minimum distance between urban gardens was 487 ± 177 m.

To compare urban and rural landscapes, we selected 14 residential gardens of detached houses or farmsteads surrounding Malmö for sampling (Fig. 1). Potential gardens were identified by visually inspecting free online maps (Hitta.se and Eniro.se) to find houses with gardens within 10 km from Malmö urban border and at least 1 km from villages or larger groups of houses. The landscapes surrounding rural gardens were dominated by annual conventionally managed crop fields according to the Integrated Administration and Control System (IACS), a database of spatially explicit data on land use on farmland fields



Sources: Esri, HERE, Garmin, USGS, Intermap, INCREMENT P, NRCan, Esri Japan, METI, Esri China (Hong Kong), Esri Korea, Esri (Thailand), NGCC, (c) OpenStreetMap contributors, and the GIS User Community

Fig. 1. Map showing the location of the 39 urban gardens (circles) and the 14 rural gardens (quadrats) in and surrounding Malmö, Sweden, that were sampled for wild bees and hoverflies during July 2017. Background map: © Open Street Map.

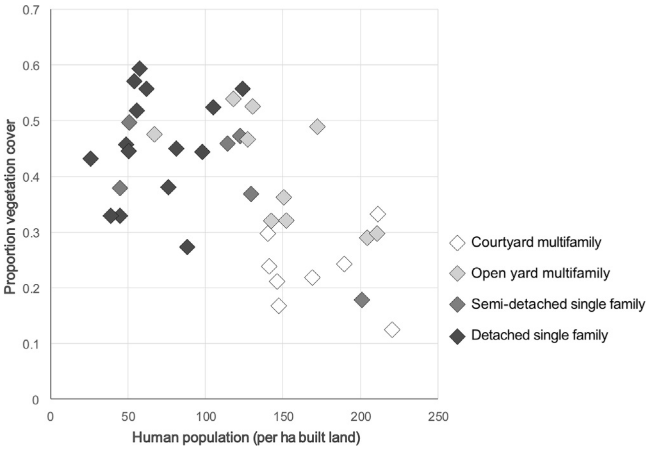


Fig. 2. Distribution of urban garden types over the design gradients: human population per ha built land and vegetation cover, measured at 500 m radius from each garden. While courtyards and detached houses were separated along the gradients, open yards and semi-detached houses were inter-dispersed with all other garden types.

administered by the Swedish Board of Agriculture. The mean minimum distance between rural gardens was 920 ± 282 m.

2.2. Insect and plant surveys

We focused on wild bees (Apoidea) and hoverflies (Syrphidae) but also included soldier flies (Stratiomyidae), because although often not treated as pollinators they have a similar life history to hoverflies (Bayless, 2008). We hereafter include them in the group hoverflies, if not otherwise stated. We surveyed pollinators using pan-traps for 30 days during summer 2017, from 2nd July until 2nd August. Three pan-traps (one yellow, one blue, one white) 15 cm in diameter and 5.5 cm deep, sprayed with UV-fluorescent paint (Sparvar Leuchtfarbe), were placed together on a black plastic tray in each garden in connection to vegetation typical of each garden, clearly visible and without shade or with only light shade for part of the day. Each bowl was half-filled with 50% propylene glycol and a drop of non-scented detergent. Traps were left in gardens, and contained liquid, for the whole period and emptied every 10 days (i.e. three times). Insects were preserved in ethanol until pinned and identified to species by entomologists at the Biological Museum, Lund University. We pooled data per pollinator taxon (bumblebees, solitary bees and hoverflies) at the individual garden level (three pan-traps) and calculated species richness, giving us three data points per garden. One urban site (multifamily open yard) was dropped from analyses because pan-traps were tampered with, leading to reduced sampling effort, resulting in 39 urban gardens. Two rural gardens were not surveyed for flowers because of time constraints, and were thus not included in models where flower data was a predictor, resulting in 12 rural gardens in those models.

We surveyed plants in each garden twice during the study period. Each time we surveyed 50 m^2 each of lawn/grass and flowerbeds/ornamental shrubs, depending on the characteristics of each garden. Hence, in total 100 m^2 per garden was surveyed. However, in 12 urban gardens less than 50 m^2 of either habitat was available, and for these we surveyed the entire habitat whilst assessing the total area surveyed to be able to control for area in analyses. We noted all flowering entomophilous plant species and estimated the total number of “flower units”, i.e. an easily countable structure that requires pollinators to fly between units (Szigeti, Kőrösi, Harnos, Nagy, & Kis, 2016). Thus, a single flower for species of Rosaceae and Campanulaceae, a raceme or flower head for most Fabaceae, flower heads for Asteraceae, a flower stalk or umbel for Lamiaceae and Apiaceae, were treated as flower units, respectively. This method gives an estimate of flower resources comparable between sites, while greatly reducing the time spent counting (cf. Williams & Kremen, 2007). We summed the number of species and flower units from the two habitats (lawn and flowerbed/shrub) per site. Summing the species numbers is reasonable because lawns and flowerbeds/shrubs largely contain different sets of plant species. We averaged the number of species and flower units across the two survey rounds, calculating abundance and richness of native species separately, defined according to Mossberg et al. (1992). Finally, to account for the smaller areas of 12 gardens, we calculated flower density as flower units/area.

