The Effect of Urbanisation on Pollinator Abundance and Reproductive Success

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Abstract

Pollinators are the basis of ecosystem services across all land-use types. Current global trends reveal that pollinators and their services are declining due to a variety of anthropogenic threats, including habitat fragmentation, pesticide use, climate change, and parasites and pathogens from commercially reared bees. Wild pollinator declines will increase global food security risks, especially the supply of vital dietary vitamins and micronutrients. Urban areas have been found to provide more improved habitat quality than some rural landscapes and provide refuge from the combination of lethal threats that occur within modern agricultural landscapes. We experimentally tested accessible food resource provision for solitary bees found within landscapes across an urban gradient, by introducing standardised tube nests seeded with Osmia bicornis pupae and measuring the reproductive output of the adults that emerged from those pupae. In addition, pollinator group richness and abundance were surveyed at every nest site. The urban gradient encompassed highly urbanised landscapes, suburban landscapes with increasing green cover, grasslands, and woodlands, Osmia bicornis reproduction was lowest in highly urban sites and highest in natural landscapes. In suburban landscapes reproductive output was lower than natural landscapes but still at sufficient levels to support stable populations. Greenspace within suburban landscapes had a negative impact on reproductive output suggesting habitat quality was higher within residential gardens than suburban parks. Hoverflies and solitary bee populations were associated negatively with urbanisation but bumblebees, Lepidoptera and honey bees were unaffected. This is proposed to be due to differences in mobility and provision of nesting and larval habitats within urban areas.

Introduction

Pollination is the transfer of pollen between male and female flower structures resulting in fertilisation and consequent reproduction. This can occur through the vectors of wind, water and animals (Potts et al. 2016). Animal pollinators are responsible for pollinating an estimated 87.5% of flowering plants globally (Ollerton et al. 2011). A range of animal taxa including birds, bats, and reptiles are known to pollinate plant but pollination services are mainly provided by insects from the families Hymenoptera (bees, wasps, and ants), Diptera (hoverflies and blowflies), and Lepidoptera (moths and butterflies; Hansen et al. 2006; Rader et al. 2020). Within agricultural systems pollination services are vital; 85% of 107 leading global crop types are reliant on animal pollinations (Klein et al. 2007). Food crops visited by pollinators have a GDP of \$780 billion (Rader et al. 2020). Although pollinated food crops only make up 35% of global food production, due to staple food crops (wheat, rice ect.) being wind pollinated (Lautenbach et al. 2012), animal pollinated crops provide critical vitamins and micronutrients (Smith et al. 2015). It is therefore imperative to understand pollinator responses to anthropogenic change.

Pollinator declines

Pollinator populations are declining globally due to threats from land-use change, pollution, and climate change, as well as the interaction between all of these stressors (Goulson et al. 2015; Potts et al. 2016). Although detailed global population trends are lacking due to insufficient data only 43.3% of European pollinators have been assessed and given a IUCN threat status (Nieto et al. 2014). Research suggests that the diversity of pollinators is declining in parallel to reduced pollination services, especially for wild bees and wild flowering plants. Biesmeijer et al. (2006) found that the degradation of plant-pollinator interaction across the UK and Netherlands resulted in declines of flowering plants and the bee species they rely up on for pollination. The same study found pollinator communities have become dominated by fewer species post 1980s and cite a reduction in functional diversity as a possible driving factor. Pollinators face threats across many landscape types. Some threats are ubiquitous such as land-use change causing landscape homogenisation and fragmentation, which reduce floral and nesting resource provisioning. Others are more specific, such as pesticide use in agricultural landscapes. Land-use change can lead to declines in pollinators particularly across agricultural and urban landscapes. Suitable habitat patches become more isolated and the matrix between patches can become increasingly difficult to disperse through (Rathcke and Jules 1993). Climate change and warming temperatures are causing rapid range shifts to higher altitudes and latitudes (Chen et al. 2011), but pollinators may not be able to track range shifts at the same rate as the environment changes, causing range contractions through the loss of suitable conditions at the range limits of a species closes to the equator and failure to colonise areas fast enough at the polar range limits (Kerr et al. 2015). Parasites and pathogens can cause major harm to pollinators. A variety of honey bee parasites can cause larval mortality, reducing the workforce of a colony and even resulting in colony mortality (Evison et al. 2015). The global trade and transportation of honey bee colonies can proliferate the spread of these diseases and spill over into wild pollinator populations, directly damaging pollinator services (Graystock et al. 2013; Ravoet et al. 2014; Goulson et al. 2015). European red list assessments indicate that, of the species with sufficient data to assess, up to 50% of bee species have been classified as nationally threatened (Potts et al. 2016, Nieto et al. 2014).

Modern agricultural landscapes bring further threats to pollinators (where their services are of such high value). Exposure of bees to pesticides like neonicotinoids can affect their nervous system and reduce the ability of bees to learn, forage and navigate (Goulson et al. 2015, Rundlof et al. 2015). Combined pesticide and fungicide exposure increases the toxicity of pesticides towards bees (Goulson et al. 2015). Herbicides can indirectly threaten pollinators by removing weeds from agricultural land, consequently reducing the diversity of floral resource for pollinators (Potts et al. 2016). Exposure to a cocktail of pesticides and fungicides, reductions in floral resource and pathogen spill over from domestic honey bees, all combine into a multifaceted assault on wild pollinators.

Many pollinators face similar threats of habitat degradation and fragmentation in urban landscapes to those in agricultural landscapes, but may be relieved of some pressures, such as exposure to agro-chemicals and the homogenous floral resource. The following sections will introduce evidence for the potential use of urban areas as a refuge for pollinators, assess which pollinators are "winners" and "losers" in urban areas, and indicate the importance of the services pollinators provide in urban areas.

Urban trends and potential refuge

Urbanisation is defined by increasingly impervious surface cover, such as concrete and builtup areas, often accompanied with decreasing levels of vegetation (UKCEH 2019). At a landscape scale, urbanisation reduces the size and connectivity of natural habitats through fragmentation, and common biotic trends show increased levels of exotic and invasive species (Fenoglio et al. 2021).

In terms of biodiversity, urbanisation is often associated with decreased species richness because it acts as a filter for species depending on their functional traits. General trends for bird species are that sedentary species, omnivores, and habitat generalist species are more successful in urban environments than insectivores, habitat specialists and ground nesting species (Gaston 2010). Floral richness can often increase with urbanisation due to the increasing numbers of introduced exotic plant species (Gaston 2010). Species of arthropod are generally declining in urban environments (Lagucki et al. 2017) due to fragmentation, heatisland effects, pollution, increases in exotic plant species and increased proportions of impervious surface cover (Fenoglio et al. 2021). Reasons for these effects include fragmentation, reducing the accessibility of resources (Merckx et al. 2018), impervious surfaces, reducing nest availability for many ground-nesting species (Banaszak-Cibicka and Żmihorski 2012), and high abundance of exotic species, which can reduce food resource quality for herbivores (Fenoglio et al. 2021). Insect pollinators are vital for pollinating vegetation that support biodiversity in higher trophic. Although the size of these effects remain unknown changes in pollinator functions will likely affect biodiversity and the functioning of the whole urban ecosystem.

Pollinator groups can also have highly mixed responses to urbanisation, with contrasting evidence for overall responses (Cardoso and Gonçlaves 2018; Banaszak-Cibicka and Żmihorski 2020; Wenzel et al. 2020). As alluded to previously, many pollinator groups are threatened by the pressures of urbanisation but in some cases, species of the order Hymenoptera (bees, wasps, ants) appear to be more tolerant (Deguines et al. 2019).

Lepidoptera, for example, rely on specific host plants during their larval stage, and so can be sensitive to the increasing proportions of exotic plant species in urban habitats. Hover flies (Syrphidae) also require separate larval and adult food resources, and larval requirements can vary widely including, deadwood, organic matter in aquatic environments, and predation on aphids (Rader et al. 2020). Bees on the other hand provision their offspring via mass provisioning like in many solitary bees or gradual provisioning like social insects, therefore relying only on floral resources for their whole lifecycle. Additionally, provisioning in nests means that offspring can develop into adults in separate locations to food resources (Van Eeckhoven 2020). These different evolutionary strategies, where bees effectively substituting separate larval and adult food requirement for a single food resource and a nesting requirement, may increase resilience of bees in urban environments compared to other pollinators, which require the simultaneous occurrence of two food resources (larval and adult) in one landscape.

Bees have widely been thought to provide the majority of pollination services (Winfree et al. 2008, Klein et al. 2007). Although recently Rader et al. (2020) reviewed 105 crop species and demonstrated that yes, 93% were visited by bees, 77% were also visited by Diptera, and mainly hover flies (Syrphidae). That being so, much of the literature is focused on domestic and wild bee responses to urbanisation, with few studies researching other pollinators (Theodorou et al. 2020). Growing evidence suggests that for pollinators, especially bees, there is potential for urban areas to support successful populations and contribute towards their conservation. Trends in wild bee abundance and species richness show potential for urban areas to be a respite from the pressures found in rural agricultural landscapes (Baldock et al. 2015). A study in Poznan (Poland) found no difference in abundance or richness between urban areas and rural areas; urban bee communities displayed higher levels of nestedness than rural communities (i.e., urban communities were mainly a subset of the more complex rural communities). In the city, 71% of the region's bee species have been observed, demonstrating the potential of urban areas to support pollinators (Banaszak-Cibicka and Żmihorski 2020). Experiments comparing bumblebee colony growth between urban and agricultural environments also show higher colony growth, reproductive success, and survival in the urban environments (Goulson et al. 2002; Samuelson et al. 2018). However, this would suggest that when compared to agricultural landscapes, urban areas could offer higher habitat quality for

important pollinator species. The quality of habitat within urban areas for all pollinators remains a knowledge gap that requires further attention.

Urban "winners" and "losers"

A review of 59 studies concluded that species richness of wild bees declined with increasing urbanisation - seemingly opposing results to the ones previously stated (Hernandez et al. 2009). The explanation for this contradiction is that functional traits determine how species respond to urbanisation and which species are effectively urban 'winners' and 'losers' (Hernandez et al. 2009). Bumblebees have shown increased species richness in urban areas, with one study comparing urban areas to disturbed and continuous forest showing such trend (Winfree et al. 2007 in Hernandez et al. 2009). In contrast, bees in the families Colletidae and Andrenidae (solitary bees) were scarcely found in urban areas and exhibit lower species richness compared to rural areas (Hernandez et al. 2009). A pairwise comparison of high-quality urban environments to high quality rural sites observed bumblebee species and honeybees making up for declines in overall insect richness and abundance in urban areas, and specifically declines in Lepidoptera (Theodorou et al. 2020).

In summary, evidence suggests that responses by wild bees to increasing levels of urbanisation follows a pattern as a result of filtering pollinator communities by functional traits. Urban winners tend to be cavity-nesting species, generalists and social species. Conversely, solitary, ground-nesting and specialised species are found to be negatively associated with urbanisation (Hernandez et al. 2009; Banaszak-Cibicka and Żmihorski 2012; Cardoso and Gonçlaves 2018; Wenzel et al. 2020).

Urban pollinator services

Within urban areas, pollinators are deeply important to ecosystem health. Pollination services maintain wild fruit trees - necessary to support migrant and resident bird populations, perpetuate vegetation in urban greenspaces and brownfield sites, and ultimately support ecological integrity of urban ecosystems (Kearns 1998). They also pollinate urban food crops reducing food security risks. Urban food security is becoming an increasingly important issue,

with estimates from 2000 including 15-20% of global food production taking place within urban area and an estimated 800 million people sourcing food from urban agriculture (Armar-Klemesu 2000).

Biodiverse greenspace within urban areas promotes physical activity, psychological well-being, and public health for city dwellers (Wolch et al. 2014). Urban trees have been found to provide health benefits to residents but also social, economic, visual and aesthetic benefits (Roy et al. 2012). Plant-richness and the number of greenspaces are also positively associated with psychological well-being measures (Fuller et al. 2007). Pollinators are a fundamental part of perpetuating urban vegetation and helping to maintain the quality of greenspaces (Cane 2005). In return, greenspaces can support healthy populations of some wild pollinators, which could potentially spill-over into agricultural systems and provide pollination services there (Langelloto et al. 2018). Understanding how urban environments affect pollinator populations and their services is therefore crucial.

