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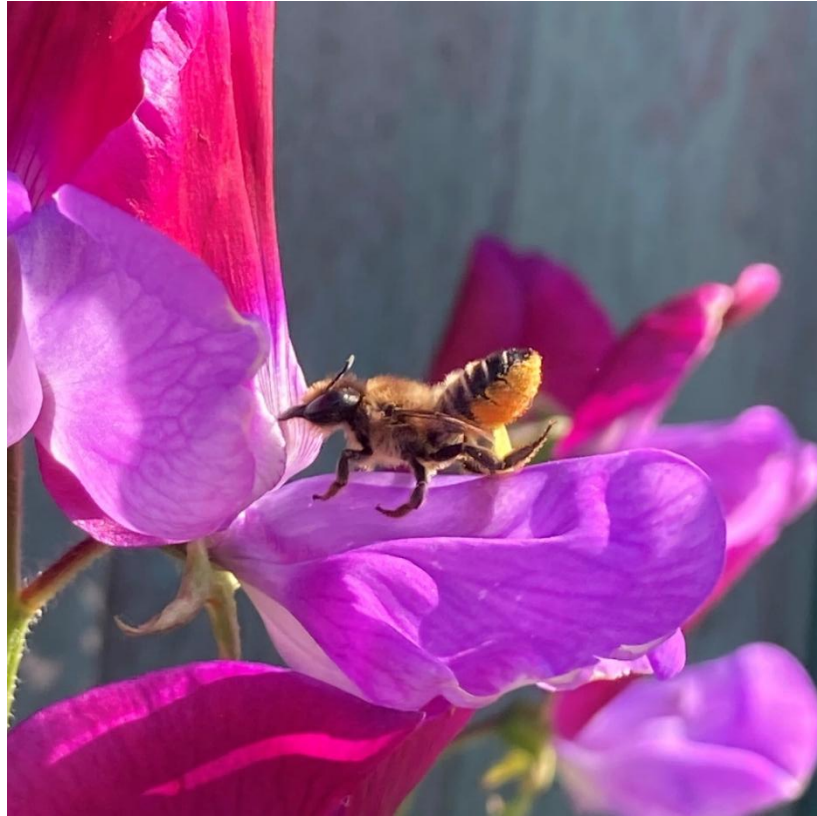
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Investigating pollinator diversity, traits, and interaction networks among urban green spaces

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Megachile centuncularis visiting *Lathyrus odoratus* in an allotment in Glasgow, Scotland

Submitted in fulfilment of the requirements for the Degree
of Doctor of Philosophy

School of Biodiversity, One Health and Veterinary Medicine

College of Medicine, Veterinary and Life Sciences

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Abstract

Global urbanisation raises concerns for biodiversity due to the negative impact on a range of taxa including invertebrate pollinators. However, cities may be hotspots for certain species, including some species of conservation relevance. Urban areas are characterised by a mosaic of land use types that range in their value as pollinator habitats. Private green spaces, such as gardens and allotments, offer great conservation potential due to the proportionally large area they cover and their high floral abundance. Management of these privately owned spaces varies and therefore understanding how these green spaces support pollinator diversity, their interactions with plants, and their functional traits are knowledge gaps critical to informing their future management.

In this thesis I have assessed the environmental drivers of pollinator diversity, plant-pollinator interaction networks, and trait assembly within gardens and allotments across Glasgow, Scotland. I collected data in 18 gardens and 8 allotment sites across two years, where I used cameras and visual observations to record plant-flower visitor interactions by bees, hoverflies and butterflies. Alongside this I also collected local and landscape level environmental data.

Results showed no effect of green space type on pollinator diversity or plant-flower visitor network structure. However, I found four key patterns. 1) Greater floral richness supported higher pollinator diversity. 2) Native plants received more flower visits; however non-native plants were still important forage for flower visitors particularly later in the season. 3) Floral richness was positively associated with network specialisation. 4) No evidence of trait filtering was revealed at the urban green space scale but did occur at the regional-city interface. This regional-city filtering may be indicated by the high prevalence of *Bombus pascuorum* in the city which was responsible for 25% of all flower visits, suggesting that generalist species are dominant within Glasgow's pollinator community.

Together, these results suggest that management interventions within gardens and allotments can support greater pollinator diversity through increases in floral richness. However, these strategies may only support greater taxonomic diversity, rather than directly increasing functional diversity. As such, I suggest management interventions should be implemented at broader spatial scales to facilitate the movement of pollinators surrounding cities into the core urban

area. Gardens could offer the opportunity to scale up pollinator conservation interventions across urban environments, given that gardens contribute to approximately 30% of green space within cities.

Table of Contents

Abstract	ii
Table of Contents	iv
List of Tables	vi
List of Figures	vii
List of Accompanying Material	viii
Acknowledgement	ix
Author's Declaration	x
Chapter 1 Introduction.....	1
Urbanisation.....	1
Green spaces in cities.....	1
Urbanisation and pollinator diversity.....	5
Urbanisation and pollinator traits.....	18
Plant-pollinator networks.....	21
Knowledge gaps and thesis aims.....	32
Chapter 2 Visual observations are more effective than cameras for recording flower visits	35
Abstract	35
Introduction.....	35
Methods	38
Data analysis.....	44
Results	44
Discussion.....	50
Conclusion	54
Chapter 3 Supporting pollinators in urban gardens: floral richness and abundance influence flower visitor interactions regardless of the surrounding landscape	56
Abstract	56
Introduction.....	56
Methods	59
Data analysis.....	63
Results	66
Discussion.....	78
Conclusions	82

Chapter 4 Floral richness drives flower-insect networks in city gardens and allotments ...	84
Abstract	84
Introduction.....	85
Methods	87
Data analysis.....	93
Results	95
Discussion.....	105
Conclusion	110
Chapter 5 Pollinator community assembly in urban green spaces is shaped by trait filtering at broader spatial scales.....	112
Abstract	112
Introduction.....	113
Methods	116
Data analysis.....	120
Results	122
Discussion.....	130
Conclusion	134
Chapter 6 Discussion	135
Summary of research findings	135
Biodiversity in cities.....	136
Environmental drivers of pollinator diversity.....	137
Plant-pollinator networks.....	140
Pollinator traits.....	141
Implications for pollinator conservation and policies	142
Limitations and future work.....	143
Conclusion	144
Appendices.....	145
Appendix A: Supplementary material for chapter 1	145
Appendix B: Supplementary material for chapter 2	146
Appendix C: Supplementary material for chapter 3	155
Appendix D: Supplementary material for chapter 4	168
Appendix E: Supplementary material for chapter 5	197
List of References	219

List of Tables

Table 1.1: Land cover in cities	3
Table 1.2: Environmental drivers of network indices	24
Table 2.1: Sample sites.....	39
Table 2.2: Network indices for cameras and visual observations	46
Table 2.3: Final models for cameras and visual observation methods	50
Table 3.1: Final model results for flower visits and network indices.....	68
Table 3.2: Flower visitor plant preferences.....	77
Table 4.1: Environmental variables in gardens and allotments	95
Table 4.2: Flower visitor plant preferences.....	104
Table 5.1: Bee and hoverfly traits	119
Table 5.2: Community weighted means in urban and regional pollinators	129

List of Figures

Figure 1.1: Land cover maps in five Scottish cities.....	4
Figure 1.2: Green space cover in five Scottish cities	5
Figure 1.3: Network nestedness diagram	22
Figure 1.4: Network modularity diagram	23
Figure 1.5: Network specialisation diagram	23
Figure 2.1: Field sampling locations	39
Figure 2.2: Camera set up in the field	42
Figure 2.3: Flower visitor stills from cameras.....	45
Figure 2.4: Comparison of flower visits between cameras and visual observations	47
Figure 2.5: Example networks from cameras and visual observations.....	E48
Figure 2.6: Comparison of network indices between cameras and visual observations.....	49
Figure 3.1: Seasonal floral resource availability	70
Figure 3.2: Floral abundance, plant origin and flower visits.....	72
Figure 3.3: Seasonal flower visits by <i>Bombus pascuorum</i>	73
Figure 3.4: Flower visitor community dissimilarity.....	75
Figure 3.5: Seasonal differences in network indices	76
Figure 4.1: Field sampling locations	89
Figure 4.2: Seasonal floral resource availability	97
Figure 4.3: Environmental drivers of flower visits.....	99
Figure 4.4: Environmental drivers of flower visitor richness.....	101
Figure 4.5: Environmental drivers of network indices	103
Figure 4.6: Patterns in visits to crop plants	105
Figure 5.1: Field sampling locations	117
Figure 5.2: Species responses to environmental drivers.....	124
Figure 5.3: Variance partitioning of environmental drivers for species occurrence	126
Figure 5.4: Species co-occurrence patterns	129

List of Accompanying Material

Table A.1: Definitions of 18 green space categories from OS MasterMap.	145
Table B.1: Urban land use definitions from Copernicus Urban Atlas.	146
Table B.2: Flower visitors from visual observations.....	148
Table B.3: Flower visitors from camera.....	150
Table B.4: Plant species list	151
Table C.1: Flower visitor species list	156
Table C.2: Plant species list	158
Table C.3: Plant preferences by pollinators.....	162
Table C.4: Optimal models.....	166
Table D.1: Garden and allotment plot details	168
Table D.2: Plant species list	169
Table D.3: Flower visitor species list.....	180
Table D.4: Final model results table	182
Table D.5: Model AIC values	185
Table D.6: Flower visitor plant preferences.....	187
Table E.1: Urban bee and hoverfly species list from garden and allotments....	207
Table E.2: Urban pollinator species collated from the NBN Atlas.....	209
Table E.3: Model WAIC scores	213
Table E.4: Regional species list for bees and hoverflies.....	214

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Author's Declaration

I certify that the thesis presented here for examination for PhD degree of the University of Glasgow is solely my own work other than where I have clearly indicated that it is the work of others (in which case the extent of any work carried out jointly by me and any other person is clearly identified in it) and that the thesis has not been edited by a third party beyond what is permitted by the University's PGR Code of Practice.

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I declare that this thesis has been produced in accordance with the University of Glasgow's Code of Good Practice in Research. I acknowledge that if any issues are raised regarding good research practice based on review of the thesis, the examination may be postponed pending the outcome of any investigation of the issues.

Publications and co-author declarations:

- Chapter 2, Cameras record fewer insect visitors but reveal similar plant-pollinator networks to visual observations, was co-authored by Dominic McCafferty, Davide Dominoni and Ria Dunkley. This chapter is in preparation for Ecology and Evolution.
- Chapter 3, Supporting pollinators in urban gardens: floral richness and abundance influence flower visitor interactions regardless of the surrounding landscape, was co-authored by Dominic McCafferty, Davide Dominoni and Ria Dunkley. This chapter was published in the Journal of Urban Ecosystems on 14/11/2025. DOI: 10.1007/s11252-025-01848-7
- Chapter 4, Floral richness drives flower-insect networks in city gardens and allotments, was co-authored by Dominic McCafferty, Davide Dominoni, Ria Dunkley and William McGhee. Chapter 4 is under review in the Journal of Ecological Entomology.
- Chapter 5, Pollinator community assembly in urban green spaces is shaped by trait filtering at broader spatial scales was co-authored by Dominic

McCafferty, Davide Dominoni, Ria Dunkley, William McGhee and Juan Morales. This chapter is in preparation for Ecology Letters

I confirm that I was responsible for the majority (95%) of the work in all chapters, with co-authors either providing supervision, editing or help with data collection.

Chapter 1 Introduction

This chapter introduces the concept of urbanisation in the context of its effects on pollinator diversity. To explore this topic in depth, I review the literature to address the following aims:

- 1) Assess the impact of urbanisation on pollinator diversity in studies using urbanisation gradients.
- 2) Investigate whether urban green space type influences pollinator diversity.
- 3) Determine environmental drivers that influences urban pollinator diversity.
- 4) Evaluate which pollinator traits play a role in determining a species' ability to cope with urban environmental drivers.
- 5) Assess how urbanisation may influence plant-pollinator network structures.

Alongside these aims, I mapped urban land uses across 5 Scottish cities to provide a broader understanding of our study location, Glasgow and assess how it compares to other cities. This mapping also provides insight into the importance of considering the urban habitat matrix when assessing urban pollinator diversity.

Urbanisation

Urbanisation is the process by which natural landscapes are converted to those dominated by impervious surfaces coinciding with higher human density in these areas (Moll et al., 2019; United Nations, 2019). Since 1950, the proportion of the global population living in cities has risen from 20% of to 40% in 2025. Moreover, between 1975 and 2025, the extent of urban areas grew twice as fast as the population growth (United Nations, 2025). This rapid expansion is of particular concern due to the potential negative effects of urbanisation on biodiversity. Amid ongoing global biodiversity loss, it is important to understand the impacts of urbanisation on species to better inform conservation.

Green spaces in cities

Urban green spaces form an integral part of green infrastructure within cities. While no single definition of urban green space exists, the term can be broadly defined as either a) green space as synonymous with nature or b) green space as explicitly urban vegetation (Taylor and Hochuli, 2017). Urban population growth and increasing population densities place urban green spaces at risk of reduction. These spaces provide valuable ecosystem services, including the regulation of ambient air temperature and the reduction of air particulate matter,

processes that become more critical as urban densification increases congestion and pollution (Gómez-Baggethun et al., 2013). In addition, green spaces can increase human physical and mental wellbeing by offering opportunities for physical exercise, social interactions and exposure to nature (Pinto et al., 2022). Biodiversity is integral to the ecosystem services provided by green spaces, with greater biodiversity associated with increased ecosystem functioning (McDonald et al., 2013).

Globally, urban green spaces are unevenly distributed. A study of the world's capital cities found that cities in Central America and Europe had higher levels of green space land cover, compared to cities in Africa and Asia (Bille et al., 2023). In particular, cities in the Global South, characterised by high population densities and lower development indices, tended to have lower green space coverage (Bille et al., 2023). However, Bille et al. (2023), used broad land cover classifications to categorise green spaces, which simplified built-up areas into a single land use category. In reality, urban environments consist of various land uses, including small green spaces such as private residential gardens.