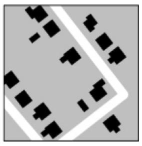
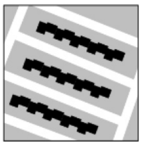
2.3. Land cover and population data

We derived detailed land cover and population data to explain pollinator species richness and to characterise the urban types. To calculate urban vegetation cover, we used a 2016 aerial ortoIR image (0.25 by 0.25 m) from Lantmäteriet (the Swedish mapping, cadastral and land registration authority) and determined the area fraction of each 100 × 100 m pixel that was either (i) trees and/or shrubs, (ii) grass or (iii) other (not vegetation), using built-in standard support-vector (supervised) machine classification in ArcGIS. Trees and grass were combined into total vegetation cover. We then extracted vegetation cover at 100 and 500 m radii surrounding each garden centre coordinate using R (packages as above). We used data on inhabitants per building from the “key code system” (NYKO) level 5 census data (2018), consisting of statistical information from almost 200 urban districts provided by Malmö municipality. As NYKO contains the total number of inhabitants in an area with several buildings, inhabitants were allocated to residential buildings relative to a building’s volume calculated as its 2D footprint multiplied by its height. Building height was determined using LIDAR data (see below). We then summed the number of residents in all buildings partially or wholly within the 100 and 500 m radii of each garden.

We extracted data on median building height within the two radii, because this is a variable with major differences between urban types and may affect pollinator movement (Johansson et al., 2018). We used LIDAR data provided by Malmö municipality and R package lidR (Roussel & Auty, 2018) to extract the LIDAR final return in a 2.5-meter

Table 1

Visual representation of garden types and typical form of neighbourhoods (100 × 100 m). Characteristics of neighbourhoods within 100 m and 500 m of the four urban garden types, and area and flower resources for all five types (mean ± std), showing model results of differences between groups (GLMs and Glimmix), see methods for details. Building height is based on the median height per site to avoid strong effects of single exceptionally tall buildings. The models of human population per built area and flower density were run with logged values, to meet asumption on normality and homogeneous variances between garden types, and building height and flower denisty were evaluated using Welch's Anova (Option Means/WELCH) to allow for heterogeneous variances.

Variable	Radius (m)	 Rural house	 Detached houses	 Semi-detached	 Open yards	 Courtyards	
Proportion vegetation cover	100	*NA*	0.50 ± 0.12	0.36 ± 0.10	0.37 ± 0.074	0.15 ± 0.050	$F_{3,35} = 23.54$; P < **0.0001**
	500	*NA*	0.46 ± 0.098	0.39 ± 0.12	0.40 ± 0.099	0.23 ± 0.066	$F_{3,35} = 10.09$; P < **0.0001**
Human population per built area	100	*NA*	245 ± 92	285 ± 85	1197 ± 327	1089 ± 252	$F_{3,14.6} = 119.76$; P < **0.0001**
	500	*NA*	5315 ± 2135	8699 ± 4526	11614 ± 3304	13433 ± 2567	$F_{3,13.45} = 12.66$; P = **0.0003**
Median building height (m)	100	*NA*	4.36 ± 0.80	4.84 ± 1.41	12.67 ± 6.18	15.30 ± 1.83	$F_{3,35} = 26.51$; P < **0.0001**
	500	*NA*	4.42 ± 0.78	4.65 ± 1.04	9.25 ± 5.44	12.71 ± 4.38	$F_{3,35} = 12.33$; P < **0.0001**
Garden area (m^2)	*NA*	3200 ± 2300	750 ± 630	130 ± 62	3000 ± 1800	990 ± 930	$F_{4,19.32} = 32.62$; P < **0.0001**
Transect flower abundance (units)	*NA*	1157 ± 632	1297 ± 593	553 ± 131	1651 ± 629	1875 ± 1467	$F_{4,46} = 2.23$; P = 0.08
Transect flower species richness	*NA*	9 ± 4	13 ± 5	12 ± 5	10 ± 4	11 ± 5	$F_{4,45,7} = 0.92$; P = 0.46
Transect flower density (units/m^2)	*NA*	12 ± 6	13 ± 10	7 ± 3	17 ± 5	30 ± 25	$F_{4,19.18} = 4.99$; P = **0.00063**

buffer around each building. Building height was calculated as the difference between the median of LIDAR returns in a building's polygon, provided by the Swedish mapping, cadastral and land registration authority (Lantmäteriet), and the surrounding buffer median final LIDAR returns. The size of gardens was measured by digitizing in ArcGIS based on the Cadastral map, aerial photos from free online sources, and notes drawn on maps from field visits. For multifamily houses with open yards, garden size was restricted to the yard in connection to the address of the participating volunteer. Thus, garden size refers to one yard even when the housing complex may contain several buildings and yards within the same property.