Characteristics of urban greenspace

Despite recent research into the trends of pollinators as a result of urbanisation, less attention has been focused on the characteristics greenspace within urban landscapes must have in order to benefit pollinators. Banaszak-Cibicka et al. (2016) provided evidence that the proximity of urban pollinator communities to large greenspace, connected by suburban areas, increases bee species richness. Another investigation into the quality of different types of urban greenspace, parks, golf courses and urban gardens, showed that all greenspace types have conservation value for wild bees. Presence of native plant species and less intensive management practices in these greenspaces also reduced the negative effects of urbanisation on floral specialists and ground-nesting species (Threlfall et al. 2015). The pairwise comparison of high-quality habitats by Theodorou et al. (2020) revealed that greater provisions of services, in the urban areas, occurred as a result of landscape-scale effects. Increased edge density and decreased proportion of arable land were associated with increased bee and wasp richness.

It is also important to consider that pollinators have the ability to forage over large areas and potentially forage from multiple habitat patches within urban landscapes. A study into honeybees in Brighton (UK) provided evidence that the bees could obtain sufficient forage within urban boundaries (Garbuzov et al. 2015), but little research has tested whether this is also the case for wild pollinators. Solitary bees can forage at distances from 100-1200 m, with a foraging range correlated with their body size (Gathmann and Tscharntke 2002). In agricultural landscapes solitary bees were found to travel out of agricultural landscapes to semi-natural habitats to forage, so proximity of natural habitat was associated with reproductive output (William and Kremmen 2007). Bumblebees have been found to regularly forage up to distances of 1750 m (Walther-Hellwig and Frankl 2000) and can certainly disperse through urban matrix to forage successfully at multiple habitat patches (Goulson et al. 2002). But the question of whether smaller ranging species can also forage successfully in urban landscapes remains unanswered.

Rural to urban gradients

Wenzel et al. (2020) suggest in their review that the key to understanding pollinator responses to urbanisation in past research lies within the underlying study systems. They theorise that that there are four key landscapes used in urban pollinator research that are often overlooked and incorporated into simple rural to urban gradients. They advocate that natural or semi-natural landscapes support the highest biodiversity, followed by urban sprawl (20-50% impervious surface), modern agriculture, and urban densification (>50% impervious surface) supporting the lowest diversity. Lack of distinction between these four landscape types can lead to very different trends in pollinator biodiversity across a "rural" to "urban" gradient.

This study addresses this issue by using a rural control that is natural or semi-natural, avoiding agricultural land and using percentage cover of suburban and urban landscapes from UKCEH land cover maps to describe sites that bridge the urbanisation gradient between urban sprawl landscapes and urban densification.

Osmia as a proxy for landscape habitat quality

Reproductive success of *Osmia bicornis* was chosen as a proxy for quality floral resource provisions in the surrounding landscape for wild pollinators, and for testing this response (reproductive success) across an urban gradient. *O. bicornis* are generalist (polylectic)

pollinators, visiting cultivated garden plants and are commonly found in residential gardens and urban greenspaces (Falk 2019). Its maximum foraging range is 600 m (Gathmann and Tscharntke 2002; Van Eeckhoven 2020) and it has a flight season of March to July, with males emerging 2-3 weeks before females (Falk 2015). *O. bicornis* is often found using a wide range of nesting sites, and as a cavity-nesting species, it divides the cavity (in our case cardboard nesting tubes) into brood cells and plugs the cavity with mud (Fig 1.; Benton 2017; Van Eeckhoven 2020). In each brood cell, females lay an egg and provision it with a food mass (pollen loaf). Approximately one egg is oviposited and provisioned each day in this way, with the body size of the resulting adult increasing with greater provisions. Females are an average of 46% heavier than males, and female body weight is positively associated with foraging ability (Van Eeckhoven 2020). Males are laid last in the nest due to the smaller amount of provision required and the reduced foraging efficiency of ageing females (Van Eeckhoven 2020). This also allows shorter foraging trips when provisioning for later laid eggs and therefore less time when the nest is left unguarded.

O. bicornis has foraging and reproductive traits that are conducive for its use as a proxy for measuring habitat guality because of its behaviour of provisioning and laying eggs individually and in the same nest, and hence the number of offspring is expected to be directly related to habitat quality. In habitats with poor floral resources a longer time will be taken to provide a sufficient pollen loaf, consequently resulting in fewer offspring (Williams and Kremmen 2007). Or females may lay eggs at the same rate but with reduced pollen provisions in poorer habitat conditions, in which case resulting pupae will be smaller due to the relationship between pupal weight and maternal food provisioning. It is expected that females foraging in poor habitat quality will result in reductions in offspring number and weight (Bosch and Vicens 2002; Evans et al 2018). This study aims to contribute towards the critical topic of whether urban landscapes can provide sufficient and accessible floral resource to solitary bees. To do this the study will assess the impacts of an urban gradient on the reproduction of a single exemplar solitary bee. Alongside this, the study aims to improve understanding of the response of different pollinator groups to urbanisation through pollinator surveys and assessment of surrounding landscape characteristics. Importantly, the urban gradient of the study system will span from urban landscapes to natural landscapes, to assess pollinator response to urbanisation irrespective of pollinator response to agricultural landscape. It is predicted that reproductive success and pollinator abundance and richness will be highest in natural

landscapes, lower in suburban areas but positively respond to the amount of greenspace within the landscape, and lower again in highly urban landscapes.



Figure 1. The life cycle of Osmia bicornis. (from Van Eeckhoven 2020, Fig 3.1)

Method overview

The study system was located around the city of Nottingham and surrounding towns of Bullwell, Hucknall, Kimberly and Netherfield situated in the East Midlands region of the UK. Data sampling took place between March 16th 2021 and August 11th 2021. Sites were positioned within the system across urban gradients. To test the habitat quality of the surrounding landscape, the present study used the introduction of solitary bee pupae (*Osmia bicornis*) in standardised nests at the centre of sites, and quantified reproductive output of the subsequently emerging adults at each site. The scale at which landscape characteristics were used to define the level of urbanisation was a 600m radius around the nest sites; the maximum foraging range of *O. bicornis* (Van Eeckhoven 2020; Gathmann and Tscharntke 2002). Pollinator surveys were also conducted at the sites to quantify the presence of other pollinators across the study system.

Site selection/urban gradient

The study used a sixlevel gradient of urbanisation that was established based on percentage cover of urban and green land cover maps (Table 1.). Potential sites that met the criteria of the urban levels were organised in regional clusters to avoid landscape scale confounding effects. Sites within clusters were randomly selected so that each cluster contained one site of all six levels of urbanisation. The study system was made up from five clusters creating a total of 30 sites (Fig 2.). Each site was initially positioned >1.2km from any other site, but this was compromised in some cases due to accessibility issues. The ownership of land used as sites in this study included public parks, household gardens, private woodland, golf courses, industrial estates, and town centre car parks.

The urban level was determined using Geographical Information System (Quantum GIS 3.18.1). Land cover maps by UKCEH 2019 with definitions of urban, suburban, improved grassland and woodland were used to describe the level of landscape urbanisation around sites (definitions of classifications in supplementary material). The six levels of urban landscapes were defined as follows: level 1 = majority urban, level 2 = majority suburban, level 3 = suburban/grassland mix, level 4 = suburban/tree cover mix, level 5 = majority grassland, level 6 = majority greenspace with tree cover. Sites were visited and ground checked by myself to visually confirm that landcovers types specified from land cover maps were present within the 600m radius of each site. The gradient of urban to green sites ground checked by myself to visually confirm that landcovers types specified from land cover maps were present within the 600m radius of each site. The gradient of urban to green sites purposefully avoided agricultural land in order to measure the effects of increasing grassland and tree cover and decreasing impervious surface

Table 1. Description of the percentage area thresholds of land cover types within the 600m radii surrounding the site centres which were used to define the urban levels in the study. The source of land cover maps for each variable are indicated by, * for land cover metrics from EDINA's Land Cover Map 2019, ** for land cover metrics from Ordinant Survey national maps, and † for land cover metrics from Bluesky's National Tree Map. (Table on following page)

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Urban	Description	% Urban	% Building	% Suburban	% Improved	% Woodland	GIS thumbnails of
Level		land	cover **	land cover*	grassland land	land cover** or	example sites showing
		cover*			cover*	Tree cover†	configuration of land
							cover and buildings
1	Urban	<u>∖50</u>	>20	(in	~5	~5	
	orban	200	20	combination			
				with urban			
				land cover)			ALLAR.
2	Suburban	<10	>15	>90	<5	<5	California -
							12N GENERAL ST
							A REAL PROPERTY OF A REAL PROPER
3	Suburban	<10	10-15	>50	>15	<10	
	+						In Participa
	grassland						
							A at a
4	Suburban	<10	10-15	>50	<10	>15	
	+ tree						ASSESSION AND
	cover						
5	Grassland	<10	<10	<20	>50	<15	
	Graddiana				200		
6	Woodland	<5	<5	<20	>80 (in	>40	
					combination		
					with woodland		
					land cover or		
					Tree cover		

cover and tree cover and decreasing impervious surface cover as the transition from urban to rural sites (agricultural land cover within site radius comprised a mean of 3% across all sites).



Figure 2. Map of site position and land covers. Urban level of the site is represented by the colour of the 600m radius surrounding the site centres (red dots). Dark grey = level 1 (most urban), Light grey = level 2, gradient of Light green – Dark green = levels 3 - 6. Land cover from EDINA lcm 2019 is indicated in the key, purple shapes indicate town and city centres, purple lines represent roads within sites radius. Transparent red shape layers encompass the 5 clustered groups of the experimental design.

Pollinator and plant surveys

Flying insect surveys were used to assess the local pollinator populations. We also measured flowering plant diversity, pollinator abundance and species richness, and recorded weather variables. Surveys took place in two sampling periods in 2021, 24th May to 9th June, and

between 5th of July and 23rd July, and were conducted between 9:00 and 16:00 (BST). Timing of the data collection took place at the most suitable conditions for foraging behaviour and lie within the following thresholds: >10°C, dry conditions without rain, Met office wind speed < 15 mph, on days with cloud conditions of sunny spells or sunshine. Measurements of condition at the time surveys were taken from the closest Met Office (Met Office 24/5/21 – 23/7/21).

Protocol for the flying pollinator surveys was a 15 minute survey in a 5m radius surrounding the site centre. Observers took a position within the 5m radius of the site centre and counted individual bumblebees, hover flies, Lepidoptera, solitary bees and honey bees. Observers moved if necessary to identify insects to genus or species level when possible. Surveys were undertaken by two observers (78%) or on by one observer (22%). When two observers were present, they positioned themselves at opposite sides of the 5m radius with one recorder and communicated sightings; abundance of species was measured as the total abundance that could be observer was present, they recorded and observed the whole 5m radius themselves. Rates of pollinator sightings were not at rates where one observer was at a noticeable disadvantage in their ability to record all pollinators within the survey time. Despite this, the discrepancy in sampling effort was included in the data analysis.

Local floral resource at sites was measured to include in statistical models and determine its importance in predicting pollinator response. Flowering plant and tree surveys were conducted on the same site visits as pollinator surveys to measure the abundance and richness of flowering plants and trees. All plants in flower at the time of the survey within a 5m radius of the site centre were counted and identified to species level or, at minimum, genus level when high diversity and hybridisation of a genus (e.g. *Taraxacum*) makes species identification in the field difficult (Ebeling et al. 2008). If separating patches of plants into discrete individuals proved impossible, an approximation of the total number was recorded by observing where plant stems entered the soil, and the use of approximation was recorded. Counting the number of flowering plants instead of using a count of individual flowers or "floral units" better suited the available sampling effort of the study, despite being a lesser measure of capturing the quantity of floral resources available to pollinators, due to the variation in floral resources provided by different species. Adult trees (>18cm diameter at breast height; dbh) and hedgerows where dbh could not be taken but were of a substantial size to provide similar resource as adult trees within 5m were counted and identified to species level (Christina et al.

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2018), resulting in 4 local floral resource measures of frequency data: abundance and richness of flowering plants and trees.

Osmia bicornis reproductive success: a proxy for floral resource

To measure the reproductive success of solitary bees across the sites within the urban gradient, tube nests seeded with *O. bicornis* pupae were placed in the field across the summer (Fig. 3). Positioned at the centre of sites, facing in a southeast direction and minimum of 1 m above the ground, nests were seeded with 5 female and 5 male *O. bicornis* pupae. The nests were mounted on woody vegetation if present, this was only compromised to ensure the nests were mounted securely and at the correct height and direction. Each nest contained 32 paper tubes of 140 mm length and 8 mm diameter. White UV paint was used on the leading edge of nests, added to improve identification and positional memory of emerging adult bees. Two nests were set up at each site between 16th and 24th of March 2021, and collected between 9th and 11th August 2021.