Although collectively urban green spaces contribute to habitat and resource provision for organisms, in an otherwise impervious landscape, their ecological value is not uniform. Amongst other factors, management of green spaces can play an important role in determining habitat quality in different green spaces. For example, mowing frequency, planting of native or non-native plants, pesticide use and vegetation structure can all influence the availability of floral and nesting resources for pollinators (Llodrà-Llabrés and Cariñanos, 2022). However, some green spaces are designed and maintained for specific functions such as recreational activities, resulting in trade-offs with biodiversity benefits (Llodrà-Llabrés and Cariñanos, 2022; Miguez et al., 2025). For example, urban green spaces often consist of highly manicured lawns, with lower biodiversity than meadows, helping to provide space for recreational activities (Paudel and States, 2023). Therefore, the proportion of different green space types within an urban area likely influences the capacity of a city to support pollinator communities. Mapping and comparing the distribution of green space types across cities therefore provides an important context for understanding variation in pollinator habitat potential. Below I map 18 green space types, as defined by the OS MasterMap (Ordnance Survey (GB), 2025), in the five major Scottish cities.

Distribution of urban green spaces in five Scottish cities

I assessed the contribution of 18 urban green spaces to land cover within Edinburgh, Glasgow, Stirling, Dundee and Aberdeen. To do this, I used the green space layer from the OS MasterMap (Ordnance Survey (GB), 2025) which defines green spaces as all public and private green spaces within an urban area, for which polygons were given specific attributes that relate to their function. The functions attributed to green space polygons in the green space layer categorise green space type, the definitions of which can be seen in (Appendix A, Table A.1). I used council boundaries to define the city area, which for Stirling Council, encompassed a greater area than Stirling City itself. Green spaces were mapped using QGIS version 3.40.8 (QGIS Development Team, 2026) (Fig.1.1 a-e).

I used the Topography Layer within the Ordnance Survey OS MasterMap to classify all remaining land use not identified as urban green space. From this dataset, grey space (impervious surface) polygons were separated from natural land cover. I defined grey space as all manmade structures associated with transport infrastructure (e.g. rail and road networks) and buildings. Land not defined as grey space was categorised as other land use. Finally, grey space and other land use polygons that lacked descriptive terms were removed from the analysis. Overall, the combined mapping of urban green space, grey space and other land use accounted for 98.2% of Aberdeen City Council, 99.9% of Stirling Council, 98.7% of Dundee City Council, 94.5% of Glasgow City Council and 95.2% of Edinburgh City Council (Table 1.1).

The proportion of green space within city boundaries ranged from 4.1% to 55.7%. Grey space consistently represented a smaller proportion of the total city area ranging from 1.5% to 31.7%. In contrast, other land use exhibited the greatest variation, comprising between 7.1% to 94.3% of the total city boundaries (Table 1.1).

Table 1.1: Total area of land cover (green space, grey space and other land use) km² and as a percentage of the area of each Scottish City Council. The area of each council is provided.

City	Total green space km ² (% of total area)	Total grey space km ² (% of total area)	Other land use area km ² (% of total area)	City council area km ²
Glasgow	97.36 (55.7%)	55.32 (31.7%)	12.38 (7.1%)	174.65
Edinburgh	99.01 (37.6%)	45.18 (17.2%)	106.56 (40.5%)	263.35

Aberdeen	65.06 (35.1%)	27.85 (15.0%)	89.31 (48.1%)	185.56
Stirling	92.48 (4.1%)	33.07 (1.5%)	2123.94 (94.3%)	2252.60
Dundee	33.12 (55.4%)	15.82 (26.5%)	10.11 (16.9%)	59.81

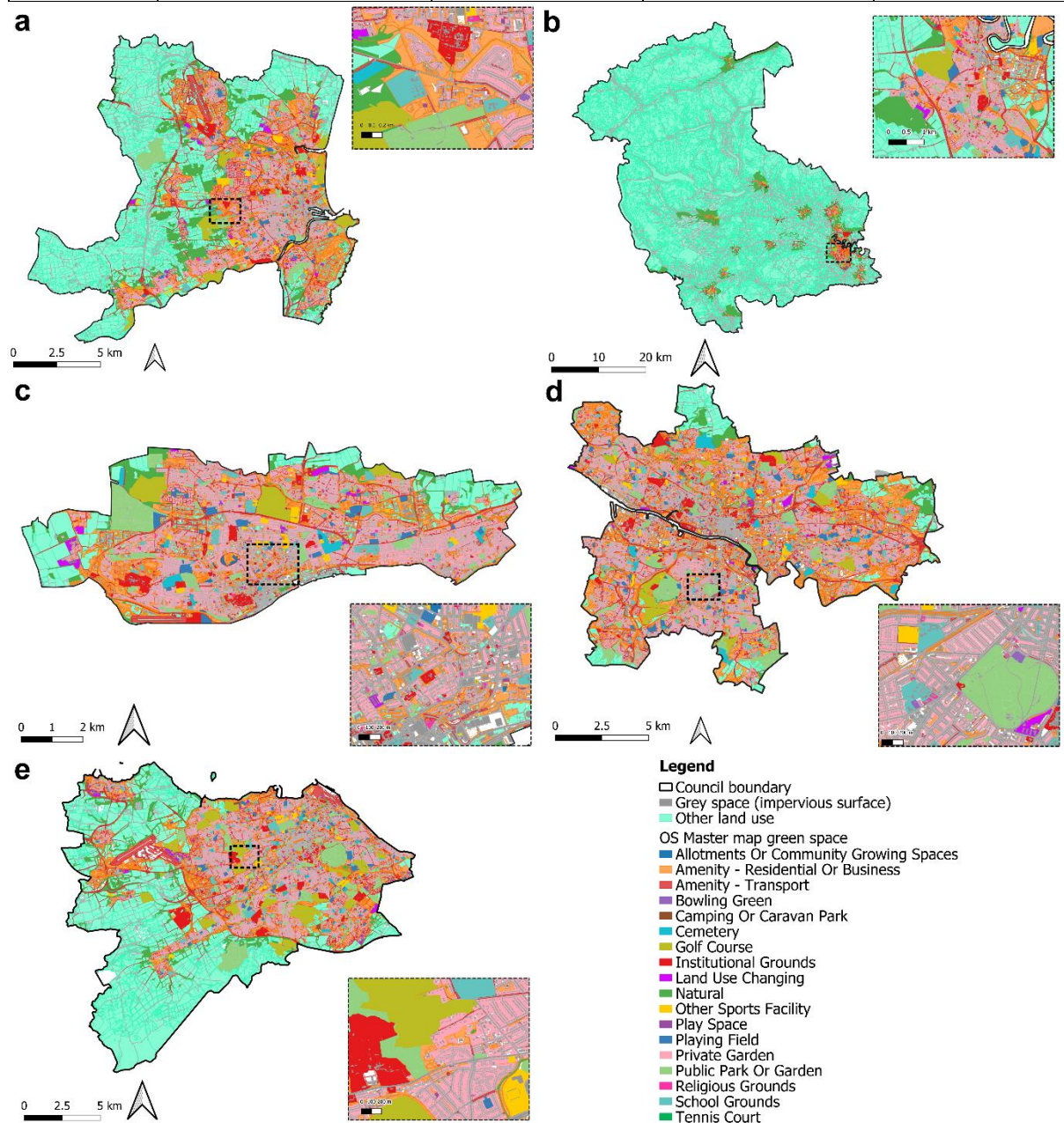


Figure 1.1: The distribution of land cover, across a) Aberdeen, b) Stirling, c) Dundee, d) Glasgow and e) Edinburgh. 18 urban green space types are mapped within each city from the green space layer in OS MasterMap, alongside grey space (impervious surface associated with transport and infrastructure), and other land use (non-manmade surfaces or green spaces from the topography layer in OSMasterMap). Rectangles to the right of each city show overviews within the core urban areas at higher resolution.

In four out of five cities, private residential gardens contributed to the largest proportion of land cover (mean $\pm$ SD: 28.2% $\pm$ 9.3%) (Fig.1.2a) which equated to a mean area of 20.9km² $\pm$ 0.1km² (Fig.1.2b). In contrast, natural green space

represented the largest proportion of green space in Stirling Council area. Amenity (residential or business) was the second largest proportion of green space in four cities ($18.9\% \pm 7.0\%$, $14.4\text{km}^2 \pm 8.2\text{km}^2$). Again, Stirling differed from other cities with private residential gardens contributing to the second largest proportion of green space. Public parks were the next largest proportion of green space for four of the five cities ($9.9\% \pm 4.6\%$, $7.7\text{km}^2 \pm 5.4\text{km}^2$). Multiple types of green spaces covered less than 1% of a cities green space, these were religious grounds ($0.3\% \pm 0.09$, $0.2\text{km}^2 \pm 0.1\text{km}^2$), allotments or community growing spaces ($0.3\% \pm 0.1$, $0.2\text{km}^2 \pm 0.1\text{km}^2$), bowling greens ($0.1\% \pm 0.09$, $0.1\text{km}^2 \pm 0.1\text{km}^2$), play spaces ($0.1\% \pm 0.06$, $0.08\text{km}^2 \pm 0.04\text{km}^2$), camping or caravan parks ($0.07\% \pm 0.09$, $0.06\text{km}^2 \pm 0.08\text{km}^2$) and tennis courts ($0.04\% \pm 0.01$, $0.03\text{km}^2 \pm 0.01\text{km}^2$).

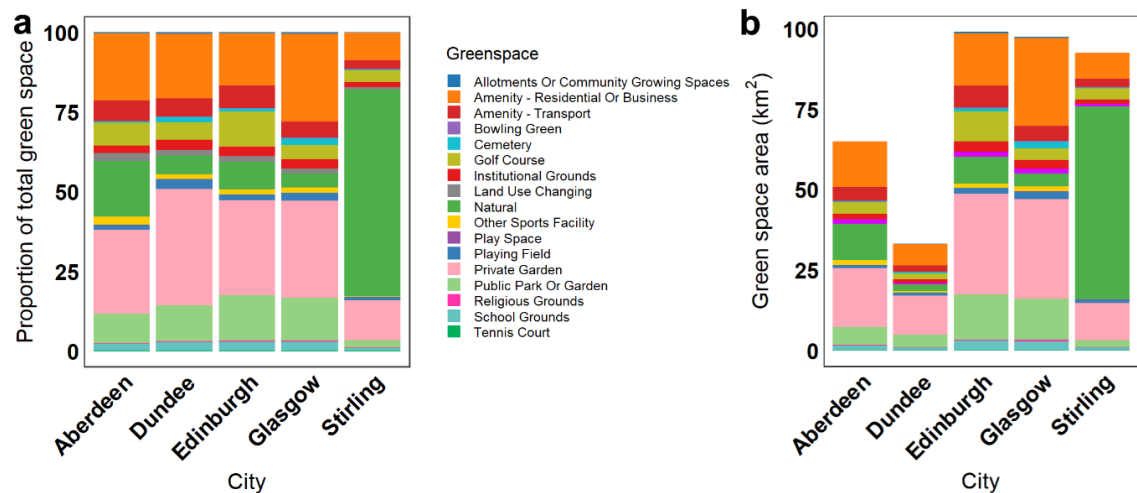


Figure 1.2: Contribution of different green space types, defined by the OS MasterMap, to land cover in cities presented as a) the proportion of total green space in that city and b) the total area of each green space (km²) in each city.

Overall, the mapping of green spaces in these five Scottish cities demonstrates the heterogeneous nature of urban landscapes. If green space types support different pollinator communities, this may increase beta diversity among different urban green spaces and, in turn, contribute to greater pollinator diversity across the urban landscape. This raises an important consideration; the varied land use types within cities should be accounted for when considering the effects of urbanisation on pollinator diversity. For example, the substantial proportion of gardens within cities could mean that these spaces are valuable in maintaining pollinator diversity. However, gardens are privately managed, and their

management may be related to the habitat quality they provide. Allotments are similarly managed by individuals; however, they cover less than 1% of green space within a city. Despite their limited spatial extent, allotments may nevertheless provide important habitat for pollinators and contribute to overall pollinator diversity within cities.

Urbanisation and pollinator diversity

As major providers of ecosystem services through their contribution to plant reproduction, pollinators provide key ecosystem services, and therefore there is a need to understand factors influencing their populations, including urbanisation (Klein et al., 2007; Ollerton et al., 2011). As with other taxonomic groups, the relationship between urbanisation and pollinator diversity is nuanced. Ensuring high diversity is maintained across different pollinating taxa is vital to ecosystem functioning, and as such the ecosystem services we gain through pollination. Compared to agricultural areas, it has been suggested that urban pollinator diversity can be relatively high due to the homogenous nature of agricultural landscapes. Therefore, cities could hold greater potential for pollinator conservation compared to farming landscapes.

Pollinator diversity across urbanisation gradients

Studies assessing the effect of urban gradients on pollinator diversity commonly compare discrete land use categories such as urban, rural, natural and farmland (Baldock et al., 2015; Banaszak-Cibicka et al., 2018; Desaegher et al., 2017; Luder et al., 2018; Theodorou et al., 2020c; Udy et al., 2020). Rural sites are often characterised by agricultural land and small villages with relatively low levels of impervious surfaces (Theodorou et al., 2020c). In urban-rural studies, rural sites are selected to be a minimum distance from urban sites (Theodorou et al., 2020c). Across these studies results suggest that responses to urbanisation are taxon specific. For example, higher bee diversity has been reported in urban areas, whilst greater hoverfly diversity has been recorded in farmland (Baldock et al., 2015; Udy et al., 2020). However, Banaszack-Cibicka et al. (2018) reported comparable bee diversity between city parks and a natural area, although this study was conducted at a small spatial scale, limiting broader inference. Larger scale studies have revealed more consistent trends. Baldock et al. (2015) conducted pollinator sampling in 12 UK cities, and results were supported by

Theodorou et al. (2020b) who compared urban and rural sites across nine German cities. Here, Theodorou et al. (2020b) found lower species richness in insects within cities, but higher bee species richness when compared to rural areas. Similarly, Baldock et al. (2015) found higher bee species richness in urban compared to farmland areas, whereas hoverfly abundance was lowest in urban sites. Variation in how land use categories can be defined may lead to differences in patterns of pollinator diversity. For example, Birdshire et al. (2020) used discrete urban and rural categories of sites alongside extracting the percentage of impervious surface for each site given that some rural areas contain low levels of impervious surface. Here, bee diversity decreased from rural to urban areas.

In contrast to categorical land use comparisons, urbanisation can be quantified along continuous gradients of impervious surface cover. In these studies, sites with low impervious surface cover are usually located outwith a city and may encompass natural, agricultural or rural landscapes (Biella et al., 2022; Fortel et al., 2014). Results from both Fortel et al. (2014) and Biella et al. (2022), found that bee diversity was highest at intermediate levels of impervious surface. Additionally, gradients of increasing impervious surface cover can be used when assessing pollinator diversity within urban habitats (Bennett and Lovell, 2019; Burdine and McCluney, 2019a; Herrmann et al., 2023; Theodorou et al., 2020b). For example, Herrmann et al. (2023a), investigated pollinator diversity in urban grasslands in Belin, Germany, and found bee and butterfly species richness reduced with increased impervious surface cover.