2.4. Statistical methods

Statistical analyses were done in SAS (SAS Institute, Cary, NC) and R version 3.6.1 (R Core Team, 2019). We used Regression models (SAS Proc Reg), Pearson Correlations (SAS Proc Corr), General Linear Models (SAS Proc GLM) and Generalised Linear Models (SAS Proc Glimmix, with Poisson distribution, log-link function and F-test using Kenward-Roger approximation of degrees of freedom). For all models, residuals were visually inspected for normality and Levene's test (Means statement, Option hovtest = levene) was used to check for heterogeneous variances among groups (where applicable). The output diagnostics of Glimmix models were checked for overdispersion. We used R for analyses of species turnover and nestedness (detailed below).

First, we analysed variables related to urban typology and flower resources, to characterise urban garden types and aid interpretation of its effects on pollinators. We ran ten separate GLMs, with garden type as the fixed factor and response variables: (log) human population density, building height, and proportion vegetation cover (at either local (100 m) or landscape (500 m) scale), (log) garden size, (log) flower abundance (total or native) or (log) flower density. Heterogeneous variances between garden types were found for building height at 100 m and 500 m scales, garden size and flower density, and we therefore used Welch's Anova (Means statement, Option Welch) to obtain test statistics. We assessed differences in flower species richness (total and native, respectively) between garden types with two Glimmix models, assigning garden type as the fixed factor. The model for total species richness was overdispersed, and we therefore included an observation level random effect.

Second, we analysed how pollinator species richness differed between contrasting landscapes and garden types using two Glimmix models. We used the containment method for the F-test to estimate degrees of freedom because the model did not converge when using the Kenward-Roger method. The response variable was the number of pollinator species per garden. Fixed factors were pollinator taxon (bumblebees, solitary bees, hoverflies), and either landscape type (urban or rural), or garden type (rural, detached, semi-detached, open yard or courtyard), and the interaction between pollinator taxon and either landscape type or garden type. To control for differences in flower resources between gardens, we included (log) total flower abundance as a fixed factor. To account for spatial dependence of abundances of the three pollinator taxa within a garden, we assigned garden id as a random factor. For significant interactions, we used the Slice option to test which pollinator taxa differed between landscape or garden types. There were no signs of overdispersion or heterogeneous variances between groups (pollinator types). We checked for spatial autocorrelation among urban gardens, using SAS Proc Variogram and Moran's I. There was no evidence of spatial autocorrelation (all $P > 0.46$). Because rural gardens were few ($N = 14$), we did not analyse spatial autocorrelation among those.

Third, we analysed how the design gradients (human population density and proportion vegetation cover) affected pollinator richness. We first analysed how strongly correlated these variables were, using one model (SAS Proc Corr) for each spatial scale. The result showed moderate correlations (100 m: $R_{37} = -0.54$, $P = 0.0004$; 500 m: $R_{37} = -0.58$, $P < 0.0001$). We then calculated variance inflation factors (VIF) using one regression model for each spatial scale, with pollinator species richness as dependent variable and human population density, vegetation cover and (log) flower abundance as fixed effects. Because the results showed low VIFs for all factors (< 2.51) we included them in the same models (Zuur, Leno, Walker, Saveliey, & Smith, 2009). Thus, to analyse if pollinator richness depended on the urban gradients, we used two separate Glimmix models, at 100 m and 500 m scale, respectively. Dependent variable was pollinator species richness. Fixed factors were: human population density, vegetation

Table 2

Results of Generalized linear models (SAS Proc Glimmix) on effects of landscape type, urban type and urban gradients on pollinator species richness at local (100 m) and landscape (500 m) spatial scales. All non-significant interactions were removed from models (backward selection) and models were rerun, to obtain final test statistics. Statistically significant results in bold.

Model description	Basic model	F_{df}	P	Interactions	F_{df}	P
Testing for effect of **landscape type** on pollinator richness	log flower abundance	$F_{1,92} = 2.20$	0.1417	garden type × pollinator taxon	$F_{8,92} = 5.25$	< **0.0001**
	pollinator taxon	$F_{2,92} = 27.48$	< 0.0001			
	garden type	$F_{4,45} = 3.02$	0.0273			
Testing for effect of **garden type** on pollinator richness	log flower abundance	$F_{1,98} = 0.99$	0.3229	landscape type × pollinator taxon	$F_{2,98} = 18.99$	< **0.0001**
	pollinator taxon	$F_{2,98} = 39.15$	< 0.0001			
	landscape type	$F_{1,98} = 4.12$	0.0450			
Testing for effect of **urban gradients at 100 m radius**	log flower abundance	$F_{1,28.24} = 2.36$	0.1359	human population × pollinator taxon	$F_{2,43.14} = 0.13$	0.8806
	pollinator taxon	$F_{2,43.86} = 34.13$	**< 0.0001**	vegetation cover × pollinator taxon	$F_{2,44.42} = 1.87$	0.1661
	human population	$F_{1,29.03} = 3.72$	0.0635	human population × vegetation cover	$F_{1,27.60} = 0.02$	0.8960
	vegetation cover	$F_{1,26.27} = 0.07$	0.7932			
Testing for effect of **urban gradients at 500 m radius**	log flower abundance	$F_{1,30.22} = 2.26$	0.1429	human population × pollinator taxon	$F_{2,41.72} = 0.02$	0.9756
	pollinator type	$F_{2,45.89} = 32.85$	**< 0.0001**	vegetation cover × pollinator taxon	$F_{2,42.46} = 0.15$	0.8645
	human population	$F_{1,28.82} = 7.52$	**0.0104**	human population × vegetation cover	$F_{1,30.54} = 1.07$	0.3089
	vegetation cover	$F_{1,27.84} = 0.19$	0.6636			