Figure 3. Standardised tube nests used by solitary bees to breed. Nests contained cardboard nesting tubes of 0.8mm diameter. Seeded *O. bicornis* breed using the cardboard tubes. Adult females forage in the surrounding landscape and return to the nest to make brood cells, often sealed with soil, where offspring will develop

Due to the March to July flight season of *O. bicornis*, foraging of females had ceased at the time that the nests were collected from field sites. In the lab the solitary bee nests were dismantled and cardboard nesting tubes opened to reveal the brood cells: the number of pollen balls, larva and pupa were counted, and pupa were weighed using a Mettler Toledo AX26 DeltaRange microbalance. An estimate of the sex, by size and weight, of pupae was also recorded. During the study 2 nests from 2 different sites were vandalised and removed. 4.8% of the seeded pupae were found to have failed to emerge in the foraging season when the nests were collected; this was accounted for within the analysis.

Landscape characteristics and justification of urban Levels

Urban level was chosen as the index for urbanisation following a Principal Component Analysis (PCA) used to analyse the relationship between the land-cover measurements, which revealed that 'urban level' was just as good at describing the variation in land-cover metrics and simpler to implement. Land-cover measurements of total area of tree cover from Bluesky's National Tree Map (NTM) data set, Improved grassland area from EDINA's land cover map (LCM), Buildings area from Ordinance survey (OS), Woodland area from OS, Suburban area from LCM, Urban area from LCM within the 600m of the site centre were used and I chose to analyse a covariant matrix, as all variables had the same scale. In the results, PCA1 describes a directional trend of suburban landcover to green landcover, correlating strongly with suburban area (r = 0.54), describing 53% of the total variation in the land composition data. The variation of PCA1 is significantly explained by Urban Level (F = 52.2, df = 5.24, P < 0.001).

PCA2 describes the trend in urban and building area across sites (r = 0.97, and r = 0.85, respectively) and independently describes a further 35% of the variation in the data. The variance of PCA2 is also significantly explained by urban Level (F = 23.5, df = 5,24, P=<0.001).

PCA3 represents the gradient of open grassland to woodland tree cover, correlating with Tree cover (r = 0.66), improved grassland area (r = -0.59) and woodland (r = 0.53). PCA3 describes 10% of the variation in the land composition data, and is also significantly explained by Level (F = 9.6, df = 5,24, P < 0.001). Together components 1, 2 and 3 describe 97.5% of the variation of land cover at sites, and effectively distinguish all 6 urban levels as a gradient of decreasing

urban and suburban area and increasing green area, distinguishing grassland area from woodland and tree cover. In light of these results, the categories of urban level can therefore be used as a valid single parameter that describes the intended gradient of urbanisation.

Analyses

All analyses were performed using R Studio v1.1.447 (RStudio Team 2021) and all averages reported as mean ± standard error. Mixed effects models were used to deal with complex structuring within the datasets (Evans et al. 2018). The importance of fixed effects within the models were assessed using a stepwise model comparison, sequentially dropping each predictor from the full model to assess their significance for the model fit. The following sections describe the analysis of the three main datasets: pollinator surveys, *O. bicornis* reproductive output and landscape configuration.

Surveys

Generalised linear mixed effects models (GLMM's) with quasi-poisson error structures, implemented using *glmer.nb* function from lme4 package (Bates et al., 2007), were used to analyse how pollinator abundance and richness was influenced by level of urbanisation. These models also assessed whether there was an interaction between urbanisation level and pollinator group, as well as the importance of local floral resource on pollinator abundance and richness. The four local floral resource measures of frequency data were included as fixed effects. Weather variables: cloud cover (5 categories from overcast to clear skies), temperature (°C) and wind (mph) along with number of observers were also included in models as fixed effects. Cluster ID and Site ID were included as nested random effects. All three weather variables, temperature, cloud cover and wind speed proved to significantly affect both pollinator abundance and richness (Details in Appendix Table 1 and Table 2). Number of observers was only significant for predicting honey bee abundance (Appendix Table 1). Pollinator groups were further analysed on an individual basis. Models were focused on investigating abundance and richness of bumblebees, solitary bees, Lepidoptera and hoverflies and the abundance of honey bees. The effects of weather variables on abundance and

richness of individual pollinator groups were varied (full details of the model statistics can be found in Appendix Tables 3 – 11).

Osmia bicornis nests

The effect of urban levels on pupal mass was analysed using linear fixed effects models implemented using the *lmer* function, and the total count of pupae per nest analysed using glmer.nb function with quasi-poisson error structure, both functions from the lme4 package (Bates et al. 2015). The variables Cluster ID, Site ID and Nest ID were included as nested random effects when testing total counts, as well as cardboard tube ID when analysing pupal mass, due to the likely relatedness of pupa within a single tube as females will return to the same cardboard tube to continue laying. To test if urbanisation caused bias in the sex ratio of the pupae, I analysed the ratio of males as a multibinomial response variable using a generalised linear mixed effects model implemented using the *glmer* function with binomial error structure.

Landscape measures

Further analysis of the composition of the landscape tested how additional landscape scale variables that were not used to define the urban level of sites are affected by the urbanisation gradient in the study system. This was implemented using *glm* function from *stats* package. Three continuous variables were considered; edge density, mean patch size and road density. Edge density and mean patch size were both calculated using *geometric attributes* function in QGIS after *clipping* BlueSky National Tree map dataset to the overlay layers of the 600m radii around site centres. NTM is a data set which documents the canopy size and shape of all trees > 3m tall in polygon shapefile. The *dissolved* function was used on the shape file so that individual trees with touching edges were joined into one continuous patch. Edge density was the sum length of perimeter (m) of these patches and mean patch size was the mean area (m²) within each site radius. Road density was also calculated using *geometric attributes* function in QGIS after *clipping* the OS roads data set to the overlay layers of the 600m radii around site centres and road density was the sum road length within each site radius. To investigate the effect of urban level these landscape characteristics I used individual models with level as the

only fixed variable and tested the significance of level being included in the model using ANOVA.

Results

Landscape variables

The urban level was associated with all three of the additional landscape variables: edge density (F = 4.344, df = 5,24, P = 0.00588; Fig 9.), mean patch size (F= 18.6, df = 24,5, P< 0.001; Fig 9.) and road length (F = 19.8, df = 5,24, P< 0.001). The patterns in landscape characteristics changing across the urban gradient show patch size generally increasing with increasing greenspace and decreasing urbanisation. Edge density shows a similar trend with the exception of grassland sites (urban level 5) which have a similar edge density to sites of majority suburban landcover (urban level 2), with mean edge density = 55300 ± 9550 , and 54200 ± 2060 , respectively). Road density decreases with increasing greenspace but remaining relatively high at urban level 4. These variables further justify this study's urban level categories as well as being potential variables that influence the response of hover fly and solitary bee abundance and richness to urban landscape level.

Surveys

From the total 15 hours of flying insect surveys across all study sites, 578 individuals from pollinator groups were observed. Bumblebees were the most well represented group with 224 individuals and eight identified species. Hover flies were the second most numerous group, 145 individuals and three commonly identified species. Ninety-nine honeybees were observed. Solitary bees and Lepidoptera were the least observed groups with 55 individuals each, and 6 and 12 identified species, respectively. The most abundant pollinator species were the Honey bee *Apis melifera*, Tree bumblebee, *Bombus hypnorum*, and White and Buff-tailed bumblebees, *B. terrestris* and *B. lucorum* (grouped: splitting the two species was not possible in the field) observed 98, 79, and 62 times respectively (Appendix Table 16.). For flowering plants across the sample sites Common Mouse ear, *Cerastium fontanum*, Lesser trefoil,

Trifolium dubium, and Small-flowered crane's-bill, *Geranium pusillum,* <u>were observed</u> 508, 378, 351 times respectively (Appendix Table 15.).



Figure 9. Mean \pm standard error of landscape variables, road density (Total length of road within the landscape; m), mean patch size of connected tree cover (m²) and edge density (total perimeter of tree cover patches within the landscape; m), across the gradient of landscape scale urbanisation from sites surrounded by landscape of high urbanisation (dark purple) to low urbanisation (dark green). Description of landscape composition for each urban level; 1 = majority urban, 2 = majority suburban, 3 = suburban/grassland mix, 4 = suburban/tree cover mix, 5= majority grassland, 6 = majority greenspace with tree cover.

When exploring the effect of urbanisation on the abundance of pollinators, urban level (χ^2 = 13.3, df = 5; P= 0.0205), pollinator group (χ^2 = 93.0, df = 4; P < 0.001), and the interaction between urban level and pollinator group (χ^2 = 49.6, df = 20; P < 0.001) were all important (Fig 4). Other variables that also had effect on pollinator abundance were: flowering plant richness (χ^2 = 8.75, df = 1; P = 0.00310), wind speed (χ^2 = 12.9, df = 1; P < 0.001), cloud cover (χ^2 = 14.3, df = 5; P= 0.0139), and temperature (χ^2 = 20.9, df = 1; P < 0.001). See appendix Table 1. for the full model. Urban level (χ^2 = 13.6, df = 5; P = 0.0187), pollintor group (χ^2 = 53.9, df = 3; P < 0.001) and flower richness (χ^2 = 13.9, df = 1; P < 0.001) also had a significant effect on total

pollinator species richness, but the inclusion of interaction between pollinator group and urban level was non-significant (See appendix Table 2. for full model)

The significant effect of the interaction of pollinator group and urban level on pollinator abundance justifies the need to further analyse the pollinator groups individually. Urban level influenced the abundance of hover flies (χ^2 = 33.0, df = 1; P < 0.001), but not the abundance of



Figure 4. Mean \pm standard error abundance and richness of pollinators across a gradient of landscape scale urbanisation from high urbanisation (1; dark grey) to low urbanisation (6; light grey). Description of landscape composition for each urban level; 1= majority urban, 2 = majority suburban, 3 = suburban/grassland mix, 4 = suburban/tree cover mix, 5 = majority grassland, 6 = majority greenspace with tree cover.

Bumblebees, Lepidoptera, solitary bees or honey bees (Fig 5; see Appendix Table 5 to 9 for full models). Hover fly abundance was greatest at woodland dominated sites (urban level 6;, 5.1 ± 0.58) and lowest at grassland sites (urban level 5; 1.3 ± 0.66). Hover flies also had low abundance at sites in highly urban landscapes (urban level 1; 1.3 ± 0.025) and solitary bees had low abundance at sites of a mix of suburban and tree cover (urban level 4; 0.3 ± 0.2 ; Fig 5.). The influence that the interaction between urban level and pollinator group has on total pollinator abundance is likely to predominantly be driven by the response of hover flies to urban landscape variables.



Figure 5. Mean \pm standard error abundance for pollinator groups across the gradient of landscape scale urbanisation from sites surrounded by landscape of high urbanisation (dark purple) to low urbanisation (dark green). n.s, *, ***, **** indicate no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Description of landscape composition for each urban level: 1 = majority urban, 2 = majority suburban, 3 = suburban/grassland mix, 4 = suburban/tree cover mix, 5 = majority grassland, 6 = majority greenspace with tree cover.

Species richness of hover flies and solitary bees were associated with urban level ($\chi^2 = 14.4$, df = 5, P = 0.0135; $\chi^2 = 13.5$, df = 5, P = 0.0190, respectively; Fig 6.). Richness in both groups following a similar pattern to that of abundance with the highest richness at woodland sites (hover fly 2.2 ± 0.37, solitary bees 1 ± 0.39). Lowest richness for hover flies and solitary bees was at grassland sites (0.9 ± 0.4, 0.3 ± 0.2), and solitary bees observed similarly low levels of richness at level 4 suburban/tree cover mix sites (0.3 ± 0.2).