Other gradients have also been used to quantify urbanisation (Gerner and Sargent, 2022; MacInnis et al., 2023). Gerner and Sargent (2022), used a combination of impervious surface cover and tree canopy cover as the study gradient due to potential confounding effects of these variables. Furthermore, MacInnis et al., (2023), used a gradient of honeybee abundance within the city of Montreal (Canada) and found that wild bee richness was negatively associated with honeybee abundance, but not impervious surface. Finally, increases along a gradient of human density had a stronger negative effect on butterfly occurrence than a gradient of built-up areas (Kuussaari et al., 2021). However, built-up area is not a direct measure of actual impervious surface in a city, and the weaker effect on butterfly occurrence indicates that built up areas can encompass small green spaces that are valuable habitats for pollinators (Kuussaari et al., 2021).

Together, these results suggest that increasing impervious surface cover may not be the only environmental driver of urban pollinator diversity.

Studies within cities may lack replication across geographical regions but they often include a greater number of sampling sites within the focal area. This can enhance the generalisability and validity of findings by capturing fine scale heterogeneity within urban landscapes. For example, Burdine and McCluney (2019a) sampled bees across 30 parks and gardens in Toledo, Ohio (USA) and found that bee abundance declined with increasing impervious surface cover. Similarly, Baldock et al. (2015) assessed pollinator diversity across different land use categories, sampling one urban, one farmland and one village site with replication across 12 cities. In this study sites were 1km x 1km meaning at the urban end of the gradient different urban land uses were encompassed in the sampling area. Thus, sampling many urban green spaces helps to characterise the complex habitat heterogeneity in urban environments.

Overall, previous research suggests a positive association between urbanisation and certain taxa, such as bees, while reducing the diversity of others. This highlights the importance of assessing pollinator responses at species level. Furthermore, studies employing urban gradients, particularly those with multiple replicates across cities or sites within cities, enable broader inferences about the general effects of urbanisation on pollinator diversity. Specifically, the urban sprawl, consisting of residential housing and lower levels of impervious surface cover, was positively associated with urban pollinator diversity. (Wenzel et al., 2020). The urban sprawl typically consists of various land use types, some of which can be beneficial pollinator habitat (Wenzel et al., 2020). Despite this, in this field, the complex mosaic of land-use types is often overlooked, potentially obscuring sources of habitat heterogeneity that may influence pollinator diversity.

Pollinator diversity between green spaces

Differences in pollinator diversity between urban green space types have been examined (Baldock et al., 2019; Daniels et al., 2020; Dylewski et al., 2020; Fischer et al., 2016; Fournier et al., 2020; Guenat et al., 2019; Zaninotto et al., 2023a). However, green space type is defined differently across studies. For example, green spaces are either defined by their land use (e.g. allotments, parks, cemeteries) (Baldock et al., 2019; Dylewski et al., 2020; Fournier et al., 2020;

Guenat et al., 2019), or by their management intensity (e.g. mown lawns, grasslands) (Daniels et al., 2020; Fischer et al., 2016; Zaninotto et al., 2023a). Moreover, there are strong biases in urban pollinator research towards studying parks, with the fewer studies in urban agroecosystems (Silva et al., 2023). Sampling a variety of green spaces in urban areas can help to better understand the influence of urbanisation on pollinators occurring in different habitats. For instance, Guenat et al. (2019) sampled 126 individual sites that consisted of three habitat types (gardens, farms and informal green spaces), across two cities and along a gradient of built infrastructure. Here, a reduction in bee abundance was associated with urbanisation in farmed sites, but no such reduction was found in informal green spaces.

Across multiple studies, allotments (also referred to as community gardens), were found to have the highest pollinator abundance (Baldock et al., 2019; Fournier et al., 2020). Baldock et al. (2019) provides a comprehensive investigation into the effect of green space type on pollinator abundance, sampling ten individual sites in each of the nine major green space types, across four UK cities. Importantly, the high pollinator abundance recorded in allotments was attributed to greater floral abundances in these green spaces (Baldock et al., 2019); this suggests that differences in pollinator diversity are likely mediated by variation in management intensity and the resulting plant community composition. Dylewski et al. (2020) found, pollinator abundance was greater in urban grasslands than in parks and housing estates. However, the relationship between plant cover and butterfly abundance varied between land use type, being positive in urban grassland and housing estates but negative in parks.

Together, these findings highlight the complex effects of land use and management on pollinator diversity, emphasising the need for extensive sampling of green spaces within cities. Furthermore, an important step towards unravelling complex green space-pollinator associations is to assess how environmental variables influence pollinator diversity between green spaces.

Urban environmental drivers of pollinator diversity

The urbanisation process presents a novel set of environmental characteristics operating across different spatial scales which can interact to shape pollinator diversity. However, these drivers are unlikely to be uniform across different urban

green spaces which will vary in their management intensity, floral resources, and surrounding landscape context. Despite this heterogeneity, studies often examine environmental variables within a single green space type, limiting our understanding of how habitat variation contributes to pollinator diversity at the city scale. Consequently, we lack knowledge on how different green spaces may contribute to supporting pollinators within cities. Below I discuss the effects of different landscape and local urban environmental driver on pollinator diversity.

Landscape scale variables

Impervious surface

Studies have shown negative (Bates et al., 2011; Bennett and Lovell, 2019; Birdshire et al., 2020; Burdine and McCluney, 2019a; Fortel et al., 2014; Geslin et al., 2016; Grossmann et al., 2023; Herrmann et al., 2023; Neumann et al., 2024), positive (Dietzel et al., 2023; Egerer et al., 2020; Wilson and Jamieson, 2019) and no associations (Guenat et al., 2019; Lanner et al., 2020; Wilson and Jamieson, 2019) between impervious surface and pollinator diversity.

Despite being commonly assessed, the scale of analysis varies between studies and taxa, with buffer zones ranging from 100m to 2000m across studies. The spatial resolution of the analysis can be predetermined by authors based on the average foraging range of their focal taxa. However, even within bees, foraging range can vary between species with larger bees capable of greater foraging distances (Kendall et al., 2022). To overcome this, certain studies use various buffer zones over different spatial scales, and compare model fit to select the most appropriate buffer (Herrmann et al., 2023; Wilson and Jamieson, 2019). However, using discrete buffer zones to measure the effects of impervious surfaces has been criticised (Miguet et al., 2017). Concentric buffer zones can oversimplify organisms' responses to landscape effects by assuming a uniform response across the entire buffer and no effect after a certain threshold (Miguet et al., 2017).

Importantly, variations in spatial scale may not only influence statistical outcomes but also reflect different ecological mechanisms. At broader spatial scales impervious surfaces may confine pollinators within certain green spaces, concentrating pollinator diversity in these sites (Dietzel et al., 2023; Sivakoff et al., 2018). In contrast, at finer scales, impervious surfaces around sites may

restrict colonisation of habitat patches themselves, resulting in reduced pollinator diversity (Sivakoff et al., 2018).

Mechanisms behind the impact of impervious surface on pollinator diversity are complex and not yet resolved. Impervious surface may be negatively associated with amount of green space or vegetation cover, and thus the amount of floral and nesting resources available in the landscape (Baldock, 2020; Nowak and Greenfield, 2020). On the other hand, impervious surfaces can increase the number of man-made cavities which cavity nesting bee species may utilise, thereby having a positive effect on their diversity (Matteson et al., 2008).

Surrounding habitat/ vegetation cover

In contrast to impervious surface, the role of surrounding habitat or vegetation cover has had comparatively less attention in the literature. The mechanism by which vegetation influences pollinator diversity in urban environments may differ from those associated with impervious surface. Surrounding habitat cover has shown either positive (Martini et al., 2025), negative (Philpott et al., 2025; Sirohi et al., 2025) or no associations (Matteson and Langellotto, 2010) with pollinator diversity. One explanation for positive associations with surrounding habitat cover is the enhanced resource availability in the landscape, facilitating pollinator spillover into study sites (Martini et al., 2025). Conversely, pollinators may prefer to forage within these surrounding habitats, resulting in a dilution effect and reduced pollinator richness within study sites (Philpott et al., 2025). Additionally, vegetation cover within the landscape may interact with impervious surface cover to influence pollinator diversity (Liao et al., 2025). While Liao et al. (2025), found an association between impervious surface and more homogenised pollinator communities whereas vegetation cover increased pollinator community heterogeneity with vegetation cover being the primary driver of Hymenoptera species richness.

Importantly, not all surrounding habitats are equivalent in their influence on pollinator diversity. Distinctions between natural habitat and developed green spaces (i.e. manicured lawns), can influence pollinator species occurrence (Ulrich and Sargent, 2025). Ulrich and Sargent (2025) reported a positive relationship between natural green space (defined as green spaces with limited anthropogenic influences such as green belts and nature reserves) and hoverfly species

occurrence, but no such association was found for developed green spaces (e.g. heavily managed parks or gardens). Similarly, the negative association observed by Sirohi et al. (2025), may reflect the inclusion of all managed and unmanaged land, when quantifying green space at the landscape level. Typically, managed land are maintained to suit anthropogenic purposes such as the intense mowing regimes within golf courses to allow the use of these spaces for golf, contrasting unmanaged sites which are allowed to develop spontaneously due to a lack of human intervention. This suggests that only certain types of green spaces that are resource rich, may positively influence pollinator diversity. Thus, results from studies investigating habitat availability within the surrounding landscape may largely depend on how green space is measured. However, studies often use land cover data to measure habitat availability without directly quantifying floral or nesting resources in the landscape.

Availability of both floral and nesting resources alone may not be the only determining factor explaining patterns in pollinator diversity and its association with surrounding habitats. Land use diversity may play an important role, as heterogeneous landscapes likely provide more diverse resources (Bottero et al., 2023). Therefore, assessing the extent and composition of green spaces surrounding sites, as opposed to solely assessing the proportion of impervious surface, may provide a more comprehensive insight into landscape effects on pollinator diversity.

Urban heat island

Higher proportions of impervious surface are also related to warmer urban temperatures, known as the urban heat island effect (UHI) (Chapman et al., 2017; Hua et al., 2020). The UHI results in higher urban temperatures compared to surrounding rural areas because of urban construction and human activities within cities. Built surfaces such as roads and buildings absorb solar radiation while reduced vegetation cover limits evapotranspiration; additionally anthropogenic heat production can contribute to urban warming (Mohajerani et al., 2017). Urban warming can have direct physiological effects on pollinators, for example the UHI effect has been associated with smaller body sizes in *Bombus* species compared to their rural counterparts (Theodorou et al., 2020a). However, species may vary in their tolerance to urban warming due to differences in their critical thermal

maximum and critical water contents. Critical thermal maximum and critical water content are defined, respectively, as the sub-lethal threshold for an organisms' maximum body temperature and minimum body water content (Burdine and McCluney, 2019b). Furthermore, warmer temperatures could lead to phenological mismatch between pollinators and their plants' resources (Fisogni et al., 2020). Ultimately, the combination of temperature effects on both pollinator physiology and phenology are thought to negatively impact pollinator diversity in cities.

Along an urban-rural gradient, bee abundance was negatively associated with a temperature increase of 2.5°C in urban areas (Hamblin et al., 2018). However, the proportion of impervious surface in the surrounding landscape explained similar levels of variation in bee abundance. Hamblin et al. (2018) also noted significant species level variation in response to warming. In contrast, no association between temperature and pollinator community composition has been recorded (Zaninotto et al., 2023a). However, the temperature gradient was greater in Hamblin et al. (2018) (2.5°C) than in Zaninotto et al. (2023a) (-0.89°C and +0.29°C), suggesting smaller variations in temperature may not influence pollinator communities. Furthermore, Zaninotto et al. (2023a) measured mean temperature within a 200m radius of garden sites. Therefore, temperature was collected within urban green spaces which may have mitigated the urban heat island effect through high vegetation cover (Wu et al., 2021). Thus, considering UHI effects as an environmental driver on pollinator diversity is likely more relevant to studies across large landscape scales such as urban-rural comparisons rather than studies that investigate pollinator diversity within urban green spaces in the same locality.

Habitat connectivity/isolation

Increased impervious surface cover can also fragment urban pollinator habitat, potentially impeding pollinator movement between suitable habitat patches. Habitat connectivity describes the degree to which the landscape facilitates movement between suitable habitat patches (CMS, 2020). The isolation of suitable habitat may make floral and nesting resources difficult to find and reduces the area in which resources can be utilised.

Connectivity can be evaluated by quantifying structural connectivity which work to evaluate physical landscape patterns such as the distance of a site to the nearest habitat patch. Wild bee community dissimilarity in Berlin's urban grassland habitats was associated with habitat isolation but not impervious surface (Buchholz et al., 2020). Here, spatial isolation of a grassland sites were determined using a continuous score from 0 (low isolation) to 12 (high isolation), incorporating both natural and artificially built barriers. While this finding demonstrates the role of habitat isolation in shaping urban bee communities, this measure considers the isolation of grassland patches from other similar sites but may not account for other green space types that could provide resources for pollinators. Furthermore, increasing habitat connectivity has been shown to positively influence pollinator richness and abundance, but the scale of this relationship was more pronounced in urban than peri-urban and non-urban landscapes (Graffigna et al., 2024). Thus, when comparing results of habitat connectivity on urban pollinator diversity between studies, it is important to consider the scale of urbanisation. Graffigna et al. (2024) used data on pollinator diversity collected in previous studies and extracted connectivity scores from assessing satellite images. Whilst this approach enables assessment across multiple cities and provides a standardise way to measure connectivity, the study is unable to control for any other environmental characteristics that could influence pollinator diversity.

More recently, three dimensional (3D) connectivity has been proposed as a measure of habitat connectivity in urban pollinator studies, where high 3D connectivity equates to low habitat isolation. (Grossmann et al., 2023; Herrmann et al., 2023). Unlike previous studies that assess habitat connectivity by considering the horizontal arrangement of habitat patches, measures of 3D connectivity also incorporate vertical barriers to movement. Therefore, 3D connectivity may provide a more informative measure of habitat connectivity in urban environments, where landscapes are often characterised by large vertical structures that could obstruct pollinator flight paths. Grossmann et al. (2023) found wild bee richness and abundance reduced with increased 3D connectivity, although hoverfly diversity was not influenced by this variable. Difference between bee and hoverfly responses in this study is likely due to hoverflies having higher mobility and bees using central place foraging strategies.