cover, pollinator type, (log) flower abundance, and all possible two-way interactions between human population, vegetation cover, and pollinator type. We assigned garden id as random factor. The test for heterogeneous variances between pollinator taxa was significant (at $P = 0.039$), and we therefore modelled the residuals accordingly (using Option random _residual_/group = pollinator type). We did not include the variable building height in these models, because it describes similar aspects of urbanisation as human population density per built area, and the two were strongly correlated (100 m: $R_{37} = 0.80$, $P < 0.0001$; 500 m: $R_{37} = 0.77$, $P < 0.0001$).

Fourth, we analysed heterogeneity in the contribution of urban and rural gardens to the pollinator species assemblages. We constructed species accumulation curves to compare urban and rural gardens, bees and hoverflies, using R and function specaccum() in package vegan based on presence-absence matrices, by adding sites (gardens) in random order with 999 permutations. We analysed if landscape types (urban/rural) differed in species nestedness and spatial turnover partitioned from community dissimilarity matrices using package betapart (Baselga, Orme, Villeger, Bortoli, & Leprieur, 2012). We first calculated Sörensen's dissimilarity based on presence-absence matrices, and then calculated the nestedness and turnover components of these dissimilarity matrices. Thereafter we analysed the nestedness and turnover matrices using permutational analysis of variance (function adonis() available in package vegan; (Oksanen et al., 2019)), with P-values derived based on 999 permutations. Because of different sample sizes in urban and rural areas, we assessed whether multivariate variance differed between urban and rural sites (using the function betadisper() in package vegan). As permutational analysis of variance is sensitive to heteroscedasticity, we analysed species nestedness and turnover only in cases where we found no signs of heteroscedasticity between groups ($P \geq 0.10$). In these models, we combined bumblebees and solitary bees into wild bees because bumblebees were too species poor to be run separately. We combined hoverflies and soldier flies for the same reason (few soldier fly species). We removed gardens with no recorded species from analyses, resulting in 48 gardens (35 urban, 13 rural) for bees, while all gardens were included for hoverflies. Lastly, we tested for species nestedness and turnover along the urban gradients (human population density and vegetation cover) at the 500 m landscape scale, using methods and packages mentioned above.

3. Results

In total, we collected 1132 specimen of wild bees (Apoidea) from 40 species (nine bumblebee and 31 solitary species), 2028 hoverflies (Syrphidae) from 35 species, and 48 soldier flies (Stratiomyidae) from seven species (Tables S1 and S2). The five most common solitary bee species were all from the genus *Lassioglossum* which are polylectic, soil nesting, and small bodied bees (4.5–6 mm long). The dominating bumblebee was *Bombus terrestris*. The five most common hoverflies were of different genera, but all are long distance migrants with aphidophagus diets. Of these, *Eupoedes corollae* and *Episyrphus balteatus* were highly dominating.

3.1. Characteristics of garden typologies

The garden types differed in size, such that rural gardens and yards between multifamily houses were largest while enclosed backyards and gardens of detached houses were intermediate and semi-detached gardens smallest (Table 1). Flower species richness did not differ between garden types (total richness, native abundance or richness, all $P > 0.27$), while there was a non-significant tendency for a difference in total flower abundance and a significant difference in flower density, both with lower numbers in semi-detached gardens (Table 1).

As intended by our design, urban garden types differed in vegetation cover, population density and median building height at both 100 m and 500 m radius (Table 1). Detached and semi-detached houses had a similarly high vegetation cover, low population density, and low surrounding buildings, while open yards and courtyards had similarly high population density and high surrounding buildings. However, open yards were surrounded by similar levels of vegetation as detached and semi-detached houses, while courtyards had lower surrounding vegetation cover (Table 1).

3.2. Pollinators in urban and rural landscapes

We found a significant effect of the interaction between pollinator type and landscape type (urban or rural) on species richness (Table 2). This was because both bumblebees ($F_{1,98} = 3.97$; $P = 0.049$) and hoverflies ($F_{1,98} = 28.75$; $P < 0.0001$) were more species rich in rural than in urban gardens, while solitary bees showed the opposite pattern ($F_{1,98} = 4.54$; $P = 0.036$) (Fig. 3a).