Pollinator response to flower and tree richness

Flowering plant richness was a predictor of the abundance of hover flies ($\chi^2 = 10.1$, df = 1, P = 0.00148), and honey bees ($\chi^2 = 1.05$, df = 1, P = 0.0499; Fig 7.). Flowering plant richness also predicted species richness of hover flies ($\chi^2 = 5.75$, df=1, P=0.0165) and solitary bees ($\chi^2 = 13.0$, df = 1, P < 0.001). Tree richness was a predictor of bumblebee abundance ($\chi^2 = 7.44$, df = 1, P = 0.00639) and hover fly abundance ($\chi^2 = 4.38$ df = 1, P = 0.0363) with a positive relationship (coefficient estimates from minimum adequate models = 0.181 and 0.132 respectively; Fig 7.). This could be an important explanation of the lack of response of bumblebees to urbanisation

as abundance as tree richness was also not affected by urbanisation and showed highest levels of richness at sites of majority suburban cover (level 2; Appendix Fig 11.).



Figure 6. Mean \pm standard error, of species richness for pollinator groups across the gradient of landscape scale urbanisation from sites surrounded by landscape of high urbanisation (dark purple) to low urbanisation (dark green). n.s, *, *** indicate no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Description of landscape composition for each urban level; 1= majority urban, 2 = majority suburban, 3 = suburban/grassland mix, 4 = suburban/tree cover mix, 5 = majority grassland, 6 = majority greenspace with tree cover.

Flowering plant richness and tree species richness were not significantly affected by urban level, but these local floral resource measures clearly play an important role in pollinator response to urbanisation. Flowering plant richness, for example, was highest at sites of suburban + tree cover mix (urban level 4; 7.8 ± 2.7) and then the most urban sites (urban level 1; 7.3 ± 1.7) and lowest at the level 6, (woodland sites; 2.6 ± 1.2). In contrast to this, tree richness was lowest at urban level 1 (0.6 ± 0.4) but highest urban level 2 (suburban sites; $2, 2.8 \pm 0.6$; Appendix Fig 11).

Lepidoptera abundance and richness was only significantly associated with temperature as a parameter (χ^2 = 4.26, df= 1, P = 0.039; χ^2 = 4.78, df = 1, P = 0.0432, respectively). It was therefore accepted that urbanisation of the surrounding landscape and local floral resources



Figure 7. The significant effects of local flowering plant or and tree richness on pollinator abundance or richness (A) local tree richness and bumblebee abundance. B) local floral richness honey bee abundance. (C) local floral richness and solitary bee species richness. (D and E) hover fly abundance and flowering plant richness and tree richness respectively. (F) hover fly richness and flowering plant richness. Linear predictors were fitted using *geom_smooth* function with a *"glm"* method, grey errors bars around the line represent standard error, to aid visualisation. Estimates of slope from the minimum adequate GLMM's for pollinator abundances or richness in response to the respective local floral resource measure; A = 0.17, B = 0.062, C = 0.17, D = 0.13, E = 0.071, F = 0.066. (details of full models in Appendix Tables 3, 5, 6, 10 and 11)

had no effect on Lepidoptera abundance and species richness. Bumblebee richness was not affected by urbanisation of the landscape and was not affected by any of the test parameters included in the model (Appendix Table 4). Honey bee abundance was not affected by urban level, as may be expected due to the likely proximity to domestic hives, and only temperature ($\chi^2 = 10.5$, df = 1, P = 0.0012), cloud cover ($\chi^2 = 14.5$, df = 5, P = 0.0124), in addition to the previously mentioned floral abundance were important predictors.

Nest Data

In terms of the reproductive success of the solitary bees that were seeded in the tube nest, urban level had an effect on total number of offspring per nest ($\chi^2 = 12.3$, df = 1, P = 0.0312), but, no effect of sex or any an interaction between sex and urban level. For a population to be stable the number of offspring produced and reproduce the next year needs be 1 per adult. We measured number of offspring before considering mortality pupal or adult mortality, and so the number of pupae per adult = 1 is an absolute minimum required to produce a stable population. Sites in the most urbanised landscape (urban level 1) were the only group to have a reproductive rate of <1 pupa per adult (0.744 \pm 0.30) and woodland sites (urban level 6) averaged the highest rates of reproduction with 2.35 ± 0.40 pupa per adult (Fig 8.). Sex of pupae was a significant predictor of mass; this is expected due to sexual dimorphism in O. bicornis (Appendix Table 13; Van Eeckhoven 2020). Urban level and the interaction between level and sex were not predictors of pupal mass. Urban level had no effect on sex ratio of the pupa (Appendix Table 14), which might have been expected due to the ordering of laying females first and when provisions are lowered laying males, or if adults abandon the nest or die we might expect a higher ratio of female pupa. These results show a reproductive output response to urban level and indicate that O.bicornis can successfully forage across a gradient of landscape scale urbanisation and even in highly urbanised landscapes.



Figure 8. Number of female (light green) and male (dark green) offspring pupae per adult seeded in tube nests mean \pm standard error (half width bars), and total pupa error per adult mean \pm standard (full width bars,no crossbar on errorbars) cross the gradient of landscape scale urbanisation from sites surrounded by landscape of high urbanisation (dark purple) to low urbanisation (dark green). Data averaged from individual solitary bee nests. Dotted horizontal line at y=1 represents a stable population r=0. Description of landscape composition for each urban level; 1 = majority urban, 2 = majority suburban, 3 = suburban/grassland mix, 4 = suburban/tree cover mix, 5 = majority grassland, 6 = majority greenspace with tree cover.

Discussion

O. bicornis reproductive output: response to urbanisation

This study investigated how the change in urban gradient affected the reproductive success of *O. bicornis.* The experimental introduction of *O. bicornis* at sites across a gradient of urbanisation provides evidence that *O. bicornis* exhibit lower reproductive output when foraging in highly urban landscapes. The pattern of reproductive output supports a previously

proposed effect of urbanisation on pollinators: that in urban gradients from natural landscapes to highly urban landscapes, pollinator success follows a three-step decline where natural landscapes provide more suitable habitat than suburban landscapes, which in turn provide more suitable habitat than highly urbanised areas (Wenzel et al. 2020). Reproductive success was highest in landscapes dominated by woodland and grassland, followed by landscapes dominated by suburban land cover and reproductive output was lowest in highly urban landscapes (Fig. 6). The results reveal important findings about changes in resource provisioning at landscape scales as a result of urbanision. Within highly urban landscapes there is either not high enough quality of habitat within *O. bicornis'* range to forage effectively, *O. bicornis* cannot travel through the matrix landscape to forage from available resources, mortality rates of adults were higher resulting in fewer offspring, or a combination of the three. Yet *O. bicornis* can successfully forage through suburban landscapes.

One explanation of the pattern of O. bicornis reproductive output across urban levels may be the reduced ability of bees to forage at their maximum range as a result of the absence of suitable habitat patches in urban environments. Essentially, the connectivity structure of habitat can determine the range that bees forage (Williams and Kremen 2007). For example, linear habitat structures can cause bees to forage across longer distances (Van Rossum and Triest 2010). There is also evidence that bees have smaller home ranges in urban areas, even in species with long-range flying abilities (López-Uribe et al. 2008). Greenspaces and edge density have been proposed as essential steppingstones and facilitators for longer foraging trips for bees (Hennig and Gazhoul 2012). The aforementioned study also found that the structure of greenspace within the landscape became more important at larger spatial scales. The results from this study may complement this theory, as edge density was lowest at highly urban level but with higher mean patch size than suburban landscapes suggesting fewer intermediary tree patches within the landscape creating larger distances and a harsher matrix to cross, less connectivity and ultimately forcing bees to forage in a smaller range. In general, the trend of landscape features across the urban gradient in Nottingham followed typical patterns of urbanisation; higher road density and smaller patch sizes with increasing urbansation, often the result of habitat loss and fragmentation (Shilling et al. 2010; Haddad et al. 2015). So, matrix quality between tree patches perhaps also played a role in the differences of reproductive success between urban and suburban landscapes. The quality of provision accessed directly from areas of suburban land cover is potentially greater than first expected

and will be later discussed in relation to landscapes comprised of suburban + green cover. Further research into the importance of small steppingstone patches on the ability of bees to forage at their full range would be highly valuable. Increased mortality rates with increasing road density should not be overlooked either; mortality of Hymenoptera has been found to be at 26.8/km/day on major roads (Baxter-Gilbert et al. 2015). Car speeds were a lot faster than what would occur within the urban areas of our study system but road density was highest at urban level 1 (Fig. 6).

Pollinator abundance and richness: response to urbanisation

The study also investigated the response of pollinators, in terms of their abundance and richness, to urban landscape change. Pollinator survey results suggested that the abundance of pollinators was affected by landscape scale urbanisation, but this trend was mainly driven by the response of hover fly abundance (Fig. 4). Persson et al. (2020) similarly found hover fly declines in abundance and richness across a gradient of increasing human population density, and a comparison of urban landscapes to both natural and agricultural landscapes similarly found lowest levels in the urban landscapes (Baldock et al 2015). Hover flies, unlike bees, are not pollen collectors and are not central place foragers (returning to a nest site). They can disperse in a linear fashion alternating between feeding and ovipositing. Hover flies rely on extremely species-specific selection of micro-habitats for larvae to feed on, such as rotting organic matter, dung heaps, and aphids and other soft-bodied insects (Rothery and Gilbert 2011). If habitats for larvae are reduced in urban and suburban areas, irrespective of the quality of floral resource or the ability to disperse through landscape, higher abundances and richness will likely be found close to where adults are emerging from larval feeding habitats (Jauker et al. 2009), perhaps with the exception of highly dispersive species such as Episyrphus balteatus (G. Stone pers. Comm.). And because offspring do not necessarily disperse from larval habitat to the same adult food resource patches as their ancestors, accumulation of adults is less like to occur at patches of adult food resources than larval food resources (Jauker et al. 2009).

Lack of larval habitat may also explain the low abundance and richness of hover flies found at majority grassland sites, as they had reduced habitat structure from lower edge density (Fig. 6) which is already known to be linked with hover fly abundance and richness (Hennig and Gazhoul 2012; Theodorou et al. 2020). This reduced habitat structure in addition to

management intensity of regular mowing (personal observation) could potentially have reduced larval microhabitats, such as deadwoods or prey species, compared to low intensity suburban areas, although this was not explicitly tested. Solitary bees similarly displayed lower species richness at grassland sites (Fig. 3), despite *O. bicornis* reproduction remaining high (Fig. 5). On account of the previously mentioned mowing regimes at these sites, this reduction in solitary bee richness may be the result of effects seen in previous research; that mowing ground disturbance reduces habitat availability for ground-nesting species (Hernandez et al. 2009; Banaszak-Cibicka and Żmihorski 2012; Cardoso and Gonçlaves 2018; Lerman et al. 2018,).

Urban filtering

The varying response to urbanisation by different pollinator groups provides evidence that pressures within urban areas manifest as a filter for the pollinator community. Reflecting findings in the literature, bumblebees were found in similar abundance and richness across the landscape gradient (Goulson et al. 2002; Hernandez et al. 2009; Banaszak-Cibicka and Żmihorski 2012; Baldock et al. 2015; Theodorou et al 2018). Bumblebees were found to be affected by urban gradients in this study, this could be linked to the maintenance of tree richness across the urban gradient, which although lowest in highly urban areas, was not significantly affected by urban level (Apendix Fig 10). During experimental introduction of their nests to urban areas, Bombus terrestris bees wer e able to take advantage of high density and diversity of flowers in suburban gardens, and high levels of moth parasitism by Aphomia sociella suggested that bumblebee hosts were already abundant in the area (Goulson et al. 2002). The large foraging range and generalist foraging behaviour of some bumblebee species allows them to take advantage of the heterogenous nature resources provided across urban landscapes (Goulson et al. 2002). Lepidoptera also remained unaffected by urban level in our study system, contrary to the trends found in other research. As previously mentioned, Theodorou et al. (2018) compared high quality urban areas to high quality rural areas and measured a significant reduction in Lepidoptera species. Lepidoptera share similarities with hover flies in that they can linearly disperse through a landscape but have dispersal ranges that are usually larger (100m – 1000m compared to <200m; Van Rossmun and Triest 2010). Similarly to bees, this can determine their success within urban environments. Urbanisation has been shown to drive shifts towards increased body size in Lepidoptera, as larger bodied

individuals are more mobile, which can mitigate reduced levels of connectivity in urban landscapes (Merckx et al. 2018).