Honeybee density

Beekeeping is the anthropogenic practice of maintaining honeybees, most commonly *Apis mellifera*, within artificial hives (apiaries) in order to harvest honey (Kritsky, 2017). The introduction of apiaries within cities can result in unnaturally high densities of honeybees in urban areas. While *Apis mellifera* native to Europe, Asia and Africa, urban bee keeping may negatively impacting wild pollinators through competitive effects for floral resources (Ropars et al., 2019a). Increased honeybee colony density has been negatively associated with wild pollinator flower visits (Ropars et al., 2019a), and wild bee species richness (MacInnis et al., 2023). In contrast, honeybee abundance has been positively associated with wild bee diversity (Herrmann et al., 2023), or shown no effect (McCune et al., 2020). Herrmann et al. (2023) measured honeybee abundance as the total number of flower visits at the site; thus, the positive association with wild bee visits may represent the general attractiveness of the site to all bees. McCune et al. (2020) and MacInnis et al. (2023) used pan traps to record honeybee abundance however, comparisons between these studies are difficult due differences in floral diversity within sites. Future research carried out under experimental conditions may provide more insights into the impacts of honeybees on wild pollinator diversity.

Local variables

Floral richness and abundance

Across studies, measures of floral resource availability vary considerably. Floral abundance is often estimated by calculating the mean number of flowers per individual plant, from a set of representative plants for each species, and multiplying this value by the approximate number of plants for each species (Nicholls et al., 2023). Alternatively, species level percentage cover of a plant within a given area may be used as an indirect proxy for floral abundance and quantified using the *Braun-Blanquet* scale (Dylewski et al., 2019; Grossmann et al., 2023). In other cases, floral abundance is estimated based on the proportion flower cover at a site. These approaches are commonly carried out along transects (Reeher et al., 2020), within a defined radius from the centre of a site (Pardee and Philpott, 2014), or across the entire site (Gerner and Sargent, 2022). Finally,

floral abundance may be quantified by direct counts of inflorescences for each species, although this approach is often restricted to smaller scales such as 1x1m (Philpott et al., 2025).

Regardless of these different approaches to assessing floral resource availability, results are consistent across many studies. Floral richness has been found to be positively related to pollinator abundance (Egerer et al., 2020; Gerner and Sargent, 2022; McCune et al., 2020; Neumann et al., 2024; Theodorou et al., 2020b) and richness (Egerer et al., 2020; Herrmann et al., 2023; Philpott et al., 2025; Theodorou et al., 2020b; Wilson and Jamieson, 2019). Similarly, floral abundance was positively associated with pollinator abundance (Baldock et al., 2019; Bates et al., 2011; Bennett and Lovell, 2019; Burdine and McCluney, 2019a; Dylewski et al., 2019; Gerner and Sargent, 2022; Pardee and Philpott, 2014; Reeher et al., 2020) and richness (Baldock et al., 2019; Bates et al., 2011; Dylewski et al., 2019; Gerner and Sargent, 2022; Grossmann et al., 2023; Hamblin et al., 2018; Pardee and Philpott, 2014). While results show a consistent positive effect of floral resource availability on urban pollinator diversity, the effect of floral resources can depend on the group studied. Philpott et al. (2025) and Herrmann et al. (2023) found only bee richness increased with floral richness, whereas butterfly/moth and fly richness showed no response.

The differential response of pollinator groups to floral resource availability may point to aspects of vegetation quality rather than quantity having a greater effect on certain pollinators. For example, butterfly diversity in urban green spaces has been positively associated with host plant richness but negatively associated with floral richness (Gordon and Kerr, 2025). Moreover, vegetation height increased butterfly and hoverfly visits to flowers (Herrmann et al., 2023); here the provision of shelter from longer vegetation may particularly benefit these taxa. Finally, some studies quantify the floral availability of “pollinator-friendly” plants (Grossmann et al., 2023), while others assess the availability of all plants (Egerer et al., 2020), although more commonly only those that are in bloom are counted (Burdine and McCluney, 2019a).

Non-native plants

The relationship between floral resource availability and pollinator diversity is more nuanced once plant origin is considered. The lack of shared evolutionary

history between non-native plants and pollinators are thought to make non-native plant species unsuitable resources for pollinators (Seitz et al., 2020). Across many studies native plants have been shown to support more pollinator diversity than non-native plants in urban green spaces (Egerer et al., 2020; Fukase, 2016; Pardee and Philpott, 2014; Zaninotto et al., 2023b). These studies have assessed how the proportion of non-native plants have impacted pollinator diversity. However, studies have found no effect (Wilson and Jamieson, 2019) while others have shown positive effects of non-native plants on pollinator diversity (Grossmann et al., 2023; Martini et al., 2025). Considering the seasonal availability of floral resources is important as pollinators require these resources across seasons. Some research highlights the seasonal role of non-native plants in supplementing pollinator forage (Poole et al., 2025; Seitz et al., 2020). For example, higher pollinator diversity has been recorded in parks that are planted with a mix of native and non-native plants (Poole et al., 2025), and early and late blooming non-native plants received more flower visitors than their native counterparts (Seitz et al., 2020).

Habitat size

The species-area relationship suggests larger habitat areas may promote higher pollinator diversity in urban green spaces (Connor and McCoy, 2013). This relationship is largely driven by greater resource availability in larger habitats (Stewart et al., 2018). Studies have related habitat size to increased pollinator richness (Egerer et al., 2020; Grossmann et al., 2023; Stewart et al., 2018; Zaninotto et al., 2023a), abundance (Grossmann et al., 2023; Stewart et al., 2018; Zaninotto et al., 2023a) and bee diversity (Buchholz et al., 2020). However, results for multiple pollinator taxa have also found no effect of patch size on their abundance or richness within gardens (Neumann et al., 2024). Here, Neumann et al. (2024), concluded that the management of green spaces in terms of their floral resources determines floral resource availability more than garden area.

Area of habitat is often measured as the area of the green space being sampled, excluding large water bodies or areas of impervious surfaces (Buchholz et al., 2020; Grossmann et al., 2023). However, within urban areas, patch size may be more complex as certain habitats can be located within larger green areas, for example garden sites that are directly surrounded by more gardens. This was

overcome in one study that measured green space area as the total area of continuous green space, until separated by >5m of impervious surface (Zaninotto et al., 2023a). However, results from Zaninotto et al. (2023a) still support a positive relationship between habitat size and pollinator diversity.

Urbanisation and pollinator traits

Variation in responses to urbanisation among pollinators is likely driven by species traits. Urban environmental variables filter pollinator communities according to their traits, allowing pollinator species with certain traits to persist in urban habitats. However, research on trait-environmental relationships within pollinators is biased toward bees and primarily focuses on environmental drivers within single green space types (Brasil et al., 2024; Gathof et al., 2022; Theodorou et al., 2020b). Fournier et al. (2020) demonstrated that urban filtering of bee communities can occur at both the city and green space scale, highlighting the need for more comparative assessments of trait-environmental relationships across green spaces.

Body size

Urbanisation is hypothesised to select for body size in two opposing ways. Firstly, fewer floral resources associated with higher proportions of impervious surface are thought to favour smaller pollinators with lower energetic requirements (Banaszak-Cibicka and Żmihorski, 2012; Eggenberger et al., 2019). Secondly, mobility is directly related to body size in insect pollinators, and larger more mobile species are likely to be more successful at finding resources in highly fragmented urban areas (Merckx et al., 2018).

Body size has been positively associated with floral richness at sites (Theodorou et al., 2020b). Moreover, increased proportions of impervious surface favoured small bees whilst 3D connectivity favoured larger bees (Gathof et al., 2022). Together, these findings support the theory that smaller bees which require fewer resources are more suited to denser urban environments, while larger more mobile species are able to cope in fragmented urban environments.

For hoverflies, no association between environmental variables and body size was found (Gathof et al., 2022). Results for hoverflies may contrast those of bees due to differences in their foraging behaviour. Bees are central place foragers that must return to a fixed nesting location, making body size particularly sensitive to

environmental conditions such as habitat fragmentation (Philpott et al., 2025). In contrast, hoverflies are not constrained by nest locations and may respond differently to urban landscape variables. Hoverflies are also highly mobile species capable of migrating over large distances (Luder et al., 2018), thus body size may not confer mobility advantages at the city scale.

Lecty

Lecty refers to the degree of pollen specialisation in bees, which are commonly categorised into polylectic (pollen generalist) and oligolectic (pollen specialist) species (Ritchie et al., 2016). While lecty provides a measure of pollen use breadth, it represents only one dimension of the broader ecological concept of ecological specialisation and does not specialisation in nectar use nor other resources. The broader concept of specialisation versus generalisation has been widely discussed in ecological literature across taxa (Devictor et al., 2010). In ecological terms, specialism is generally defined as niche breadth (Devictor et al., 2010). However, in this review we assess the impacts of urbanisation on lecty as this is the indicator of specialisation that has been previously investigated. Thus, although lecty is used here to examine impacts of urbanisation on pollen specialisation it cannot inform drivers on entire niche breadth. Pollen specialisation, is of particular interest when assessing the impacts of environmental change as oligolectic species are considered more sensitive to disturbance due to their limited capacity for resource switching (Devictor et al., 2010). Consequently, polylectic species are often expected to be more tolerant of urban environmental pressures. Higher abundances of polylectic bees have been found in urban environments across multiple studies (Banaszak-Cibicka and Żmihorski, 2012; Normandin et al., 2017). The relationship between lecty and urban environmental drivers are often discussed in the context of the high proportion of non-native plants in urban areas as a mechanism for reducing oligolectic bees (Baldock et al., 2015; Zaninotto et al., 2023a, 2023b).

Comparisons between studies are difficult due to inconsistencies in the environmental drivers assessed. Several studies have reported a positive relationship between polylectic species and the proportion of impervious surface (Buchholz et al., 2020; Gathof et al., 2022). Others report a higher probability of finding oligolectic species with increased impervious surface (Brasil et al., 2024), or with increased proportion of residential cover (Theodorou et al., 2020b). Fewer

studies examined relationships between lecty and floral resources (Brasil et al., 2024; Theodorou et al., 2020b). Polylecty was positively associated with higher floral richness, but no such relationship was found with oligolectic bees (Theodorou et al., 2020b). These results suggest that greater floral richness in urban areas may only benefit generalist species, potentially due to the increased proportion of non-native plants. While studies have linked the availability of native and non-native plants to pollinator abundance in general, no studies have assessed the relationship between plant origin and pollinator traits, highlighting an area of future research.

Nesting sites

The greater provision of man-made cavities associated with high impervious surface cover can increase nesting resources for cavity nesting bees. In contrast, ground nesting bees likely confer a disadvantage due to the lack of bare soil available for nesting (Matteson et al., 2008). However, studies show varying results for the relationship between bee nesting strategies and environmental variables. Below-ground nesting has been positively correlated to bare soil availability (Theodorou et al., 2020b), while the proportion of impervious surface has been positively associated with cleptoparasites and tunnel nesting species (Buchholz et al., 2020), and below ground nesting species (Gathof et al., 2022). Results from Gathof et al. (2022) are counterintuitive, however authors believe that the result is specific to the urban grasslands sampled. Here, sample sites themselves may have provided ample nesting opportunities despite the high levels of impervious surface surrounding sites.

Sociality

Eusociality has evolved repeatedly in Hymenoptera, including bees (Silva and Jack, 2021). Division of labour can confer a selective advantage over solitary bees under resource scarcity (Fronhofer et al., 2018) and in heterogeneous urban landscapes (Banaszak-Cibicka and Żmihorski, 2012; Wenzel et al., 2020). These advantages may arise through their flexibility in resource use, ecological dominance and the ability of eusocial bees to store food, thus buffering against temporal variation in resource availability (Chapman and Bourke, 2001; Hinnert et al., 2012). Consistent with this, analysis has shown positive relations between urbanisation and eusociality (Gathof et al., 2022). In contrast, Wilson and

Jamieson (2019) found solitary bee abundance increased with urbanisation, whilst decreasing eusocial bee abundance, unless bloom cover was high. These results suggest that large colony sizes in eusocial species can increase overall resource demand, indicating floral resource availability may be a limiting factor of eusocial bee abundance in urban areas (Wilson and Jamieson, 2019).

Traits in other pollinators

Patterns of pollinator trait responses to urbanisation beyond bees remains a key knowledge gap. To date, only one study has examined trait-environmental relationships in hoverflies (Gathof et al., 2022); urbanisation was positively associated with terrestrial saprophagous larvae and negatively associated with migratory species. Unlike bees, hoverfly larvae exploit a wide range of food resources, potentially resulting in a dependence on specific habitats that provide these resources (Gathof et al., 2022). Butterfly larvae are also dependent on specific host plants, yet trait-environmental responses to urbanisation have yet to be assessed in butterflies. Overall, extending trait-environmental analysis to a wider range of pollinator taxa is essential to increase understanding of how urbanisation shapes pollinator communities, given the substantial variation in life history strategies which urbanisation may act on.

Plant-pollinator networks

Interactions between plants and pollinators form mutualistic bipartite networks (Dormann et al., 2009). Analysis of network topology allows inference of ecosystem stability and functioning, therefore providing useful conservation insights (Tylianakis et al., 2010). For instance, bipartite network analysis allows the identification of pollinators and plants that are vulnerable to extinction based on their position within the network. Furthermore, network topology can enable predictions of how disturbance and resulting species loss may propagate through the wider community. Consequently, network-based approaches can provide greater insights than patterns of diversity metrics by recognising that a species persistence within an environment is partly determined by its interactions with other species.

Certain topological properties are characteristic of plant-pollinator networks and are particularly important for determining ecosystem resilience. One such property is the significantly nested structure (Bascompte and Scheffer, 2023;

Dormann et al., 2009) (Fig.1.3a). This results in asymmetries in specialisation whereby specialists interact with a subset of species that generalists also interact with (Bascompte et al., 2003). Such nested structures increase network stability by providing alternative interactions following species extinctions, as generalist species tend to be less sensitive to disturbance than specialist species (Aizen et al., 2012).