3.3. Pollinators in different garden typologies

There was a significant effect of the interaction between pollinator type and garden type on species richness (Table 2). Slices showed that

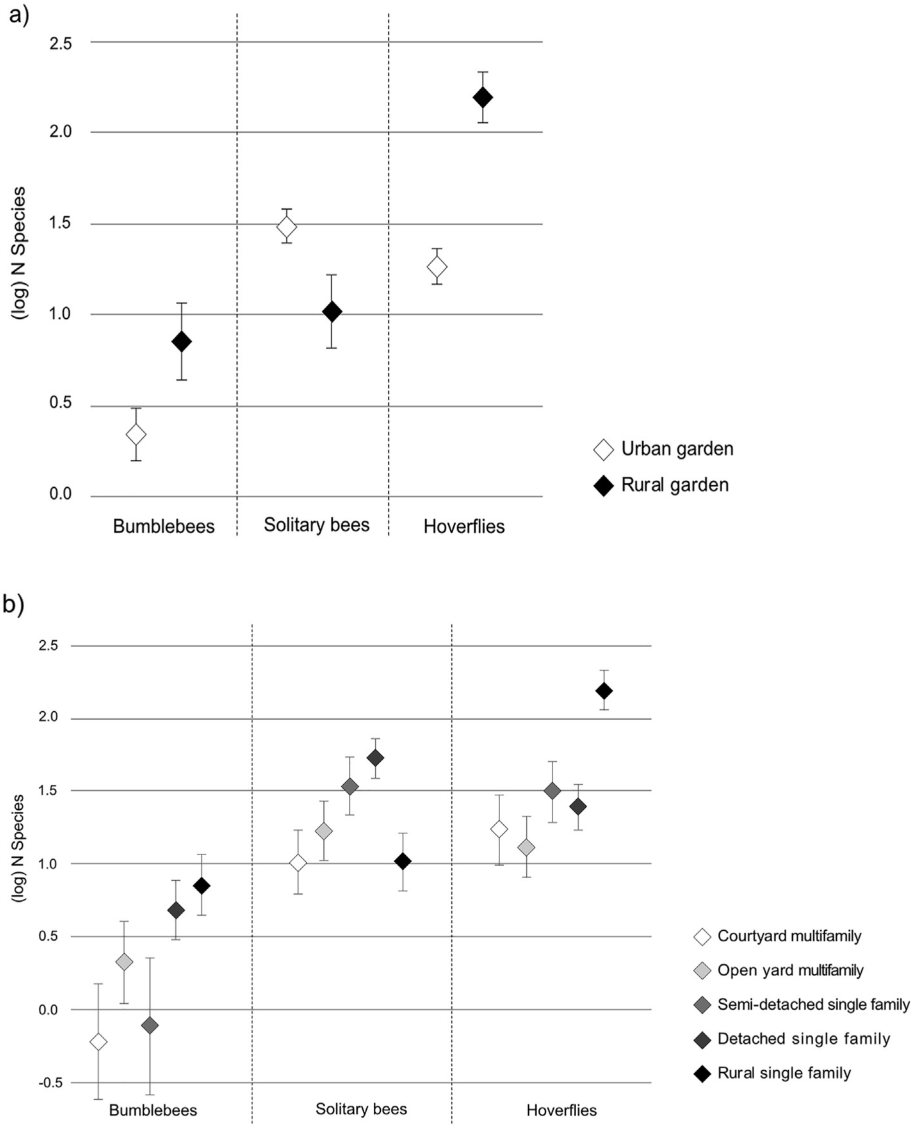


Fig. 3. Species richness per garden (model estimated mean ± SE) of bumblebees, solitary bees and hoverflies in Malmö, a) comparing rural and urban gardens, and b) comparing rural and four types of urban gardens.

richness of solitary bees ($F_{4,92} = 2.68$; $P = 0.036$) and hoverflies ($F_{4,92} = 8.09$; $P < 0.0001$) differed significantly between garden types, while bumblebees showed a marginally non-significant difference ($F_{4,92} = 2.25$; $P = 0.070$) (Fig. 3b). Hoverflies were more species rich in rural compared to all urban garden types, while solitary bees showed a more complex pattern with a higher richness in gardens of detached and semi-detached houses compared to rural gardens. Bumblebees showed a tendency for more species in gardens of rural and detached houses compared to enclosed backyards and semi-detached gardens, while open yards were intermediate in richness.

Flower abundance had no significant effect in any of the models (all $P > 0.14$). We also ran models with abundance of native species only, species richness (total and native), and flower density, but none had a significant effect or changed the model results qualitatively in any way. We therefore present only model results with flower abundance.

3.4. Pollinators across urban gradients

Species richness of pollinators was negatively related to increasing human population density at the 500 m scale, and tended to be so at the local 100 m scale (Table 2, Fig. 4). In contrast, there was no effect of vegetation cover at either spatial scale, nor of any of the two-way interactions (vegetation cover × population density, pollinator type × population density, pollinator type × vegetation cover) (all $P > 0.16$). Hence, pollinator groups did not differ in their response to human population density, and vegetation cover did not moderate the response.