Mobility appears to be a principal factor in pollinator response to urbanisation in our system. Mobile and large bodied species are generally more successful when habitat fragmentation prevents smaller less mobile species from reaching enough quality food resource from nest sites (Harrison and Winfree 2015). The trends from the pollinator survey of bumblebees, honey bees and Lepidoptera remaining unaffected by urban level and hover fly responding to urban level suggests that pollinator groups with better mobility were able to cope with the pressures of urbanisation in our system. For *O. bicornis*, this isolation from suitable food resource perhaps occurred at the most urban landscapes and potentially within some suburban landscapes but not to a detrimental level. This variation in reproductive success within different suburban landscapes will be discussed in the following section.

Suburban gardens vs greenspace

It is important to note that *O. bicornis* had significantly higher reproductive success in the suburban landscapes (urban level 2) than both landscapes of suburban + grassland (urban level 3), and suburban + tree cover (urban level 4). As a result, habitat quality within suburban landscapes cannot be said to follow a simple linear pattern that increasing green and reduced suburban land cover leads to decreased habitat quality for wild pollinators within the landscape for wild pollinators. It should be considered that the suburban landscapes were mainly composed of residential gardens, and landscapes of suburban + grassland or tree cover often included greenspace embedded within suburban sprawl and were rarely connected to any natural areas. Therefore, although the quantity of greenspace was increased within the landscape, the quality of resource appears to be higher in suburban residential gardens. Daniels et al. (2020) compared urban greenspaces. Similarly, across four UK cities, urban gardens have been predicted to support 54 – 83% of the urban pollinators found in the study, outperforming public managed greenspace despite having similar total areas (Baldock et al. 2019).

Multiple local variables could also contribute to the variation of habitat quality within different suburban landscapes. Specific variables have been found to influence pollinator populations in

suburban gardens. These include the structure in which floral resources are provided, with wild bees preferring clusters of resource as opposed to more evenly dispersed resources (Plascencia and Philpott 2017), as well as local variables such as flower abundance and richness, herbaceous plant richness, mulch cover, and leaf litter, which have varying effects on different bee species (Quistberg et al. 2016). The mix of exotic and native plants can have a positive effect on pollinators by increasing the temporal stability of floral resource availability (Kaluza et al. 2016). Richness of flowering plants and trees from this study's survey were key predictors of pollinator abundance and richness, yet these floral resource variables were not linked to urban level. High tree species richness in urban level 2 (Appendix Fig.9) could help explain differences in *O. bicornis* reproductive success at urban levels 2 - 4, along with potential variation in other specific local scale variables that have been shown to be important within suburban gardens (Kaluza et al. 2016; Quistberg et al. 2016; Plascencia and Philpott 2017).

Threats to population sustainability

Populations of O. bicornis in highly urbanised landscapes are unsustainable; (Fig 8.) demonstrates the number of offspring per adult within urban level 1 was on average less than one (0.744 \pm 0.295). Meaning the population failed to replace itself after one generation (even before late pupal and adult mortality or failure to reproduce), which would eventually lead to local extinction if that rate of reproduction remained. At sites in suburban + tree cover landscapes (urban level 4) number of offspring per adult was on average more than one (1.12 ± 0.26), but error bars indicate that it is close to dropping below one and potentially also at risk of exhibiting a decreasing population trend in some areas. Secondary risk may also occur through decreased foraging ability of female offspring in future years. Weight of females of O. bicornis is associated with foraging ability (Van Eeckhoven 2020), and although in this study pupal mass was not significantly affected by urban level, female weights showed a decreasing trend with increasing urbanisation, with female weights at urban levels 1 and 4 were on average 90±4% and 90±3%, respectively, of female weights in woodland landscapes. These variations may be at too small an effect size to be statistically significant after one year of sampling but have the potential to manifest as a positive feedback loop if smaller females emerge, have poorer foraging capabilities due to their small body size, leading to further reductions in body size of offspring or a drop in total number of offspring. This is relevant as

some landscapes within suburban areas of the city may be population sinks over a longer time scale than encompassed within this study, instead of providing suitable habitat initially thought. This may be less of an issue when taking into consideration dispersal from nearby source populations, which could stabilise populations over the wider landscape through meta-population dynamics (Hanski 1998). It is important to state that our measure of pupa per adult is not a measure of replacement rate or population success as it does not include variables that may cause failure to reproduce between pupa and reproductive stages. Here we can only indicate which populations will be declining by not reaching the minimum number of pupae per adult, but this does not guarantee that populations above this threshold will be stable or increasing.

Conservation recommendations

Increased public attention towards the conservation of pollinators has largely been focused on the services they provide for humans. Honey bees and bumblebees often being the focus species and little public attention on other wild pollinator groups or even species of bee that are not honey and bumblebees (Drossart and Gérard 2020, Wilson et al. 2017). This is also reflected in the literature, with honey bee declines being subject to more research attention than other pollinator species (Potts et al. 2010).

Opportunities for conservation of pollinators, especially bees, lie within suburban landscapes with high tree and flowering plant richness. This study has shown that, when provided with nesting habitat, solitary bees can successfully reproduce in suburban environments, and pollinators respond positively to flowering plant and tree richness irrespective of urban level. The variation in reproductive output at urban levels 2, 3, and 4 (Fig 8.) suggest that there is potential for improvement of habitat quality of greenspace within suburban landscapes. Improving the floral provisions of city parks and greenspace by increasing abundance of common species (*Belis perenis, Taraxacum* agg., *Trifolium repens*) has been modelled to have conservation benefits for urban pollinator (Baldock et al. 2019). Blackmoore and Goulson (2014) demonstrated that simple intervention methods of sowing amenity grasslands with wildflower seed can greatly improve conditions for wild pollinators, observing 50 times more bumblebees and 13 times more hover flies than control sites.

Increased nesting provisions will benefit wild bees as the more nesting spaces provided for bees the more chance (on average) that some emerging adults will be closer to resources, and consequently have to invest less in foraging for longer distances. It is clear that there are accessible floral resources within suburban landscapes for O. bicornis, but many other solitary bee species have far smaller foraging ranges (<150; Gathmann and Tscharntke 2002), so proximity of nesting sites to floral resource will be increasingly important for such species. In addition, the combination of finding suitable nesting and floral resource within home range will become increasingly unlikely with increasing habitat fragmentation. Nesting provisions for multiple cavity-nesting species can be easily provided with a simple tube nest like those used in this study (Fig 3.), and a variety size of cardboard tube diameters (4 -10 mm) including red mason bees O. bicornis, leafcutter bees Megachile sp., potter wasps Ancistrocerus sp., blue mason bees Osmia caerulescens, and solitary bees of the genus Hylus (Evans et al. 2018). Ground-nesting species are more sensitive to urbanisation likely due to decreasing nest habitat availability (Hernandez et al. 2009, Banaszak-Cibicka and Żmihorski 2012, Wenzel et al. 2020). To combat this pressure, gardens and greenspaces should aim to provide bare ground free of dense shrub undergrowth (Banaszak-Cibicka et al. 2016). Other variables that benefit groundnesting species are areas of low cover of mulch and leaf litter (Quistberg et al. 2016). Reducing mowing intensity from once per week to once every three weeks can increase bee species richness generally by improving floral richness and habitat heterogeneity (Lerman et al. 2018) For hover fly species the availability of habitat for larvae - microhabitats of rotting organic matter or availability of prey species, is important for reducing the impact of urbanisation. Residential gardens have the potential to supply these increased conservation benefits (Persson et al. 2020). Although gardens are managed at small scales, when garden guality improves over neighborhood or city scale they can offer positive conservation outcome (Goddard et al. 2010). Improving suburban habitat quality and connectivity with large natural greenspaces can lead to better infiltration of bees into more urbanised landscapes (Banaszak-Cibicka et al. 2016), although as this study shows, quality of greenspace is imperative.

Conservation of pollinator populations in urban landscapes is vital for the health of ecosystems, which is the fundamental basis to human health and economic security. Fifty five percent of people now live in urban areas and set to rise to 68% by 2050 (UN, 2018). Wild pollinators are critical to providing urban ecosystem services and cannot be substituted by domestic honey bees in terms of pollination efficiency. A study in Berlin, Germany, measured

visits to urban trees by different pollinators. Visits by wild pollinators to urban trees were positively associated with tree reproductive success but visits by honey bees were not (Hausmann et al. 2016). Higher quality habitat in gardens can benefit pollination and output of food crops in urban community gardens (Werell et al. 2009), in turn supporting urban communities through access to healthy foods and economic relief (Siegner et al. 2018). In the UK, encounters with wild birds are highly valued by the public and food sources for these birds are directly supported by pollinators (Birkin 2017). Public interest and support for conservation of pollinators has been increasing, but public knowledge remains mainly related to bumblebees and honey bees (Wilson et al. 2017). The public engagement with pollinator conservation within urban areas offers an opportunity for residents to engage with nature in their local area, leading to the potential further support of biodiversity conservation (Dunn 2006). Hall and Martins (2020) summarise the diverse roles pollinators can play as a focus: "Insect pollinators are optimal conservation focal species simultaneously filling roles of: flagship (evoking public support), umbrella (having conservation needs that incidentally protect other species), indicator (sensitive to change/degradation), and keystone species (having ecological impact disproportionate to their abundance)". Personal observations from this study highlighted the conservation potential within the Nottingham region. Leafcutter bees Megachile sp. were regularly found to use the tube nests and the enthusiasm from the public when either inquiring about the experiment or volunteering their gardens clearly showed a desire to contribute towards bee conservation, which is reassuring.

Recommendations for further research

Overall, this is an observational study with many parameters that may be resulting in the observed patterns of pollinator abundance, richness and reproductive success of *O. bicornis*. As highlighted in the PCA of landscape variables used to describe our urban gradient there are many changing variables across urban gradients that become difficult to extract causal effects in this study. For better management of pollinators in urban areas these specific drivers need to be identified. Multi-year research should be undertaken to measure the possible accumulative effect of reduced female size and the knock-on effect of reduced foraging ability in subsequent years. As some trends in female pupal weight were present in this study but were at an effect size too small to be recognised by the statistical models in data from just one-year. Limitations of this study were that pollinator surveys from only one year of observations can be produce variable results.

Multi-year studies overcome this by being able to measure underlying trends and cutting through yearly variability in pollinator communities (Hernandez et al. 2009). Further research should investigate the capability of connected suburban gardens to be host source populations of pollinator species and how they compare to and combine with nearby greenspaces. This would be highly beneficial for city planners and conservation charities to know where to focus conservation energy as it may reduce reliance on parks and large greenspace as the main population sources for pollinators in urban landscape.

Conclusion

Insect pollinators respond to landscape and local scale variables within urban environments. The provision of quality habitat for pollinator species within urban area largely depends on functional traits and ecological requirements at adult and larval stages. Mobility through urban landscapes likely relieves pressures of habitat fragmentation, and tree and flowering plant richness are key local factors that support pollinators across the urban gradient. This allows some pollinator species to take advantage of heterogenous habitats found in urban landscapes and sustain successful populations. Conservation opportunities within the regions surrounding Nottingham (UK) potentially lie within suburban landscapes where sufficient floral resource can be provided for wild pollinators such as *O. bicornis*, so long as nesting requirements are met.

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References

Baldock, K. C. (2020). Opportunities and threats for pollinator conservation in global towns and cities. *Current Opinion in Insect Science*, *38*, 63–71. https://doi.org/10.1016/J.COIS.2020.01.006

Baldock, K. C., 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: Biological Sciences*, 282(1803). https://doi.org/10.1098/RSPB.2014.2849

Baldock, K. C., 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., Stone, G. N., Vaughan I. P., & Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature ecology & evolution*, *3*(3), 363-373.

Banaszak-Cibicka, W., Ratyńska, H., & Dylewski, Ł. (2016). Features of urban greenspace favourable for large and diverse bee populations (Hymenoptera: Apoidea: Apiformes). *Urban Forestry & Urban Greening*, *20*, 448–452. https://doi.org/10.1016/J.UFUG.2016.10.015

Banaszak-Cibicka, W., & Żmihorski, M. (2012). Wild bees along an urban gradient: Winners and losers. *Journal of Insect Conservation*, *16*(3), 331–343. https://doi.org/10.1007/S10841-011-9419-2

Banaszak-Cibicka, W., & Żmihorski, M. (2020). Are cities hotspots for bees? Local and regional diversity patterns lead to different conclusions. *Urban Ecosystems*, 23. https://doi.org/10.1007/s11252-020-00972-w

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(8). https://doi.org/10.1371/JOURNAL.PONE.0023459

- Bates D, Mächler M, Bolker B, Walker S (2015). "Fitting Linear Mixed-Effects Models Using Ime4." *Journal of Statistical Software*, 67(1), 1–48. doi: 10.18637/jss.v067.i01.
- Baxter-Gilbert, J. H., Riley, J. L., Christopher, •, Neufeld, J. H., Litzgus, J. D., & Lesbarrères, D. (2015). Road mortality potentially responsible for billions of pollinating insect deaths annually. *Journal of Insect Conservation*, *19*. https://doi.org/10.1007/s10841-015-9808-z
- Beverly J. Rathcke, & Erik S. Jules. (1993). Habitat fragmentation and plant–pollinator interactions. *Current Science*, 65(3), 273–277.