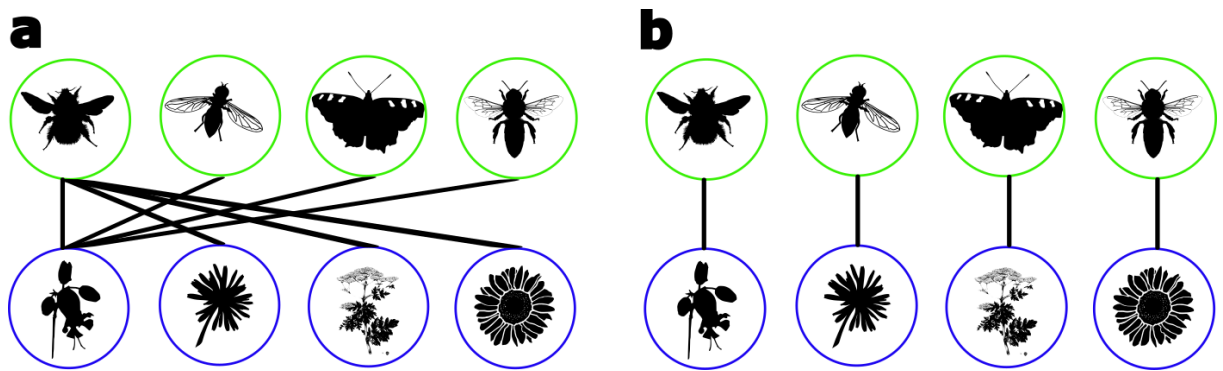


Figure 1.3: A schematic representation of a) nested and b) non-nested plant-pollinator network. In (a), nestedness quantifies the extent to which specialist species (plants and pollinators on the right) interact with a subset of species visited by generalists (plants and pollinators on the left).

Another key architectural property of plant-pollinator networks is modularity, where groups of species (modules) interact with each other more strongly than with species in other modules (Olesen et al., 2007) (Fig.1.4). In plant-pollinator networks, different modules represent coevolutionary units formed by trait matching between the two trophic levels (Bascompte, 2014). For example, a module may consist of short-tongued pollinator species that primarily interact with flowers with short corollas (Ollerton, 2021). Modularity is thought to increase network resilience to extinctions, as species losses are confined within modules, rather than across the whole network (Dormann et al., 2017). Additionally, species can have two main roles acting as either hubs (highly linked species in their own module), or connectors (species that link different modules) (Olesen et al., 2007). Thus, assessing species roles as hubs or connectors within a network can help to identify priority species for conservation actions.

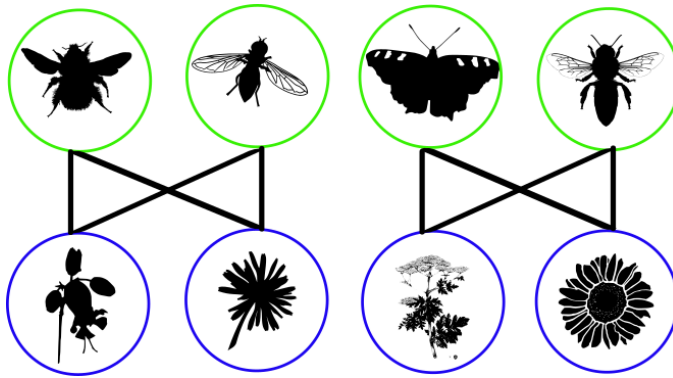


Figure 1.4: A schematic representation of modularity within a plant-pollinator network. The network forms two modules where species within each module interact more closely with each other than with species in other modules.

Other measures of network topology include specialisation at both the species and network level, link density, connectance, and interaction evenness. These metrics capture different dimensions of ecological network structure including niche partitioning, interaction density and sensitivity to species loss. Network specialisation (H_2') is defined as the degree of partitioning in both plants and pollinators across the whole network (Blüthgen et al., 2006) (Fig.1.5). In contrast, species level specialisation (d'), describes the level of selectivity of a species over its interaction partners (Blüthgen et al., 2006). Measures of interaction density include connectance, which is the proportion of realised interactions relative to the total possible interactions (Blüthgen et al., 2006), and link density which is the mean number of interactions per species (Bersier et al., 2002). Finally, interaction evenness quantifies the spread of interactions within a network (Blüthgen et al., 2008).

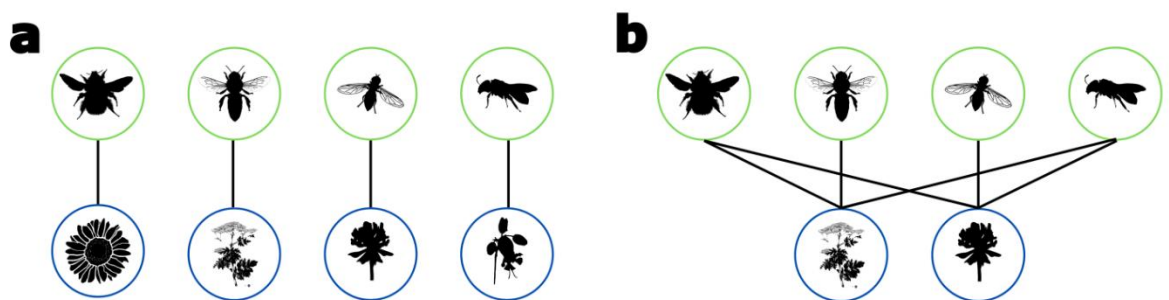


Figure 1.5: Schematic diagram showing plant-pollinator networks with a) high specialisation b) low specialisation. Although pollinators show similar species-level specialisation in both networks, the overall niche breadth of pollinators is narrower in (a) than in (b).

Urbanisation and plant-pollinator network structure

Studies revealed inconsistent effects of urbanisation on plant-pollinator network topology (Table 1.2), reflecting differences in study gradients, focal taxa and environmental drivers explored. However, most research has focused on urban-rural gradients or specific green spaces within cities. Only one study compared network robustness between urban green space types (Baldock et al., 2019), and other structural features (e.g. specialisation) have been largely unexplored in this context. Consequently, understanding of how the urban mosaic may influence plant-pollinator networks is limited.

Table 1.2: A list of network indices, their definitions and their response to urban environmental drivers found in the literature

Network Indices	Definition	Environmental drivers	Association of network indices with environmental driver
Nestedness	The extent to which specialists interact with a subset of species that generalists also interact with (Bascompte et al., 2003).	Landscape diversity	(-) Graf et al., (2024)
		Non-native plant richness	(+) da Cunha-Silva et al., (2025)
		Floral richness	(+) Olsson et al., (2021); Schmack and Egerer, (2023) (-) Philpott et al., (2025)
Modularity	The extent to which species interactions are organised into modules (link dense regions) (Olesen et al., 2007).	Impervious surface cover	(+) Herrmann et al., (2023) (no association) Tavares-Brancher et al., (2024)
		Tree cover (landscape)	(no association) Tavares-Brancher et al., (2024)
		Landscape diversity	(no association) Graf et al., (2024)

Network specialisation	The degree to which plants and pollinators discriminate over their interaction partners across the whole network. Higher specialisation relates to narrower niche breadth (Dormann, 2011).	Urbanisation as land use comparisons	(+) Baldock et al., (2015); Suni et al., 2022 (-) Proesmans et al., (2024) (no association) Fisogni et al., (2022); Silva et al., 2025; Sirohi et al., (2022); Theodorou et al., (2017)
		Landscape diversity	(-) Graf et al., (2024)
		Non-native floral richness	(-) Baldock et al., (2015); Deguines et al., (2016); Zaninotto et al., (2023b)
		Impervious surface (landscape)	(-) Tommasi et al., (2021) (no association) Tavares-Brancher et al., (2024)
		Tree cover (landscape)	(no association) Tavares-Brancher et al., (2024)
Connectance	Proportion of actual observed interactions compared to the total number of all interactions (Blüthgen et al., 2006).	Urbanisation as land use comparisons	(-) Proesmans et al., (2024)
		Impervious surface (landscape)	(+) Tavares-Brancher et al., (2024)
		Tree cover (landscape)	(+) Tavares-Brancher et al., (2024)
Linkage density	Average number of interaction partners per species (Bersier et al., 2002)	Urbanisation as land use comparisons	(+) Proesmans et al., (2024) (no association) Amado De Santis et al., (2023); Fisogni et al., (2022); Sirohi et al., (2022)

		Floral richness	(+) Theodorou et al., (2017)
Interaction evenness	The spread of interactions in the network (Blüthgen et al., 2008)	Urbanisation as land use comparisons	(+) Geslin et al. (2013) (-) Udy et al. (2020)
		Floral richness	(-) Philpott et al., (2025)
		Impervious surface (landscape)	(+) Tavares-Brancher et al., (2024)
		Tree cover (landscape)	(+) Tavares-Brancher et al., (2024)

Network and species specialisation

When assessing network specialisation across land use gradients or comparing urban with rural, farmland or natural land use, empirical findings are mixed, with positive (Baldock et al., 2015; Suni et al., 2022), negative (Proesmans et al., 2024; Tommasi et al., 2021) and no effects (Fisogni et al., 2022; Silva et al., 2025; Sirohi et al., 2022; Tavares-Brancher et al., 2024; Theodorou et al., 2017) of urbanisation on network specialisation reported. Despite this inconsistency at the network level, many studies reported increased specialisation of flower visitors along an urbanisation gradient, with a lower proportion of the available plant species visited (Baldock et al., 2015; Herrmann et al., 2023; Martins et al., 2017; Suni et al., 2022; Theodorou et al., 2017).

Contrasting results suggest that changes in specialisation metrics can arise from various mechanisms. Firstly, changes in specialisation may reflect pollinator turnover driven by altered floral availability in urban environments. For instance, urban environments are associated with a greater richness of non-native plants which may disproportionately attract generalist species, thereby reducing network

specialisation (Baldock et al., 2015; Deguines et al., 2016; Zaninotto et al., 2023b). However, specialisation metrics may also reflect behavioural responses to altered floral resources within habitats. In resource-rich urban habitats, generalist pollinators may restrict their foraging to abundant floral resources to optimise foraging efficiency through frequency dependent foraging (Eckhart et al., 2006), or to maintain floral constancy and reduce competition in areas with high pollinator diversity (Chittka et al., 1999). Thus, under high floral diversity, pollinator specialisation may increase, despite their potential to occupy broader niches. Consequently, shifts in specialisation do not necessarily imply loss of specialist species, but may reflect plasticity in behavioural responses to urbanisation.

Suni et al. (2022), found that urban pollinators were more specialised than rural counterparts, despite no differences in floral diversity. However urban sites contained a higher abundance of flowers per plant species, leading to the conclusion that frequency dependency foraging influences species specialisation. In contrast, Baldock et al. (2015) found urban pollinators foraged on a narrower proportion of available plants but used a wider range of plants compared to natural areas. Here, patterns were attributed to the high floral richness in urban environments, combined with lower pollinator richness and greater community homogenisation in urban habitats. Together, these results suggest that urbanisation may result in a loss of specialist species whilst promoting narrower foraging behaviours by generalist pollinators in florally diverse habitats.

Beyond floral resources, specialisation may be influenced by habitat patch size. Specialist pollinators are thought to be more reliant on larger habitats in order to meet their narrower resource requirements. Accordingly, one study found species specialisation was positively associated to patch size in urban grasslands (Herrmann et al., 2023).

Interaction density and distribution metrics

When assessing interaction complexity along urbanisation gradients, numerous structural metrics can be employed, complicating cross-study comparison. Moreover, some metrics are sensitive to network size (number of plants and pollinators). Therefore, contrasting findings may reflect differences in metric choice rather than ecological impacts.

Proesmans et al. (2024), reported lower connectance but higher link density with increasing urbanisation. While this pattern appears contradictory, as both metrics relate to the number of interactions, it highlights differences in scaling properties between the two indices. Connectance is standardised by the total number of possible interactions, which increases multiplicatively with species richness. In contrast, linkage density reflects the mean number of realised interactions per species and scales linearly with network size. Thus, greater floral richness can increase potential interactions more sharply than realised interactions increase, resulting in lower connectance despite species interacting on average with more partners.

The relationships between interaction density metrics and urbanisation are not consistent across studies. Several authors reported no effect of urbanisation on connectance (Amado De Santis et al., 2023; Fisogni et al., 2022; Sirohi et al., 2022). Instead, floral richness may be a more important driver of connectance and linkage density. For instance, Theodorou et al. (2017) used structural equation modelling to demonstrate that urbanisation increased floral richness which in turn was positively associated with linkage density. These findings indicate that observed shifts in interaction density may arise through changes in floral resource availability rather than from urbanisation.

When investigating interaction evenness, Geslin et al. (2013), reported a positive association with urbanisation, whereas Udy et al. (2020), reported the opposite effect. Contrasting patterns may be a result of differences in community composition, with interaction evenness being sensitive to dominant species that interact strongly with a few plant species. Both studies established experimental plant communities along their study gradients, thereby partially controlling for plant community composition. Thus, in study systems such as Geslin et al. (2013) where urban sites are dominated by a small number of pollinators, interaction evenness declined due to the disproportionate frequency of interactions with a small proportion of plant species. Conversely, in Udy et al. (2020) urban pollinator communities were diverse, with no clear dominating taxa, resulting in more evenly distributed interactions.

Floral richness itself may influence interaction evenness. Phillpott et al. (2025) demonstrated that interaction evenness decreased with increasing plant richness. Interactions may become concentrated on a subset of highly abundant or

rewarding plant species under conditions of high plant richness, generating a skewed pattern in network interactions. Thus, along urbanisation gradients where floral richness is altered, changes in interaction evenness may reflect both shifts in pollinator communities as well as floral resource availability. However, no studies have compared interaction evenness across gradients of both floral richness and urbanisation.

Structural organisation

Given that specialists are more sensitive to habitat loss and alteration (Aizen et al., 2012; Resasco et al., 2021; Spiesman and Inouye, 2013), urbanisation is likely to alter the nestedness of plant-pollinator networks.

Nestedness may decline due to a loss of interactions between specialists as well as specialist-generalist interactions (Spiesman and Inouye, 2013). Urbanisation has been shown to reduce nestedness, where land use diversity, used as a proxy for urbanisation, was negatively associated with nestedness (Graf et al., 2024). In their study, Graf et al. (2024) proposed that reduced landscape diversity lowered floral resource availability, thereby limiting specialist interactions and reducing nestedness; however, floral resource availability was not explicitly measured.

On the other hand, urbanisation may also increase nestedness through shifts in community composition, specifically through an increase in generalist pollinators driven by non-native plant richness. A greater prevalence of generalists can promote more opportunistic interactions and increase overlap between species' interaction partners, in turn increasing nestedness (da Cunha-Silva et al., 2025). Prendergast and Ollerton (2021), compared urban bushland remnants and residential gardens within the same urban area, finding higher nestedness in gardens. This pattern was attributed to the high frequency of interactions between honeybees and non-native plants, acting as supergeneralists linking otherwise weakly connected species. However, results from da Cunha-Silva et al. (2025) found the relationship between urbanisation and nestedness was indirect and mediated by pollinator richness as opposed to the proportion of non-native plant species. Their findings suggest any positive association between nestedness and urbanisation arises due to a loss of interaction partners, and potentially a lack of specialist interactions.