3.5. Pollinator community composition

Species accumulation curves revealed a threefold number of hoverfly species in rural compared to urban gardens at a comparable number of sites ($N = 10$), whereas the total number of wild bees were equal amongst rural and urban gardens (Fig. 5). For hoverflies, species nestedness analysis showed that urban communities were a subset of rural communities ($R^2 = 0.31$; $F_{1,51} = 22.72$; $P = 0.001$), whereas urban and rural sites did not differ in species turnover ($R^2 = 0.0072$; $F_{1,51} = 0.37$; $P = 0.70$). Nineteen species of hoverflies were unique to rural sites, but only two species were unique to urban sites (Table S1). In contrast, wild bee communities showed a significant species turnover ($R^2 = 0.18$; $F_{1,46} = 10.16$; $P = 0.001$), demonstrating that different sets of species preferred rural and urban sites. Eight bee species were unique to rural sites, and 15 species unique to urban sites (Table S2). The data matrix for nestedness of wild bees showed signs of variance

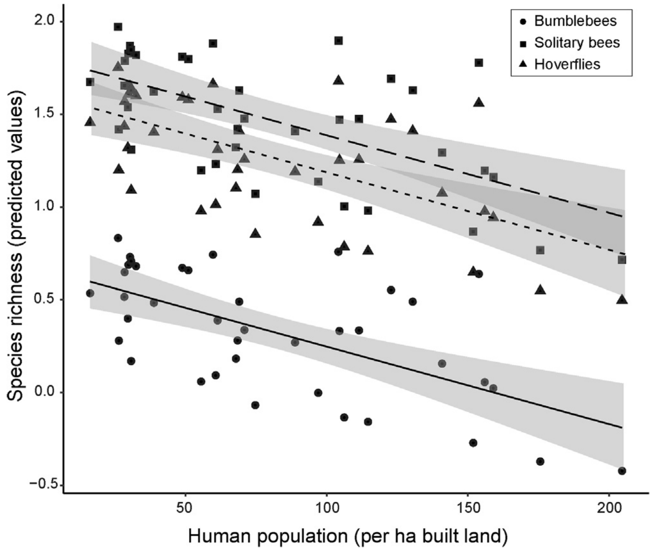


Fig. 4. Model predicted values of pollinator species richness of the three taxonomic groups, illustrating the negative effect of landscape scale human population density (within 500 m radius), with fitted linear trend lines and 95% confidence intervals (grey shade). Model estimated slope: −0.26 ± 0.093 (standard error). Solid line: bumblebees; dashed line: solitary bees; dotted line: hoverflies. For test statistics, see Table 2.

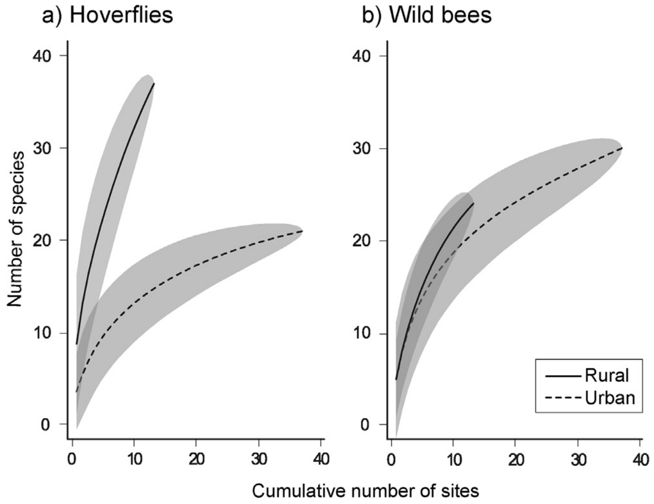


Fig. 5. Species accumulation curves with 95% confidence intervals (grey shade) for a) hoverflies and soldier flies and b) wild bees (bumblebees and solitary bees), for rural (solid line) and urban (dashed line) gardens in Malmö. The curves for hoverflies differ significantly between urban and rural gardens, while wild bees show similar patterns of species accumulation in.

heterogeneity ($F_{1,46} = 3.42$; $P = 0.07$) and was therefore not analysed further.

Wild bees showed no signs of species nestedness or turnover along the gradients, neither for solitary bees alone, nor for solitary and bumblebees combined (all $P > 0.12$). Hoverfly species nestedness was related to human population density ($R^2 = 0.10$; $F_{1,36} = 4.22$; $P = 0.042$), such that species were consistently lost as human population increased, leaving a subset of the total hoverfly community in densely populated areas. We found no effect of vegetation cover on species nestedness, nor of vegetation cover or population density on community turnover (all $P > 0.22$).

4. Discussion

Using detailed data on urban landscape characteristics and local habitat quality, we found contrasting responses to urbanisation for bee and hoverfly species richness during summer among urban and rural residential gardens, and among urban gardens of different types (urban form). In addition, and in contrast to garden type, species richness of all taxa was consistently negatively related to surrounding human population density, while the proportion of vegetation cover had no detectable effect. Furthermore, we found significant differences in pollinator species composition between urban and rural gardens. While differences in pollinator species richness between rural and urban gardens can be attributed to the highly contrasting characteristics of those environments, our results strongly suggest that differences between urban garden types are caused by a combination of human population density and built form, which in turn affect building height, garden size, tenure and management practices, at both local and landscape scales.