Biesmeijer, J. C., Roberts, S. P., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., ... & Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, *313*(5785), 351-354.

Birkin, L. J. (2017). *Pollination ecosystem services and the urban environment*. (Doctoral dissertation, University of Essex).

Blackmore, L. M., & Goulson, D. (2014). Evaluating the effectiveness of wildflower seed mixes for boosting floral diversity and bumblebee and hoverfly abundance in urban areas. *Insect Conservation and Diversity*, 7(5), 480–484. https://doi.org/10.1111/icad.12071

Bosch, J., & Vicens, N. (2002). Body size as an estimator of production costs in a solitary bee. *Ecological Entomology*, 27, 129–137.

Breeze, T. D., Bailey, A. P., Balcombe, K. G., & Potts, S. G. (2011). Pollination services in the UK: How important are honeybees? *Agriculture, Ecosystems & Environment*, 142(3–4), 137– 143. <u>https://doi.org/10.1016/J.AGEE.2011.03.020</u>

Buchholz, S., Gathof, A. K., Grossmann, A. J., Kowarik, I., & Fischer, L. K. (2020). Wild bees in urban grasslands: Urbanisation, functional diversity and species traits. *Landscape and Urban Planning*, *196*. https://doi.org/10.1016/J.LANDURBPLAN.2019.103731

Cardoso, M. C., & Gonçalves, R. B. (2018). Reduction by half: the impact on bees of 34 years of urbanization. *Urban Ecosystems*, *21*(5), 943–949. https://doi.org/10.1007/s11252-018-0773-7

Chen, I. C., Hill, J. K., Ohlemüller, R., Roy, D. B., & Thomas, C. D. (2011). Rapid range shifts of species associated with high levels of climate warming. *Science*, 333(6045), 1024-1026.

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

Daniels, B., Jedamski, J., Ottermanns, R., & Ross-Nickoll, M. (2020). A "plan bee" for cities: Pollinator diversity and plant-pollinator interactions in urban greenspaces. *PLoS ONE*, *15*(7 July). https://doi.org/10.1371/journal.pone.0235492

Drossart, M., & Gérard, M. (2020). insects Beyond the Decline of Wild Bees: Optimizing Conservation Measures and Bringing Together the Actors. *Insects*, *11(9)*, *649*. https://doi.org/10.3390/insects11090649

Dunn, R. R., Gavin, M. C., Sanchez, M. C., & Solomon, J. N. (2006). The pigeon paradox: dependence of global conservation on urban nature. Conservation biology, 20(6), 1814-1816.

Ebeling, A., Klein, A.-M., Schumacher, J., Weisser, W. W., & Tscharntke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower

visits? *Oikos*, *117*(12). https://doi.org/10.1111/j.1600-0706.2008.16819.x Evans, A. N., Llanos, J. E. M., Kunin, W. E., & Evison, S. E. F. (2018). Indirect effects of agricultural pesticide use on parasite prevalence in wild pollinators. *Agriculture, Ecosystems and Environment*, *258*, 40–48. https://doi.org/10.1016/j.agee.2018.02.002

Evison, S. E. (2015). Chalkbrood: epidemiological perspectives from the host-parasite relationship. *Current opinion in insect science*, *10*, 65-70.

Falk, S. (2019). Field guide to the bees of Great Britain and Ireland. Bloomsbury Publishing.

Fenoglio, M. S., Calviño, A., González, E., Salvo, A., & Videla, M. (2021). Urbanisation drivers and underlying mechanisms of terrestrial insect diversity loss in cities. *Ecological Entomology*, 46(4), 757–771. https://doi.org/10.1111/een.13041

Fischer, L. K., Eichfeld, J., Kowarik, I., & Buchholz, S. (2016). Disentangling urban habitat and matrix effects on wild bee species. *PeerJ*, 2016(11). https://doi.org/10.7717/PEERJ.2729

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

Garbuzov, M., Schürch, R., & Ratnieks, F. L. W. (2015). Eating locally: dance decoding demonstrates that urban honey bees in Brighton, UK, forage mainly in the surrounding urban area. *Urban Ecosystems*, *18*(2), 411–418. https://doi.org/10.1007/s11252-014-0403-y

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A.,
Kremen, C., Carvalheiro, L. G., Harder, L. D., Afik, O., Bartomeus, I., Benjamin, F., Boreux, V.,
Cariveau, D., Chacoff, N. P., Dudenhöffer, J. H., Freitas, B. M., Ghazoul, J., Greenleaf, S., ... Klein,
A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey

bee abundance. *Science*, *340*(6127), 1608–1611. https://doi.org/10.1126/SCIENCE.1230200 Gathmann, A., & Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of Animal*

Ecology, 71(5), 757–764. https://doi.org/10.1046/J.1365-2656.2002.00641.X

Gaston, K. J. (Ed.). (2010). Urban ecology. Oxford University Press.

Goddard, M. A., Dougill, A. J., & Benton, T. G. (2010). Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution*, 25(2), 90–98. https://doi.org/10.1016/J.TREE.2009.07.016

Goulson, D., Hughes, W. O. H., Derwent, L. C., & Stout, J. C. (2002). Colony growth of the bumblebee, Bombus terrestris, in improved and conventional agricultural and suburban habitats. *Oecologia*, *130*(2), 267–273. https://doi.org/10.1007/S004420100803

Goulson, D., Nicholls, E., Botias, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of

flowers. *Science*, *347*(6229). https://doi.org/10.1126/science.1255957 Graystock, P., Yates, K., Evison, S. E., Darvill, B., Goulson, D., & Hughes, W. O. (2013). The

T rojan hives: pollinator pathogens, imported and distributed in bumblebee colonies. *Journal of Applied Ecology*, *50*(5), 1207-1215.

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

Jenkins, C. N., King, A. J., Laurance, W. F., Levey, D. J., Margules, C. R., ... Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, *1*(2). https://doi.org/10.1126/sciadv.1500052

- Hall, D. M., & Martins, D. J. (2020). Human dimensions of insect pollinator conservation. In *Current Opinion in Insect Science* (Vol. 38, pp. 107–114). Elsevier Inc. https://doi.org/10.1016/j.cois.2020.04.001
- Hansen, D. M., Beer, K., & Mü, C. B. (2006). Mauritian coloured nectar no longer a mystery: a visual signal for lizard pollinators. *Biol. Lett*, *2*, 165–168. https://doi.org/10.1098/rsbl.2006.0458
- Hanski, I. (1998). Metapopulation dynamics. In NATURE (Vol. 396). www.nature.com
- Harrison, T., & Winfree, R. (2015). Urban drivers of plant-pollinator interactions. *Functional Ecology*, 29(7), 879–888. https://doi.org/10.1111/1365-2435.12486
- Hausmann, S. L., Petermann, J. S., & Rolff, J. (2016). Wild bees as pollinators of city trees. *Insect Conservation and Diversity*, 9(2), 97–107. https://doi.org/10.1111/ICAD.12145
- Hernandez, J. L., Frankie, G. W., Thorp, R. W., Hernandez, J. L.;, & Frankie, G. W.; (2009). Ecology of Urban Bees: A Review of Current Knowledge and Directions for Future Study. In *Cities and the Environment (CATE)* (Vol. 2, Issue 1).
- Ireneusz Hennig, E., Ghazoul, J., Hennig, E. I., & Ghazoul, J. (2012). *Pollinating animals in the urban* environment. 15, 149–166. https://doi.org/10.1007/s11252-011-0202-7
- Jauker, F., Diekötter, T., Schwarzbach, F., & Wolters, V. (2009). Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. *Landscape Ecology*, *24*(4), 547–555. https://doi.org/10.1007/s10980-009-9331-2
- Kaluza, B. F., Wallace, H., Heard, T. A., Klein, A. M., & Leonhardt, S. D. (2016). Urban gardens promote bee foraging over natural habitats and plantations. *Ecology and Evolution*, 6(5), 1304– 1316. https://doi.org/10.1002/ECE3.1941
- Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. In *Proceedings of the Royal Society B: Biological Sciences* (Vol. 274, Issue 1608, pp. 303–313). Royal Society. https://doi.org/10.1098/rspb.2006.3721
- Lagucki, E., Burdine, J. D., & McCluney, K. E. (2017). Urbanization alters communities of flying arthropods in parks and gardens of a medium-sized city. *PeerJ*, *5*, e3620.
- Langellotto, G. A., Melathopoulos, A., Messer, I., Anderson, A., Mcclintock, N., & Costner, L. (2018). Garden Pollinators and the Potential for Ecosystem Service Flow to Urban and Peri-Urban Agriculture. *Sustainability*, *10*(2047). https://doi.org/10.3390/su10062047
- Lautenbach, S., Seppelt, R., Liebscher, J., & Dormann, C. F. (2012). Spatial and temporal trends of global pollination benefit. *PloS one*, *7*(4), e35954.
- Lerman, S. B., Contosta, A. R., Milam, J., & Bang, C. (2018). To mow or to mow less: Lawn mowing frequency affects bee abundance and diversity in suburban yards. *Biological Conservation*, 221, 160–174. https://doi.org/10.1016/J.BIOCON.2018.01.025
- Li, T., Shilling, Fraser, Thorne, J., Li, F., Schott, Heidi, Boynton, R., & Berry, A. M. (2010). Fragmentation of China's landscape by roads and urban areas. *Landscape Ecology*, 25, 839– 853. https://doi.org/10.1007/s10980-010-9461-6
- María, M., ´Opez-Uribe, L., Oi, C. A., Antonio, M., & Lama, D. (2008). Nectar-foraging behavior of Euglossine bees (Hymenoptera: Apidae) in urban areas*. *Apidologie*, *39*, 410–418. https://doi.org/10.1051/apido:2008023
- Merckx, T., Aur, |, Hans, K. |, & Dyck, V. (2018). Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. https://doi.org/10.1111/gcb.14151
- Met Office. (2021). Met Office Lenton, Nottngham and Watnall Forcast, accessed (24/5/21 23/7/21), https://www.metoffice.gov.uk/weather/forecast/gcrjjnz9t#?date=2021-09-20
- Nieto, A., Roberts, S.P.M., Kemp, J., Rasmont, P., Kuhlmann, M., García Criado, M., Biesmeijer, J.C., Bogusch, P., Dathe, H.H., De la Rúa, P., De Meulemeester, T., Dehon, M., Dewulf, A., Ortiz-Sánchez, F.J., Lhomme, P., Pauly, A., Potts, S.G., Praz, C., Quaranta, M., Radchenko, V.G., Scheuchl, E., Smit, J., Straka, J., Terzo, M., Tomozii, B., Window, J. and Michez, D. (2014). European Red List of bees. Luxembourg: Publication Office of the European Union.

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? *Oikos*, *120*(3), 321–326. https://doi.org/10.1111/J.1600-0706.2010.18644.X

Persson, A. S., Ekroos, J., Olsson, P., & Smith, H. G. (2020). Wild bees and hoverflies respond differently to urbanisation, human population density and urban form. *Landscape and Urban Planning*, *204*, 103901. https://doi.org/10.1016/J.LANDURBPLAN.2020.103901

Plascencia, M., & Philpott, S. M. (2017). Floral abundance, richness, and spatial distribution drive urban garden bee communities. *Bulletin of Entomological Research*, *107*(5). https://doi.org/10.1017/S0007485317000153

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353. https://doi.org/10.1016/J.TREE.2010.01.007

Potts, S. G., Imperatriz-Fonseca, V., Ngo, H. T., Aizen, M. A., Biesmeijer, J. C., Breeze, T. D., Dicks, L. v., Garibaldi, L. A., Hill, R., Settele, J., & Vanbergen, A. J. (2016). Safeguarding pollinators and their values to human well-being. *Nature*, *540*(7632), 220–229. https://doi.org/10.1038/NATURE20588

Pufal, G., Steffan-Dewenter, I., & Klein, A. M. (2017). Crop pollination services at the landscape scale. *Current Opinion in Insect Science*, *21*, 91–97.