Furthermore, studies report either increased (Olsson et al., 2021; Schmack and Egerer, 2023) or decreased (Philpott et al., 2025) nestedness with floral richness. Greater floral richness may enhance interaction complexity and thus nestedness within networks. Alternatively, if higher floral richness promotes greater network specialisation, nestedness may decline. Methodological differences may have contributed to this variation in results. Sampling duration varied considerably within studies; Schmack and Egerer (2023) and Olsson et al. (2021) sampled pollinators in 5 minute and 30-minute blocks respectively. In contrast, Philpott et al. (2025) collected plant-pollinator interaction data over a 4-hour sampling period. However, sampling of sites was not repeated across days or months in Philpott et al. (2025) unlike the other two studies. Specifically, it has been shown that shorter sampling times result in increased recording of common pollinators (Chacoff et al., 2012). Therefore, differences in sampling intensity and frequency may bias the resulting networks.

Modularity reflects the degree to which interactions within networks are divided into distinct clusters or modules (Olesen et al., 2007). Such compartmentalisation of plant-pollinator networks may arise from habitat heterogeneity, divergent trait selection or phylogenetic clustering of closely related species, all of which are not mutually exclusive (Olesen et al., 2007). For example, habitat heterogeneity can promote modularity by filtering species into distinct communities within habitat patches, thereby reinforcing interactions between specific groups of species in these habitats (Grass et al., 2018).

The literature is sparse on the effects of urbanisation on plant-pollinator network modularity. Tavares-Brancher et al., (2024) and Graf et al. (2024), found no association between network modularity and urbanisation when assessed along an urbanisation gradient. The lack of association between modularity and urbanisation may indicate that modules are primarily structured through trait convergence and phylogenetic relationships rather than by landscape contexts (Tavares-Brancher et al., 2024). Thus, while urbanisation may alter species composition, the organisation of interactions into distinct compartments may be relatively conserved with urbanisation.

In contrast, Herrmann et al., (2023) found decreased modularity with increased impervious surface cover. Here, reduced modularity was thought to be mediated by loss of pollinator species with increased urbanisation. Smaller communities

resulting from a loss of plant or pollinator species have a tendency for fewer modules (Olesen et al., 2007; Yahaya et al., 2024). However, larger habitat sizes may mitigate the negative effects of urbanisation on modularity as a positive association between grassland patch size and modularity was demonstrated by Herrmann et al. (2023). Here, increased habitat size may enhance taxonomic and functional diversity within patches, thereby increasing network modularity through the organisation of interacting species with corresponding traits into modules (Herrmann et al., 2023).

Network stability

Network stability refers to the persistence of species and interactions over space and time (Ren et al., 2022). Beyond single species losses, stability also encompasses the extent of extinction cascades throughout the network. Topological indices are often used as proxies for stability. For example, nestedness is considered a key structural determinant of network stability, as interaction redundancy can provide alternative pathways following species loss, thereby preventing secondary extinctions (Grilli et al., 2016; Memmott et al., 2004). Stability of networks themselves can be quantified using different metrics such as robustness and extinction slopes in the Bipartite package (Dormann et al., 2008), or using stochastic coextinction models (SCM) (Proesmans et al., 2024).

Within the Bipartite package in R, Robustness measures the area below an extinction curve when loss of species is simulated in the corresponding level, whereas extinction slopes quantify the simulated secondary loss of species with extinction of species in the other level (Prendergast and Ollerton, 2021). Robustness has been shown to decrease with urbanisation when compared across an urban-farmland gradient (Udy et al., 2020). Reduced robustness was attributed to the presence of dominating interaction links in urban networks making the network particularly sensitive to collapse if these interactions were lost. Additionally, Prendergast and Ollerton (2021), found networks in bushland remnants had a higher robustness than those in residential gardens. However, extinction slopes showed opposite patterns to robustness, with greater extinction slopes in bushland remnants than residential gardens. Overall, Prendergast and Ollerton (2021) demonstrate that while bushland remnants are more resistant to initial species loss (high robustness), extinction cascades are more severe when they do occur (steeper extinction slopes). Higher nestedness may contribute to

increased robustness, whilst greater specialisation likely amplifies the magnitude of secondary extinctions in bushland remnants.

Using stochastic coextinction models, Proesmans et al. (2024), found higher link density and network asymmetry in urban networks due to the higher floral richness in these areas. Moreover, higher link density was found to reduce the probability of coextinction cascades, however, when cascades did occur, they were more intense. Network asymmetry similarly reduced coextinction occurrence risk. As such, the higher link density and asymmetry of urban networks in Proesmans et al. (2024) likely equated to a reduced risk of extinctions but simultaneously a higher number of species lost if extinction cascades do occur.

One study assessed plant-pollinator network robustness across nine different urban green space types (Baldock et al., 2019). Here, Baldock et al. (2019) used Bayesian network models to predict the effects of increasing areas of each land use category on network robustness at the city scale. Models predicted allotments would generate the greatest increase in city scale robustness when their area increased, owing to the high floral abundance and associated pollinator diversity in these sites. Although this study highlighted potential differences in robustness among green space types, it did not examine variation in other network metrics.

Knowledge gaps and thesis aims

Although urban pollinator ecology is now a well-established field, much of the literature treats urbanisation as a simplified gradient, often overlooking the fine-scale heterogeneity of urban green space mosaics. While patterns of pollinator diversity are relatively well documented, responses of functional traits and plant-pollinator network structures in different urban green space types remain comparatively unexplored. Furthermore, research across these themes has been strongly biased with trait-based and network approaches rarely extending to other pollinator taxa such as butterflies and hoverflies. Together, these constraints limit our broader understanding of how pollinator communities assemble and function within urban landscapes. Consequently, important conservation insights into how urban landscapes can support functionally diverse and resilient pollinator communities may be overlooked.

In this thesis I assess how variation in habitat characteristics provided by two urban green spaces (private residential gardens and allotments) influences pollinator

diversity, plant-pollinator network structure and the distribution of functional traits. I primarily focused on three main pollinator taxa: bees, butterflies and hoverflies. The aim of each of the following chapters are outlined below.

- **Chapter 2:** This chapter evaluates two different methodologies for sampling flower visits and plant-flower visitor network structure, by comparing camera derived data with traditional visual observations in private residential gardens. This enables a cost-benefit analysis of the use of cameras to record flower visits and provides recommendations for improving the use of this novel technology in future research.
- **Chapter 3:** This chapter focuses on private residential gardens to examine how environmental characteristics, including floral abundance and richness, plant origin, habitat size, surrounding green space area and land use diversity, influenced flower visits and flower visitor networks. Therefore, this chapter explicitly identifies within-green space environmental drivers of flower visits before examining across habitats.
- **Chapter 4:** Extending beyond a single habitat type, this chapter investigates how environmental variables shape flower visits and flower visitor network structure across contrasting urban green spaces (private residential gardens and allotments). It compares, plant-flower visitor network structure between green spaces, addressing a key knowledge gap in the literature.
- **Chapter 5:** This chapter assesses community assembly processes in bees and hoverflies across gardens and allotments using hierarchical modelling of species communities (HMSC), a novel analytical approach that allows assessment of trait-environmental relationships within these green spaces. The use of HMSC allows variation in species level responses to environmental drivers be explored, helping to further understand patterns of pollinator diversity within these green spaces. Furthermore, chapter 5 determines whether trait filtering occurred at the regional-city interface using biological records to acquire a regional trait pool.
- **Chapter 6:** The final chapter synthesises findings from the previous chapters to provide management suggestions for supporting pollinator diversity within cities. Study findings are further discussed in the context

of pollinator conservation strategies within the UK and identifies areas of future research.

Collectively, the chapters progress from assessing environmental drivers of diversity to understanding community assembly processes in urban green spaces. Overall, this research extensively explores pollinator responses to urbanisation and contributes to greater understanding of pollinator diversity patterns in urban green spaces. Together the chapters allow for more informative insights into the potential of conservation practices within these green spaces.

Chapter 2 Visual observations are more effective than cameras for recording flower visits

Abstract

The global economic value of pollinators makes their ongoing decline especially concerning and necessitates their long-term monitoring. Recent studies have highlighted the need to investigate relationships between pollinators and the flowers they visit, as plant-pollinator networks underpin the maintenance of diversity within an ecosystem. However, flower visitor networks are often affected by sampling bias and in some cases involve lethal sampling, raising ethical concerns. Advancements in technology means cameras can be effective tools of monitoring flower visitor interactions, yet studies comparing network structure determined by camera and visual observation methods are relatively scarce. Thus, we aimed to compare flower visits (Anthophila, Syrphidae and Papilionoidea), and flower visitor network structures recorded by cameras and visual observations. We found cameras recorded fewer flower visits than visual observations. Furthermore, due to the relatively low image resolution of the camera used, species level identification could not be determined in video recordings. Despite these differences between the two methodologies, network structures (specialisation, connectance and interaction evenness) were similar. Overall, we show that cameras can be an effective tool for recording flower visitor network structure and could potentially be used for long term deployment in the field to reduce sampling bias. We discuss our results in the context of the benefits and limitations to using cameras in flower visitor studies.

Introduction

Insect declines have been reported across the world (Sánchez-Bayo and Wyckhuys, 2019). Understanding this decline requires increased monitoring of insects, both longitudinally and in cross-sectional studies using standardised methodologies. As a key ecosystem service provider (Ollerton et al., 2011), pollinators (particularly

Hymenoptera and Lepidoptera) are central to insect research (Sánchez-Bayo and Wyckhuys, 2019), with many studies focusing on plant-pollinator interactions. These interactions provide vital insights into how certain habitats can support pollinator diversity (Elle et al., 2012; Kaiser-Bunbury and Blüthgen, 2015). Citizen science schemes such as the UK Pollinator Monitoring Scheme (UK Pollinator Monitoring Scheme, 2025), have been employed to increase sampling effort through volunteer recruitment to monitor plant-pollinator interactions. However, these schemes can be expensive to run (Breeze et al., 2021) and the data collected can be biased from differing spatial, temporal and taxonomic sampling efforts, as well as observer error (Díaz-Calafat et al., 2024; Johnston et al., 2023). Thus, research on plant-pollinator interactions is often still carried out by trained researchers. As technology advances it is important that researchers consider new techniques in monitoring insects as both budget and time constraints remain a constant issue.

Traditionally, plant-pollinator interactions are recorded through visual observations of plants, or less commonly by using the pollen carried by pollinators (Chacoff et al., 2012; Memmott, 1999). This sampling frequently involves lethal sampling by removing pollinators from the study system for later identification. Whilst lethal sampling allows species level identification of pollinators, it raises considerable ethical concerns as well as having a potential disruptive effect on future plant-pollinator interactions. Alternatively, some studies do identify pollinators in the field to genus or morphospecies such as solitary bees, hoverflies, bumblebees and honeybees (Nicholls et al., 2023; Renaud et al., 2020). However, visual observations are subject to human error and require meticulous training of observers to control these errors. Furthermore, field work to collect plant-pollinator data can be extremely time and labour intensive, making them difficult to carry out under budget and time constraints (Hegland et al., 2010). Time constraints may influence plant-pollinator observations given the resulting interactions networks are subject to sampling effort biases, with shorter observation times resulting in a lower chance of recording rare species (Blüthgen et al., 2008; Manning et al., 2025; Rivera-Hutinel et al., 2012). As technology advances, new techniques for monitoring plant-pollinator observations have emerged including the use of eDNA and cameras (Banerjee et al., 2022; Sittinger et al., 2024).

Cameras have widely been used in the field of ecology, particularly being deployed to monitor larger mammals (Delisle et al., 2021). However, camera technology has advanced, allowing higher resolution images of smaller objects coinciding with lower costs (Droissart et al., 2021; Sittinger et al., 2024). In turn, there has been an increase in cameras used for insect monitoring (Høye et al., 2025).

Cameras can have distinct advantages over human observations when it comes to recording plant-pollinator interactions. Firstly, cameras do not use lethal sampling unlike many visual observation studies (Baldock et al., 2019; Herrmann et al., 2023; Zaninotto et al., 2020). This can have multiple benefits for the resulting plant-pollinator network, as the removal of individuals can result in a change in chemical queues released by plants, avoidance of plants by pollinators, and changes in the pollinator population that can ultimately influence other flower visitors and thus the network structure (Brosi et al., 2017). Moreover, the lethality of studies on insects in a time of severe population declines, as well as current understanding of insect welfare, raises ethical concerns (Barrett and Fischer, 2024; Drinkwater et al., 2019). Secondly, the ability to situate cameras in the field for a long period of time has significant benefits for collecting longitudinal data compared to cross-sectional data that is often collected with human observations. Longitudinal data can help to increase the likelihood of capturing rare and elusive species and even nocturnal species that are difficult to sample via human observation, as well as providing more insight into the phenology of study organisms (Basilio et al., 2006; Dorado et al., 2011; García et al., 2024; Manning et al., 2025). Finally, cameras provide video evidence of flower visitor interactions, allowing their validation by experts in the field, helping to strengthen the quality of the data collected (Naqvi et al., 2022; Roy et al., 2016; Serra-Marin et al., 2025).

As many insects have microscopic differences that determine their species, it is often not possible to identify pollinators to species level when using cameras. Thus, cameras are often used to identify pollinators to family or morphospecies such as bumblebees, solitary bees, flies, hoverflies and butterflies (Naqvi et al., 2022). As such, data collected using cameras may not provide great insight into the diversity of pollinators hosted by plants. Moreover, to effectively study plant-pollinator networks in a system, it is common to sample a representative sample of flowers (Memmott, 1999). In systems with high floral richness, this would

require many cameras to observe individual flower species. Additionally, if these cameras are left to record for long duration, efficient battery life and data storage would be required. Large amounts of data can be generated from cameras which require processing to extract flower visitor interactions. Artificial Intelligence (AI) techniques need to be implemented to help with data processing (Ştefan et al., 2025a), otherwise filtering data from video recordings can be labour intensive, in turn reducing the benefits of the time savings with cameras in the field.