4.1. *The benefits of urban residential gardens differ between taxa*

As expected, urban gardens contained higher solitary bee species richness, including several unique species, compared to rural gardens. In addition, we found a significant turnover between urban and rural bee species assemblages, showing that the urban residential green spaces increased regional bee diversity by complementing the species pool of the rural surroundings. Our results thus support recent studies showing that urban areas can be rich in bee species, especially within regions of intensive agriculture (Wenzel et al., 2019), such as our study area. Although the value of residential gardens compared to other urban green spaces may vary (Fetridge et al., 2008; Threlfall et al., 2015), they have been shown to support distinct bee communities and contribute to species turnover (Martins et al., 2017), which is further supported by our results.

Urban areas can contain habitats such as brownfields and other low-maintenance green spaces that offer foraging and nesting habitats for solitary bees (Martins et al., 2017; Twerd & Banaszak-Cibicka, 2019). While nest sites for species using pre-existing cavities in dead wood may be limited in highly urbanised areas (Fortel et al., 2014), we suggest that urban areas contain novel habitats that some bees can exploit for nesting, such as crevices in buildings, bare patches of sand and well-drained soil around tracks and paving (pers. obs.). The differences in tenure and management of neighbouring green spaces (Aronson et al., 2017) may further support bee diversity by increasing spatial habitat variation and allow resource complementation. As long as flower resource requirements are met within foraging distance, typically a few 100 m for small bodied bees (Greenleaf, Williams, Winfree, & Kremen, 2007), such variation may provide opportunities for successful nesting and reproduction of a diverse community. The characteristics of urban environments may particularly benefit small-bodied species such as halictid bees, e.g. *Lassioglossum* spp. (e.g. Bates et al., 2011; Hinners et al., 2012; Threlfall et al., 2015), possibly because they require less food to successfully complete a nest. Small, polylectic (generalist) *Lassioglossum* spp. were indeed collected in a higher proportion of urban than rural gardens (Table S2). In addition, the urban heat island effect leads to an earlier start of the season compared to rural landscapes (Mimet et al., 2009), which could result in ample flower resources over an extended season, at least for polylectic species (Buchholz et al., 2020; Martins et al., 2017; Threlfall et al., 2015).

Green spaces, especially single-family home gardens, are often managed to provide ornamental flowers and flowering crops over a prolonged period. However, we found only minor difference in flower availability between garden types (lower density in semi-detached gardens), and flower densities were similar to semi-natural elements in the wider agricultural landscape sampled in a concomitant study (unpubl. data). Furthermore, flower availability did not have any significant effect on pollinator richness. This indicates that availability of nesting habitat could be more important in structuring local summer active wild bee assemblages in our study system (Fortel et al., 2014; Quistberg, Bichier, & Philpott, 2016), possibly in combination with barriers to movement (Buchholz et al., 2020; Johansson et al., 2018), such as enclosed courtyards. However, foraging bumblebees are known to aggregate into flower-rich patches (Blackmore & Goulson, 2014), and the low flower density of semi-detached housing could therefore explain the particularly low bumblebee species richness in those sites.

In contrast to solitary bees, species richness of bumblebees was lower in urban than in rural gardens, driven by a tendency for lower species richness in densely populated areas. Typical bumblebee nesting and foraging habitat, flower-rich semi-natural grassland, may occur in low-maintenance parks and brownfields, but is rare in most residential areas. Although contemporary agricultural landscapes largely lack such habitats, they do contain linear elements such as non-crop field borders where bumblebees nest and forage (Osborne et al., 2008; Persson & Smith, 2013). Bumblebees may be sensitive to elevated temperatures and dry conditions during heatwaves (Rasmont & Iserbyt, 2012), e.g. due to increased energy needs for fanning and thermoregulation of the colony (Heinrich, 1979), and suboptimal temperatures during queen hibernation (Iserbyt & Rasmont, 2012). Although speculative in our case, increased temperatures in highly urbanised parts of the town could therefore limit bumblebee nest establishment.

Hoverflies showed a consistently low species richness in all urban garden types and an increased species nestedness in urban compared to rural areas, and along the human population density gradient. Species were thus systematically lost as the landscape was urbanised and more densely populated, and the species in more densely populated neighbourhoods were only a subset of the more diverse communities in rural and low-density areas. Many larval habitats for hoverflies, most notably dead wood, dung, and ephemeral water bodies (Bartsch, 2009), are likely less common in urban gardens and green spaces. In our dataset, rural gardens were larger than urban ones, allowing for sections with shrubs, tall grass and woody debris (pers. obs.). Although hoverflies are not central-place foragers restricted by returning to a fixed nest, they require both larval habitats and flower resources at landscape scales (Moquet, Laurent, Bacchetta, & Jacquemart, 2018). In the rural areas, we expect such resource complementarity to occur more frequently than in urban areas, where dispersal between semi-natural larval habitats and gardens may be limited because of barriers in the built structure, reducing the potential for habitat complementarity. Thus, in line with Verboven et al. (2014), we found that hoverflies are more sensitive to urbanisation than bees and that peri-urban agricultural areas constitute important hoverfly habitat.