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

Rader, R., Cunningham, S. A., Howlett, B. G., & Inouye, D. W. (2020). Non-Bee Insects as Visitors and Pollinators of Crops: Biology, Ecology, and Management. https://doi.org/10.1146/annurev-ento-011019

Ravoet, J., De Smet, L., Meeus, I., Smagghe, G., Wenseleers, T., & de Graaf, D. C. (2014). Widespread occurrence of honey bee pathogens in solitary bees. *Journal of Invertebrate Pathology*, *122*, 55-58.

Ropars, L., Dajoz, I., Fontaine, C., Muratet, A., & Geslin, B. (2019). Wild pollinator activity negatively related to honey bee colony densities in urban context. *PLoS ONE*, *14*(9). https://doi.org/10.1371/JOURNAL.PONE.0222316

Roy, S., Byrne, J., & Pickering, C. (2012). A systematic quantitative review of urban tree benefits, costs, and assessment methods across cities in different climatic zones. *Urban Forestry & Urban Greening*, *11*(4), 351–363. https://doi.org/10.1016/J.UFUG.2012.06.006

Samuelson, A. E., Gill, R. J., Brown, M. J. F., & Leadbeater, E. (2018). Lower bumblebee colony reproductive success in agricultural compared with urban environments. *Proceedings of the Royal Society B: Biological Sciences*, 285(1881). https://doi.org/10.1098/RSPB.2018.0807

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*, *109*(40), 16083–16088. https://doi.org/10.1073/pnas.1211658109

Siegner, A., Sowerwine, J., & Acey, C. (2018). sustainability Does Urban Agriculture Improve Food Security? Examining the Nexus of Food Access and Distribution of Urban Produced Foods in the United States: A Systematic

Review. Sustainability, 10(2988). https://doi.org/10.3390/su10092988

Smith, M. R., Singh, G. M., Mozaffarian, D., & Myers, S. S. (2015). Effects of decreases of animal pollinators on human nutrition and global health: a modelling analysis. *The Lancet*, *386*(10007), 1964–1972. https://doi.org/10.1016/S0140-6736(15)61085-6

Steckel, J., Westphal, C., Peters, M. K., Bellach, M., Rothenwoehrer, C., Erasmi, S., Scherber, C., Tscharntke, T., & Steffan-Dewenter, I. (2014). Landscape composition and configuration differently affect trap-nesting bees, wasps and their antagonists. *Biological Conservation*, 172, 56– 64. https://doi.org/10.1016/J.BIOCON.2014.02.015

Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T. E., & Paxton, R. J. (2020). Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nature Communications*, *11*(1). https://doi.org/10.1038/s41467-020-14496-6

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

 UN. (2018). The 2018 Revision of the World Urbanization Prospects is published by the Population Division of the United Nations Department of Economic and Social Affairs (UN DESA) Working Paper No. ESA/P/WP.252. New York: United Nations. Retrieved from:

https://population.un.org/wup/Publications/Files/WUP2018-Methodology.pdf. (19/09/2021) Van Eeckhoven, J. (2020). From control to constraint: a study of reproduction in the eusocial honeybee

and the solitary red mason bee (Doctoral dissertation, University of Leeds).

Van Rossum, F., & Triest, L. (2010). Pollen dispersal in an insect-pollinated wet meadow herb along an urban river. *Landscape and Urban Planning*, 95(4), 201–

208. https://doi.org/10.1016/J.LANDURBPLAN.2010.01.004

Walther-Hellwig, K., & Frankl, R. (2000). Foraging habitats and foraging distances of bumblebees, Bombus spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology*, 124.

- Wenzel, A., Grass, I., Belavadi, V. v., & Tscharntke, T. (2020). How urbanization is driving pollinator diversity and pollination – A systematic review. *Biological Conservation*, 241, 108321. https://doi.org/10.1016/J.BIOCON.2019.108321
- Werrell, P. A., Langellotto, G. A., Morath, S. U., Matteson, K. C., Werrell, P. A.;, Langellotto, G. A.;, & Morath, S. U.; (2009). The Influence of Garden Size and Floral Cover on Pollen Deposition in Urban Community Gardens. *Cities and the Environment (CATE)*, 2.
- Williams, N. M., & Kremen, C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, *17*(3), 910–921.
- Wilson, J. S., Forister, M. L., & Carril, O. M. (2017). Interest exceeds understanding in public support of bee conservation. *Front Ecol Environ*, *15*(8), 460–466. https://doi.org/10.1002/fee.1531
- Winfree, R., Williams, N. M., Gaines, H., Ascher, J. S., & Kremen, C. (2008). Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania,
- USA. Journal of Applied Ecology, 45, 793–802. https://doi.org/10.1111/j.1365-2664.2007.01418.x Wolch, J. R., Byrne, J., & Newell, J. P. (2014). Urban greenspace, public health, and environmental justice: The challenge of making cities 'just green enough.' *Landscape and Urban Planning*, 125, 234–244. https://doi.org/10.1016/J.LANDURBPLAN.2014.01.017
- Woodard, S. H., & Jha, S. (2017). Wild bee nutritional ecology: predicting pollinator population dynamics, movement, and services from floral resources. *Current Opinion in Insect Science*, *21*, 83–90. https://doi.org/10.1016/J.COIS.2017.05.011
- Yong, D. L., Barton, P. S., Okada, S., Crane, M., Cunningham, S. A., & Lindenmayer, D. B. (2020). Conserving focal insect groups in woodland remnants: The role of landscape context and habitat structure on cross-taxonomic congruence. *Ecological Indicators*, *115*, 106391. https://doi.org/10.1016/J.ECOLIND.2020.106391

Appendix

Table 1. Model of effects on pollinator abundance. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total abundance of pollinators as the response variable. *, **, *** indicates significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value

Family	110018)	92.9 (4)	< 0.001***
Level	1020(17)	13.3 (5)	0.0205 *
Level:Family	1010(22)	49.6 (20)	0.000249 ***
Temperature	984 (41)	20.9 (1)	< 0.001***
Cloud	978 (37)	14.3 (5)	0.0139 *
Wind	976 (41)	12.9 (1)	0.000334 ***
Flower Richness	972(41)	8.750 (1)	0.00310 **
Tree Richness	963(42)	0.304(1)	0.582
Tree Abundance	963(43)	0.0027(1)	0.959
Flower Abundance	963(44)	0.0842(1)	0.773
Number of observers	963(44)	3.50	0.0613

Table 2. Model of effects on pollinator species richness. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Family	666(17)	53.9(3)	< 0.001***
Level	626(15)	13.6(5)	0.0187 *
Level:Family	612(20)	24.6(15)	0.0561 .
Temperature	618(19)	5.82(1)	0.0158 *
Cloud	626(15)	13.5(5)	0.0190 *
Wind	622(19)	9.68(1)	0.00186 **
Flower Richness	626(19)	13.9(1)	< 0.001***
Tree Richness	587(35)	0.177(1)	0.674
Tree Abundance	587(36)	0.0506(1)	0.822

Flower Abundance	587(37)	0.0037(1)	0.952
Number of observers	587(38)	0.0856(1)	0.770

Table 3. Model of effects on bumblebee species abundance. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	257(13)	2.83 (5)	0. 0.726
Temperature	263(6)	0.022(1)	0.882
Cloud	261(8)	4.72 (5)	0.450
Wind	263. (7)	1.75 (1)	0.185
Flower Richness	265 (6)	2.84 (1)	0.0920 .
Tree Richness	273(4)	7.44 (1)	0.00639 **
Tree Abundance	254(18)	0.0081(1)	0.928
Flower Abundance	253 (19)	0.645 (1)	0.422
Number of observers	253(20)	9e-04(1)	0.976

Table 4. Model of effects on bumblebee species richness. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	177 (13)	2.62 (5)	0.759
Temperature	178 (6)	0.311 (1)	0.577

Cloud	177 (8)	0.435 (5)	0.994
Wind	178 (7)	1.04 (1)	0.308
Flower Richness	180 (5)	1.27 (1)	0.261
Tree Richness	182 (4)	2.00 (1)	0.157
Tree Abundance	174 (18)	0.0016 (1)	0.968
Flower Abundance	174 (19)	0.0142 (1)	0.905
Number of observers	174 (20)	0.122 (1)	0.726

Table 5. Model of effects on hover fly species abundance. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	222 (12)	33.0(5)	< 0.001***
Temperature	206(16)	17.1 (1)	< 0.001***
Cloud	216(12)	27.4 (5)	< 0.001***
Wind	201(16)	12.4 (1)	< 0.001***
Flower Richness	195(16)	6.08 (1)	0.0136 *
Tree Richness	189(17)	3.33 (1)	0.0679
Tree Abundance	185(18)	1.13(1)	0.287
Flower Abundance	185 (19)	0.775(1)	0.379
Number of observers	184 (20)	0.33(1)	0.856

Table 6. Model of effects on hover fly species richness. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	157 (12)	14.4 (5)	0.0135 *
Temperature	150 (16)	7.13 (1)	0.00758 **
Cloud	160 (12)	17.3 (5)	0.00395 **
Wind	149 (16)	6.56 (1)	0.0104 *
Flower Richness	148 (16)	5.75 (1)	0.0165 *
Tree Richness	143 (17)	0.675 (1)	0.411
Tree Abundance	142 (18)	0.612(1)	0.434
Flower Abundance	141 (19)	0.428 (1)	0.513
Number of observers	141 (20)	0.207 (1)	0.649

Table 7. Model of effects on Lepidoptera species abundance. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable.,*, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	152 (5)	9.59 (5)	0.0877
Temperature	157 (4)	4.26 (1)	0.039 *
Cloud	143 (10)	11.0 (5)	0.0510
Wind	132 (15)	0.146 (1)	0.702
Flower Richness	132 (17)	1.35 (1)	0.245
Tree Richness	132 (16)	0.407 (1)	0.523
Tree Abundance	132 (18)	0.161 (1)	0.688
Flower Abundance	132 (19)	0.0347 (1)	0.852
Number of observers	131 (20)	0.0098	0.921

Table 8. Model of effects on Lepidoptera species richness. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	136 (5)	8.46 (5)	0.132
Temperature	137 (4)	4.78 (1)	0.0288 *
Cloud	128 (10)	10.3 (5)	0.0662
Wind	117 (15)	0.0044(1)	0.947
Flower Richness	117 (16)	2.59 (1)	0.107
Tree Richness	116 (17)	0.0343(1)	0.853
Tree Abundance	115 (18)	2e-04 (1)	0.999
Flower Abundance	115 (19)	0.493 (1)	0.483
Number of observers	114 (20)	0.101 (1)	0.750

Table 9. Model of effects on Solitary bee species abundance. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	140 (10)	14.0 (5)	0.0157 *
Temperature	127 (15)	1.22 (1)	0.270
Cloud	148 (10)	13.1 (5)	0.0222*
Wind	140 (16)	1.51 (1)	0.218
Flower Richness	139 (14)	12.6 (1)	< 0.001***
Tree Richness	124 (17)	0.273 (1)	0.601

Tree Abundance	124 (18)	0.103 (1)	0.748
Flower Abundance	124 (19)	0.232 (1)	0.630
Number of observers	123 (20)	0.201 (1)	0.650

Table 10. Model of effects on Solitary bee species richness. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P valuie
Level	120 (10)	11.5 (5)	0.0421 *
Temperature	109 (15)	1.18(1)	0.278
Cloud	123 (10)	14.0 (5)	0.0156 *
Wind	108 (16)	0.773 (1)	0.379
Flower Richness	120 (14)	11.7 (1)	< 0.001***
Tree Richness	107 (17)	0.762 (1)	0.383
Tree Abundance	106 (18)	0.193 (1)	0.660
Flower Abundance	106 (19)	0.377 (1)	0.539
Number of observers	106 (20)	0.968 (1)	0.325

Table 11. Model of effects on honey bee species abundance. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total species richness of pollinators as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, sampling number. quasipoisson error structure was used for the model. R function used = glmer.nb

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	170 (13)	6.25 (5)	0.282
Temperature	184 (11)	14.4 (1)	< 0.001***