In this study we compared plant-pollinator interactions measured by video recordings and human observations. Specifically, we measure the effectiveness of both techniques for 1) determining pollinator abundance and richness and 2) constructing plant-pollinator visitation networks. We predict that pollinator richness will be higher in the human observation recordings due to the ability to better identify pollinators to species level (H1). As a result of the reduced ability to detect pollinators using cameras, we predict that the resulting network structure metrics (network specialisation, evenness, connectance and nestedness), will differ between camera recordings and human observation data (H2). Overall, this research provides insight into the utility of cameras in studying plant-pollinator interactions and discusses both advantages and limitations of this approach whilst outlining future improvements for this method.

Methods

We sampled plant-insect interactions in 18 gardens across Glasgow, Scotland (55° 51'46" N, 4° 15'07" W) between the 1st of June 2023 and 30th of September 2023. Sample sites recruited on a volunteer basis by advertisement on social media sites and emailing local community groups. Sites were selected then selected on a first come, first chosen basis and provided they were at least 1km apart and covered and equal split of high and low urbanisation areas. Urbanisation was quantified as the proportion of impervious surface within a 1km grid cell and sites could be located anywhere within that grid cell. High urbanisation for each grid cell was categorised as more than 50% impervious surface cover. Impervious surface data were obtained from the Copernicus Urban Atlas (European Union, 2020). The following land use categories were classified as impervious surfaces: construction sites, continuous urban fabric, discontinuous dense urban fabric and industrial, commercial, public, military and private units (Defined in Appendix B,

Table B1). Classification of site urbanisation and area can be seen in Table 2.1. Due to the difficulty in recruiting sites, the sampling area was expanded to include a 5km buffer surrounding the Glasgow City Council boundary to ensure sites were independent and covered areas of high and low urbanisation (Fig 2.1). Each garden was visited once a month on separate days for the four months of the study. Sampling was conducted under conditions similar to (Zaninotto et al., 2023b), on clear days with air temperature above 10°C, and wind speed was below 15km/h. Whilst the insects in our study are known pollinators, we recognise that our methodology cannot confirm actual pollination, thus we refer to pollinators as flower visitors throughout the manuscript.

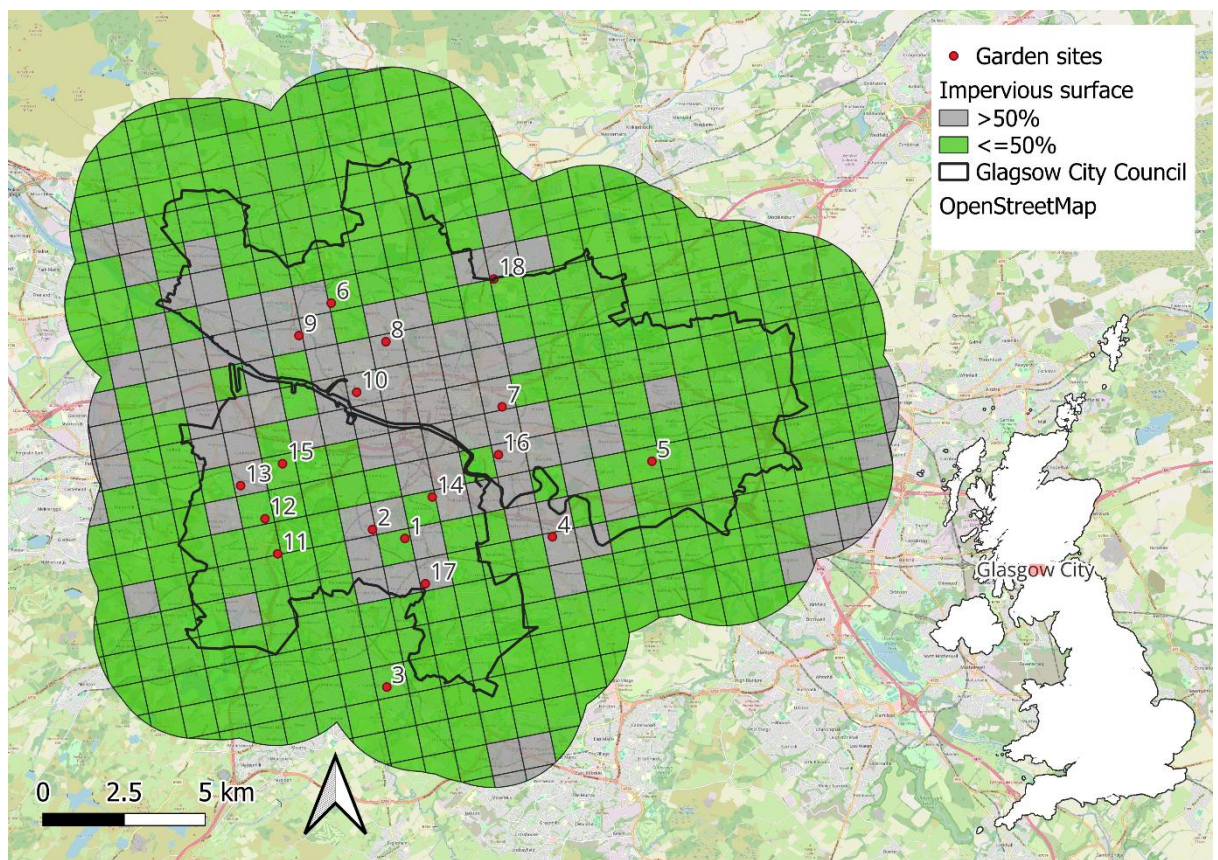


Figure 2.1: Location of 18 gardens (red points) sampled within Glasgow, Scotland. Sites fell within Glasgow City Council boundary, and a 5km surrounding buffer. Sites were stratified into high impervious surface cover within a 1km grid cell (grey squares), or low impervious surface cover (green squares).

Table 2.1: Sample site information on urbanisation categorisation and area of the garden sampled.

Site	Urbanisation	Garden area (m ²)
Battlefield	Low	49.469
Bellahouston	High	121.931
Bishopbriggs	Low	44.164
Bridgeton	Low	38.112

Broomhill	High	97.831
Clarkston	Low	411.749
Dennistoun	High	65.683
Dormanside	High	181.215
Govanhill	Low	86.948
Jedburgh	High	576.848
Kelvindale	Low	177.039
Mt Vernon	Low	173.035
Muirend	High	71.413
National Dr	Low	87.696
Neilsland	Low	37.808
Rutherglen	High	46.434
Shawlands	High	133.999
Yorkhill	High	47.535

Floral resources

Methodology for quantifying floral resources was followed from Plant et al. (2025). Floral resources at each site were measured using transects (width 0.25m) and were recorded in the morning of each sampling day from 0900. Due to variation in the shape and size of gardens, transects were established to match the length of the garden and were stratified to use one transect per 5m width of each vegetation type (grassy areas, floral borders and vegetable patches). Across all sites, transect lengths ranged from 10-60m (mean $\pm$ SD: 25.44 $\pm$ 14.60). Plants that fell within the transect were identified to genus or species, and the number of floral units (individual flowers) on each plant was counted. Apiaceae umbels and Asteraceae flower heads were counted as one floral unit. Due to the maximum height of camera tripods, only shrubs and trees up to a height of 1.5m were included in the count. One branch on each tree would be randomly selected, and the number of flowers on the branch would be counted and multiplied by an estimate of the total number of branches. To ensure consistency, one observer (E.P), carried out the recording and identification of plants. Botanical keys (Rose and O'Reilly, 2006) and information from garden owners corroborated with online resources were used to identify plants to the lowest possible taxonomic level. The International Code of Nomenclature for algae, fungi and plants was followed (Turland et al., 2025).

Flower visitor interactions

One individual of each plant species was chosen to record its flower visitor interactions via visual observations and video recording. The two methodologies were not carried out at the same time on one individual plant, to reduce the chance of one methodology influencing the other. For both methodologies the data collection was randomised between morning (0930-1130) and afternoon (1230-1700), meaning that both video recordings and visual observation of an individual plant at a site were carried out in either the morning or afternoon but never at the exact same time. Both methods were undertaken for 20 minutes at each plant after a settling in period of two minutes. Cameras were placed so that the lens was 20 - 40cm from the flower depending on where the camera tripod could be stabilised and to ensure the camera had a clear angle of view (Fig. 2.2). Flower visits were extracted from recordings by watching video playback at 2x the speed and identifying target taxa to the lowest taxonomic level. This included identifying *Bombus* and *Apis* to species level, Syrphidae to family level and other bees to genus level. Three flower visitors could not be identified in the video recordings and were removed from the analysis. The observer stood 1-2m from the flowers and collected any flower visitor that could not be identified in the field. One observer carried out all visual observations of flower visits and was responsible for the placement of cameras (E.P.)



Figure 2.2: The camera (RunCam 5) used for video recording of flower visitor interactions. Cameras were placed on tripods so that the lens of the camera was 20-40cm from flowers (here: *Ranunculus* sp.). Cameras recorded for 20minutes after a 2-minute settling in period.

Camera specifications

The cameras used in this study were the RunCam 5 (manufacturer: RunCam) in the colour black. These cameras are lightweight (56g) and small (38X38X36cm). Video quality was set to high and resolution to 4K at 30 frames per second, allowing for 90-120 minutes of battery life. Cameras were attached to a lightweight mobile-phone tripod using Velcro (Fig. 2.2).

Network indices

The resulting flower visitation data was used to build plant-flower visitor networks using the Bipartite package in R (Dormann et al., 2008). Network indices were calculated for each garden for every month they were sampled, for both the camera and visual observation data. A total of 50 camera networks and 50 and visual observation networks were constructed after removing networks that were too small to calculate indices (small networks $n=13$). We calculated network specialisation (H_2'), nestedness, interaction evenness and connectance. These network indices are commonly used in other studies (Philpott et al., 2025; Theodorou et al., 2017). Specialisation refers to the level of selectivity of all species over their interaction partners within a network. Nestedness calculated as niche overlap based on decreasing fill (NODF), describes the extent to which specialist species interact with a subset of species which generalists also interact with. Interaction evenness is the spread of interactions within the network, with higher values equating to a more even spread of interactions. Finally, connectance is the proportion of possible interactions that are realised. All the indices calculated are sensitive to network size, therefore we calculated Z-scores from these networks to standardise against network size. To do this we generated null networks using the null model function and “Vaznull” method in the Bipartite package which randomises the total number of interactions in the network whilst maintaining the actual interactions within the original network. Z scores were then calculated by: $Z = (Observed - mean(null)) / SD(null)$. *Observed* is the network index calculated from raw data and *mean(null)* is the mean value of a network index across the generated null networks and *SD(null)* is the standard deviation of a network index across the generated null networks.

Data analysis

We used Generalised Linear Mixed Models (GLMMs) in the lme4 package (Bates et al., 2015) in R (“R version 4.5.2,” 2025), to analyse flower visitor frequency and plant-flower visitor network structure. Models were checked for overdispersion, collinearity, zero-inflation and uniformity of residuals using the package performance (Lüdtke et al., 2021). Significance of variables was tested using backwards stepwise model selection using likelihood ratio tests (Zuur et al., 2009).

To address the flower visitor frequency analysis, we used the number of flower visits and the richness of flower visitors per plant species, per month, per site as response variables. The models were fitted using negative binomial distributions in the glmmTMB package (Brooks et al., 2017). Method of data collection (camera or visual observation), and day of study (first sampling day=1), were included as fixed effects. Site and plant species were included as random effects. Flower visitor frequency was also assessed for individual *Bombus* species using the same model variables as flower visitor frequency for all flower visitors.

To compare plant-flower visitor network structure, we used Gaussian distribution GLMMs. For each monthly network, in each site, the Z-scores for network specialisation, nestedness, interaction evenness and connectance were the response variables. Fixed effects included method of recording and day of sampling. Site and Day were included as a random effect.

Results

Across the 18 sites and the 4 months of data collection, 73 plants were identified to genus and 54 were identified to species. Visual observations recorded 1015 flower visits, almost two times (568) the number of flower visits recorded using cameras. Examples of flower visitations from video recordings can be seen in (Fig.2.3). No butterflies were recorded using cameras; however, the number of butterfly observations was low across the entire study (visual observations=8). Furthermore, some bee genera were not recorded by cameras, such as *Andrena*, *Anthophora*, *Halictus*, *Lasioglossum* and *Osmia* but were recorded via visual observations (*Andrena*=1, *Anthophora*=1, *Halictus*=1, *Lasioglossum*=20, *Osmia*=7). A species list of flower visitor records via visual observations and cameras can be seen in Appendix B: Table B.2 and Table B.3, respectively. Plants that received

the highest number of flower visits when measured using visual observations were *Lavandula sp.* (n=106), *Geranium sp.* (n=74) and *Brassica rapa* (n=72). With cameras the plants that received the most visits were also *Lavandula sp.* (n=79), *Brassica rapa* (n=32), and *Papaver cambricum* (n=21). A species list of plant recorded in this study can be found in Appendix B: Table B.4.



Figure 2.3: Stills from video recordings of flower visits, identified as a) *Syrphidae* on *Eriocapitella hupehensis*, b) *Apis mellifera* on *Hieracium sp.*, c) *Bombus hortorum* on *Lavandula sp.*, d) *Megachile sp.* On *Geranium sp.* Images have been cropped to focus on the flower visitor.

The mean $\pm$ SD number of flower visits per plants species recorded by cameras was 1.17 ± 2.51 , compared to 2.08 ± 3.45 flower visits by visual observations. The mean flower visitor richness to individual plants recorded with cameras was 0.49 ± 0.75 , compared to 1.22 ± 1.47 flower visiting taxa recorded by visual observations. Mean and standard deviation of network indices for both methods can be seen in Table 2.2.

Table 2.2: Mean and standard deviation of raw network indices for the camera and observation recording methods prior to Z-score calculation. Mean and standard deviation of Z-scores for corresponding network indices are also given.