4.2. Negative effects of dense urban areas for pollinator species richness

The negative relation between human population density and pollinator species richness was consistent among taxa, while vegetation cover showed no relation, thus only partly confirming our expectations. We believe that our measure of population density (people per built area) represents a combination of urban form and associated green space management. Typical dense residential areas in the studied region have homogenous green spaces with high management intensity, often by an external contractor, more physical disturbance by humans and taller buildings, thus reducing both pollinator habitat quality and accessibility (Buchholz et al., 2020; Dylewski et al., 2019). In contrast, low-density neighbourhoods contain fewer movement barriers and a higher habitat variation because landowners manage each garden individually (Aronson et al., 2017), which potentially benefit pollinators. Our results suggest that vegetation cover, as a proxy for habitat availability, does not take such differences in habitat quality or accessibility into account, while they are captured by human population density.

4.3. Limitations of the study

Our sampling lasted throughout July, with continuous use of pan-traps over 30 days. This period likely coincides with the main pollinator activity period, but does not cover the early season and therefore will not represent spring-active species of bees or hoverflies (Banaszak et al, 2014; Bartsch, 2009). Because spring-active bee species often rely on trees and shrubs for flower resources (e.g. Donkersley, 2019), they could respond differently to urban gradients than species relying on herbaceous flowers if the abundance and distribution of trees and shrubs differ from herbaceous species across urban forms. However, we expect that some important factors of urbanisation and urban form, such as barriers to movement and intensive vegetation management (Buchholz et al., 2020; Dylewski et al., 2019), affect spring and summer active pollinators in a similar fashion. Our samples contained few bumblebee species and showed large between-site variation within garden types. This may be the results of a combination of low species richness at a regional scale and low detection probability, because pan-traps are not well suited for bumblebee sampling (e.g. Roulston, Smith, & Brewster, 2007), giving less robust data for bumblebees. Although pan-trap sampling can indeed detect a high proportion of total bee species richness (Nielsen et al., 2011), and is a cost-effective means of sampling (Westphal et al., 2008), a combination of pan-traps and netting along transect would have increased the proportion of the total species pool detected (Nielsen et al., 2011). The species accumulation curves show that we only sampled a small proportion of the rural pollinator community, especially for hoverflies, while the representativeness was better for bees and for hoverflies in urban areas (Fig. 5). Thus, intensified sampling would likely strengthen the differences between urban and rural sites for hoverflies. Because our aim was not to describe the complete species pool of Malmö, but to compare how well some pre-defined residential categories cater for pollinators, we believe that the high representativeness of pan-traps suffices to draw conclusions on the relative effects of urbanisation and urban form on wild pollinator assemblages.

4.4. Conclusions and potential for pollinator conservation in residential green spaces

By combining analyses covering a variety of typical urban residential forms and two separate aspects (gradients) of urbanisation, our study improves the understanding of how urban areas affect insect pollinator communities. Our results indicate that urban areas may not be refuges for declining pollinators in an agricultural region, but that the variation in habitat provided by areas of different urban form supports a different set of bee species and thereby contribute to the regional species pool. We also add knowledge on how hoverflies respond to urbanisation; an important group of pollinators that is less well studied in the urban context (Wenzel et al., 2019). Importantly, we show that densely populated urban areas need careful design to remove barriers and improve habitat, if they are to support a rich pollinator fauna.

The lack of an effect of surrounding vegetation cover on pollinator richness indicates a possibility to benefit pollinators by improving habitat quality without increasing vegetation cover. Green spaces of multifamily houses with open yards would be especially suitable for improvements (Fischer, Eichfeld, Kowarik, & Buchholz, 2016), because they are often large with quite extensive green space, but designed and managed in ways that reduce habitat quality for pollinators. Our results suggest that it is critical to include not only flower resources, but also bee nesting and hoverfly larval habitats in recommendation for habitat design and management. A promising but so far underutilized option is to turn amenity grass into “urban meadows” with reduced moving regimes (Garbuzov, Fensome, & Ratnieks, 2015; Norton et al., 2019). Acceptance of such vegetation among the public has likely been underestimated (Fischer et al., 2018), and the main resistance may lie among planners and managers (Hoyle, Jorgensen, Warren, Dunnett, & Evans, 2017).

Residential green spaces cover a large part of urban areas but are often overlooked as a resource for biodiversity, partly because city councils have very limited control over design and management (Goddard et al., 2010). Our results show that, while hoverflies cannot utilise most urban gardens, residential gardens should be considered in conservation planning for solitary bees. There is ample scope for improvements of urban pollinator habitat within existing green spaces, especially in densely populated areas.

CRediT authorship contribution statement

Anna S. Persson: Conceptualization, Formal analysis, Investigation, Writing - original draft, Visualization, Project administration, Funding acquisition. **Johan Ekroos:** Formal analysis, Writing - original draft. **Peter Olsson:** Software, Investigation, Resources. **Henrik G. Smith:** Conceptualization, Formal analysis, Writing - original draft.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2020.103901.

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