Cloud	185 (7)	14.7 (5)	0.0115 *
Wind	170 (12)	0.173 (1)	0.677
Flower Richness	178 (11)	1.05 (1)	0.0499 *
Tree Richness	174 (18)	3.85 (1)	0.699
Tree Abundance	164 (19)	0.338 (1)	0.560
Flower Abundance	163 (20)	0.233 (1)	0.629
Number of observers	177 (11)	6.44 (1)	0.0112 *

Table 12. Model of effects on number of pupa per nest. Statistical test values for the stepwise removal of parameter terms from generalised linear mixed effects model with total number of pupa as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, nest. Gaussian error structure was used for the model. R function used = lmer

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Sex	666 (6)	8.84 (1)	0.00296 **
Level	658 (5)	9.36 (5)	0.0956
Number of emerged Adults	649 (10)	3.79 (1)	0.0514
Level:Sex	644 (11)	4.16 (5)	0.527

Table 13. Model of effects on weight of pupa. Statistical test values for the stepwise removal of parameter terms from general linear mixed effects model with weight of pupa as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, nest, nesting tube. Gaussian error structure was used for the model. R function used = Imer

Term	Residual Deviance(df)	F value(df)	P value
Sex	- 3040 (5)	808 (1)	< 0.001***
Level	- 3850(6)	4.34 (5)	0.501
Level:Sex	- 3850 (11)	4.48 (5)	0.483

Table 14. Model of effects on sex ratio of pupa. Statistical test values for the stepwise removal of parameter terms from general linear mixed effects model with a multi-binomial matrix of males-females as the response variable. *, **, *** indicates no significance or significance of the term at the level of 0.05, 0.01 and 0.001, respectively. Nested terms accounted for in the model included, site, nest, nesting tube. binomial error structure was used for the model. R function used = glmer

Term	Residual Deviance(df)	Chi-squared value(df)	P value
Level	457 (4)	3.00 (5)	0.699



Figure 10. Pupa weight mean ± standard error grouped by site ID, nest ID and tube ID. across the gradient of landscape scale urbanisation from sites surrounded by landscape of high urbanisation (dark purple) to low urbanisation (dark green). Description of landscape composition for each urban level; 1=majority urban, 2=majority suburban, 3=suburban/grassland mix, 4=suburban/tree cover mix, 5= majority grassland, 6=majority greenspace with tree cover.



Figure 11. Mean \pm standard error of flowering plant species richness and tree species richness across the gradient of landscape scale urbanisation, from local floral resource observations. Description of landscape composition for each urban level; 1 = majority urban, 2 = majority suburban, 3 = suburban+grassland mix, 4 = suburban+tree cover mix, 5 = majority grassland, 6 = majority greenspace with tree cover.

Table 15. Number of Tree and Flowering plant species surveyed within 5m radius of site centres. Frequency refers to the frequency the species was surveyed across all sites.

Туре	Genus	Species	Frequency
Flower	Achillea	millefolium	2
Flower	Ajuga	reptans	1

Flower	Alliara	petiolata	5
Flower	Allium	cristophii	10
Flower	Allium	giganteum	7

Flower	Allium	unifolium	1
Flower	America	Maritima	1
Flower	Anthriscus	sylvestris	33
Flower	Aquilegia	vulgaris	10
Flower	Arabidopsis	thaliana	2
Flower	Armeria	maritima	1
		splendens	
Flower	Aubrieta	deltoidea	1
Flower	Barabarea	vulgaris	31
Flower	Begonia	sp.	2
Flower	Bellis	perennis	138
Flower	Buddleja	davidii	2
Flower	Calystegia	sepium	41
Flower	Campanula	persicifolia	12
Flower	Campanula	trachelium	2
Flower	Cardamine	flexuosa	12
Flower	Cardamine	sp.	46
Flower	Centaurea	cyanus	4
Flower	Cerastium	fontanum	508
Flower	Cerastium	glomeratum	7
Flower	Cerastium	sp.	36
Flower	Choisya	ternata	1
Flower	Circaea	lutetiana	4
Flower	Cirsium	arvense	21
Flower	Cistus	x purpureus	1
Flower	Clematis	sp.	2
Flower	Cotoneaster	horizontalis	5
Flower	Crataegus	crusgalli	1
Flower	Crataegus	laevigata	1
Flower	Crepis	capillaris	36
Flower	Dianthus	chinensis	2
Flower	Dianthus	sp.	1
Flower	Digitalis	purpurea	1
Flower	Diplotaxis	muralis	1
Flower	Epilobium	montanum	17
Flower	Epilobium	roseum	1
Flower	Erigeron	canadensis	1
Flower	Erigeron	karvinskianus	9
Flower	Eschscholzia	californica	6

Flower	Euphorbia	sp.	1
Flower	Felicia	amelloides	1
Flower	Filipendula	ulmaria	11
Flower	Fragaria	x ananassa	1
Flower	Fraxinus	excelsior	1
Flower	Fuchsia	magellanica	4
Flower	Galium	aparine	99
Flower	Geranium	columbinum	4
Flower	Geranium	lucidum	1
Flower	Geranium	maculatum	135
Flower	Geranium	pusillum	351
Flower	Geranium	robertianum	43
Flower	Geranium	rosanne	1
Flower	Geranium	sp.	8
Flower	Geranium	versicolor	1
Flower	Geum	urbanum	300
Flower	Hemerocallis	fulva	2
Flower	Heracleum	sphondylium	13
Flower	Heuchera	micrantha	8
Flower	Hibiscus	syriacus	1
Flower	Hieracium	sp.	10
Flower	Hosta	sp.	1
Flower	Hyacinth	x massartiana	58
Flower	Hypericum	sp.	21
Flower	Hypericum	tetrapterum	1
Flower	Hypochaeris	radicata	4
Flower	Iberis	sempervirens	11
Flower	Impatiens	walleriana	54
Flower	Impatients	sodenii	1
Flower	Jasminum	sp.	1
Flower	Lactuca	virosa	2
Flower	Lamium	album	24
Flower	Lamium	purpurea	9
Flower	Lamprocapnos	spectabilis	1
Flower	Lapsana	communis	1
Flower	Lavandula	sp.	11
Flower	Leucanthemum	sp.	6
Flower	Lobellia	erinus	1
Flower	Lonicera	hispidula	1

Flower	Lupinus	sp.	2
Flower	Lysimachia	nummularia	10
Flower	Lysimachia	vulgaris	12
Flower	Magnolia	sp.	2
Flower	Meconopsis	cambrica	11
Flower	Mycelis	muralis	12
Flower	Myosotis	secunda	17
Flower	Myosotis	sp.	127
Flower	Myosotis	sylvatica	44
Flower	Nemesia	sp.	18
Flower	Oxalis	corniculata	21
Flower	Papaver	rhoeas	2
Flower	Pelargonium	x hortorum	55
Flower	Penstemon	sp.	3
Flower	Pentaglottis	sempervirens	24
Flower	Petunia	sp.	6
Flower	Phlox	paniculata	6
Flower	Phlox	sp.	1
Flower	Plantago	lanceolata	114
Flower	Primula	sp.	10
Flower	Prunella	vulgaris	226
Flower	Ranunculus	acris	170
Flower	Ranunculus	repens	186
Flower	Rorippa	nasturtium-	25
		aquaticum	
Flower	Rosa	carnina	3
Flower	Rosa	frymincot	1
Flower	Rosa	sp.	10
Flower	rubus	fruiticosus	1
Flower	Rubus	fruiticosus	168
Flower	Rubus	idaeus	2
Flower	Salvia	sp.	1
Flower	Salvia	verbenaca	2
Flower	Salvia	x jamensis	2
Flower	Saponania	acymoides	1
Flower	Saxifraga	x urbium	78
Flower	Sedum	spathulifolium	1
		pruprureum	
Flower	Senecio	jacobaea	9

Flower	Senecio	vulgaris	14
Flower	Silene	hampeana	2
Flower	Sisymbrium	officinale	10
Flower	Solanum	glasnevin	1
Flower	Solanum	lycopersicum	2
Flower	Solanum	sp.	18
Flower	Sonchus	arvensis	1
Flower	Sonchus	asper	1
Flower	Sonchus	oleraceus	2
Flower	Sonchus	sp.	3
Flower	Spiraea	japonica	2
Flower	Stachys	sylvatica	10
Flower	Stylophorum	diphyllum	1
Flower	Symphoricarpos	albus	2
Flower	Tagetes	sp.	3
Flower	Tanacetum	vulgare	5
Flower	Taraxacum	sp.	81
Flower	Trifolium	dubium	378
Flower	Trifolium	pratense	1
Flower	Trifolium	repens	190
Flower	Ulex	europaeus	2
Flower	Unknown	Unknown	12
Flower	Valerianella	locusta	35
Flower	Verbascum	thapsus	2
Flower	Veronica	arvensis	30
Flower	Veronica	chamaedrys	98
Flower	Veronica	serpyllifolia	91
Flower	Veronica	sp.	24
Flower	Vicia	hirsuta	6
Flower	Vicia	sativa	25
Flower	Vicia	villosa	1
Flower	Viola	x wittrockiana	23
Flower	Weigela	sp.	2
Flower	Wisteria	macrostachya	1
Flower	Wisteria	sp.	1
Flower	Zantedeschia	aethiopica	8
Flower	NA	NA	0
Tree	Acer	campestre	2
Tree	Acer	pseudoplatanus	2

Tree	Acer	sp.	2
Tree	Aesculus	hippocastanum	2
Tree	Alnus	glutinosa	2
Tree	Aucuba	sp.	2
Tree	Betula	pendula	34
Tree	Buddleja	davidii	4
Tree	Carpinus	betulus	2
Tree	Chamaecyparis	lawsoniana	20
Tree	Corylus	avellana	2
Tree	Cotoneaster	salicifolius	2
Tree	Crataegus	laevigata	12
Tree	Crataegus	oxyacantha	2
Tree	Fagus	sylvatica	2
Tree	Ficus	carica	2
Tree	Fraxinus	excelsior	4
Tree	llex	aquifolium	2

Tree	llex	canariensis	2
Tree	Laburnum	anagyroides	2
Tree	Leylandii	sp.	2
Tree	Ligustrum	ovalifolium	18
Tree	Malus	sp.	2
Tree	Pinus	sylvestris	8
Tree	Populus	x canadensis	2
Tree	Prunus	avium	16
Tree	Quercus	robur	16
Tree	Salix	alba	8
Tree	Sambucus	nigra	2
Tree	Syringa	vulgaris	5
Tree	Taxus	baccata	2
Tree	Tilia	cordata	2
Tree	Unknown	Unknown	2
Tree	NA	NA	0

Table 16. Number of Pollinator species surveyed within 5m radius of site centres. Frequency refers to the frequency the species was surveyed across all sites.

Group	Genus	Species	Count
Bombus	Bombus	campestris	1
Bombus	Bombus	hortorum	3
Bombus	Bombus	hypnorum	79
Bombus	Bombus	lapidarius	5
Bombus	Bombus	pascuorum	19
Bombus	Bombus	pratorum	26
Bombus	Bombus	sylvestris	2
Bombus	Bombus	terrestris/lucoru	62
		m	
Bombus	Bombus	Unknown	18
Bombus	Unkown	Unknown	9
Honeybee	apis	mellifera	1
Honeybee	Apis	mellifera	98
Hoverfly	Chrysotoxum	Unknown	1
Hoverfly	Milesia	craboniformis	1
Hoverfly	Unkown	Unknown	138

Hoverfly	Volucella	bombylans	5
Lepidoptra	Aphantopus	hyperantus	7
Lepidoptra	Artogeia	rapae	4
Lepidoptra	Inachis	io	1
Lepidoptra	Lampronia	Unknown	1
Lepidoptra	Leptidae	sinapis	1
Lepidoptra	Maniola	jurtina	3
Lepidoptra	Melanargia	galathea	1
Lepidoptra	Pararge	aegeria	1
Lepidoptra	Pieris	brassicae	3
Lepidoptra	Pieris	napi	1
Lepidoptra	Pieris	rapae	1
Lepidoptra	Unkown	Unknown	29
Lepidoptra	Vanessa	atalanta	2
Solitary	Andrena	minutula	1
Solitary	Andrena	sp.	2
Solitary	Andrena	Unknown	2

Solitary	Halictus	rubicundus	1
Solitary	Megachile	sp.	4
Solitary	Nomada	marshamella	3
Solitary	Nomada	sp.	4

Solitary	Osmia	bicornis	17
Solitary	Osmia	leaiana	2
Solitary	Unkown	Unknown	19