Recording method	Network specialisation (mean±SD)	Network specialisation Z-score (mean±SD)	Interaction evenness (mean±SD)	Interaction evenness Z-score (mean±SD)	Nestedness (mean±SD)	Nestedness Z-score (mean±SD)	Connectance (mean±SD)	Connectance Z-score (mean±SD)
Camera	0.65±0.38	1.54±1.69	0.59±0.09	-1.35±1.14	32.4±20.0	1.14±-1.38	0.47±0.15	-1.38±0.72
Observations	0.47±0.30	1.02±1.02	0.63±0.06	-1.12±1.03	28.6±13.0	1.07±1.16	0.37±0.13	-0.97±0.67

Full results for comparisons between cameras and visual observations can be seen in Table 2.3. Visual observations recorded more flower visits (Estimate=0.66, $Z=7.86$, $p<0.001$), and greater flower visitor richness (Estimate=0.92, $Z=11.91$, $p<0.001$), than video recordings (Fig.2.4). Sampling day influenced flower visitor richness recorded (Estimate=-0.005, $Z=-3.28$, $p=0.020$), with fewer species recorded at sampling points later in the year. Certain eusocial bee species such as *Bombus pratorum* and *Apis mellifera* did not differ in their number of flower visits between the two methods. However, there were higher numbers of visits recorded using the visual observation methods for *Bombus pascuorum* (Estimate=0.71, $Z=5.06$, $p=0.007$), *Bombus lucorum* agg. (Estimate=0.60, $Z=3.27$, $p<0.001$), *Bombus hypnorum* (Estimate=0.95, $Z=2.36$, $p=0.012$) and *Bombus lapidarius* (Estimate=0.68, $Z=1.84$, $p=0.05$).

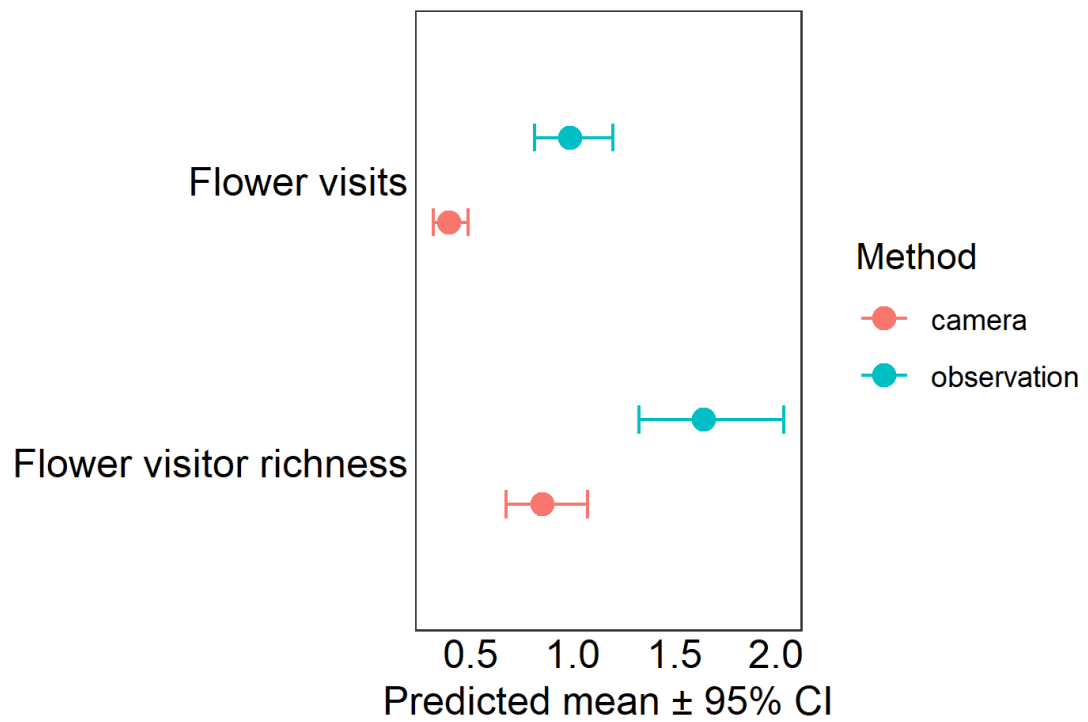


Figure 2.4: Predicted values of flower visits and flower visitor richness recorded using cameras (red) and visual observations (blue). Points represent the predicted values calculated from final models and lines represent the 95% confidence intervals.

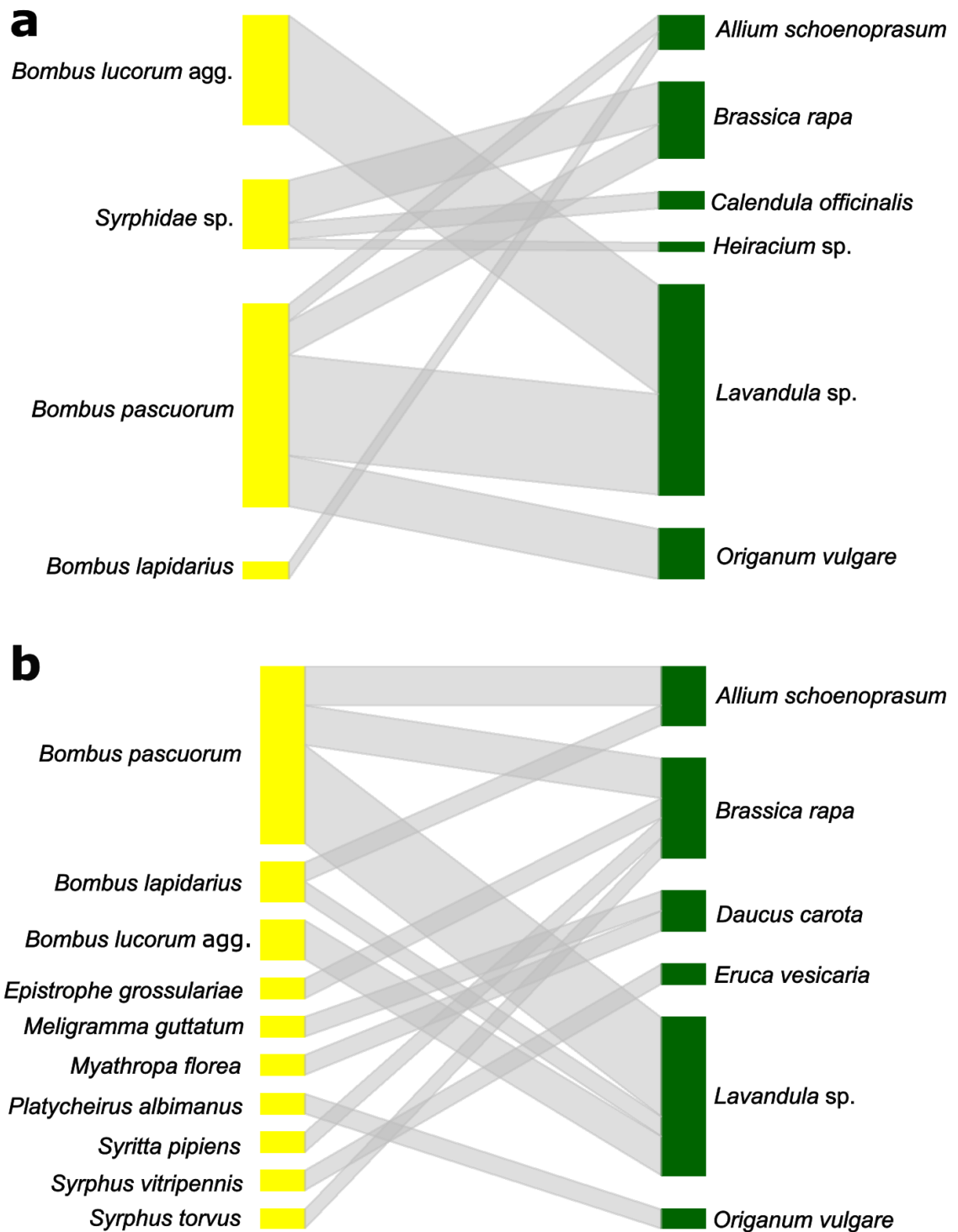


Figure 2.5: Flower visitor network structure constructed within a single garden in August using a) camera data and b) visual observation data. Flower visitors are seen in yellow, and plants in green. Grey lines indicate interactions between the flower visitor and plant level, with line thickness relative to the frequency of interactions.

An example of two networks constructed at the same sampling event using cameras and visual observations is shown in Fig.2.5. Neither network

specialisation, interaction evenness, nestedness nor connectance differed between the two methods of data collection (Fig.2.6). Sampling day did not influence any of the network indices.

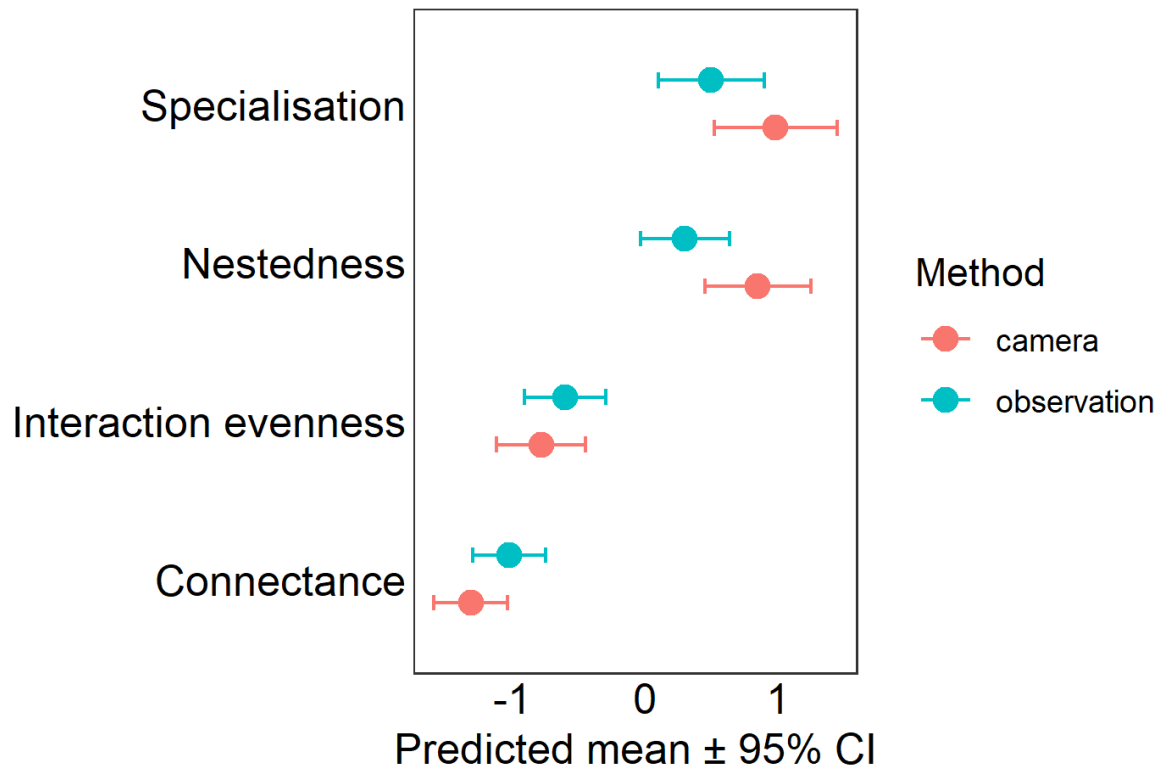


Figure 2.6: Predicted values of network indices z scores calculated from flower visitation networks recorded using cameras (red) and visual observations (blue). Points represent the predicted values calculated from final models and lines represent the 95% confidence intervals.

Table 2.3: The final models describing how method of recording influence flower visits and plant-flower visitor network structure. The table shows for each response variable the significant explanatory variables based on backwards stepwise selection of variables and likelihood ratio tests. The corresponding estimates, standard errors, z values, p values and 95% confidence intervals are shown.

Response	Explanatory	Estimate	Standard error	Z value	Conf. low - Conf. high	Adj. P value
Flower visits	Method	0.66	0.08	7.86	0.50 - 0.83	<0.001
	Day					0.390
Flower visitor richness	Method	0.92	0.08	11.91	0.77 - 1.08	<0.001
	Day	-	-	-	-	0.120
NODF	Method	-	-	-	-	0.076
	Day	-	-	-	-	0.871
	Sampling effort					0.643
H ₂ '	Method	-	-	-	-	0.525
	Day	-	-	-	-	0.181
	Sampling effort	-	-	-	-	0.643
Interaction evenness	Method	-	-	-	-	0.504
	Day	-	-	-	-	0.689
	Sampling effort	-	-	-	-	0.643
Connectance	Method	-	-	-	-	0.306
	Day	-	-	-	-	0.181
	Sampling effort	-	-	-	-	0.643

Discussion

This study directly compared video recordings of plant-flower visitor interactions to visual observations over a standardised period, contributing to the limited literature on this topic. Overall, we found video recordings were not as effective at recording plant-flower visitor interactions compared to visual observations.

Despite this, the resulting plant-flower visitor networks were similar in structure with no difference in specialisation, interaction evenness, nestedness and connectance. We discuss the difficulties in using cameras for recording flower visitor data and suggest potential improvements to this methodology.

Limitations of cameras

In our study, fewer flower visits were captured using cameras to record plants for a 20-minute period than when they were observed by a human recorder. In fact, nearly twice as many flower visits were recorded using visual observations compared to cameras. Moreover, there were fewer flower visitor species recorded using cameras, however this is to be expected as species level identification was not possible from many of the video recordings. Previously, only two studies have compared cameras to visual observations (Naqvi et al., 2022; Serra-Marin et al., 2025); although Naqvi et al. (2022) used camera traps that were set either to record every 5 minutes for 60 seconds over 3 hours or were motion activated. In these studies, cameras recorded more flower visitors than visual observations. Naqvi et al. (2022) recorded flower visits from a wider range of taxa (six insect orders), compared with the identification of only Anthophila, Syrphidae and Papilionidae in our study. Despite the difference in focal taxa and taxonomic resolution, our results still contrast those of Naqvi et al. (2022, as human observers in our study identified more flower visits than cameras across all taxa. In contrast, Naqvi et al. (2022) found scheduled cameras recorded more Hymenoptera (which includes Anthophila, recorded in our study) as well as Formicidae and Hemiptera. Finally, we undertook the two methodologies on a focal plant at different times of day, to ensure the disturbance from one method did not affect the other. This contrasts Naqvi et al. (2022) where camera recording and visual observation of focal flowers occurred concurrently. Recording flowers at different times could potentially account for the discrepancy in results between the studies. External factors influencing flower visits such as time of day and weather conditions may lead to differing numbers of flower visits between the two methods in our study. Whilst we recognise this potential limitation in our study, we believe that these external factors were controlled for by randomising the time of sampling between morning and afternoon, as well as controlling for the weather conditions.

One of the main difficulties in our study that prevented the accurate recording of flower visitor interactions with cameras was the image resolution of the cameras. As seen in Fig.2.3 the quality of plant-flower visitor interaction videos produced from the RunCam5 was relatively poor. This meant that many smaller species of bees, such as *Lasioglossum*, went undetected in videos; similar difficulties were reported in Serra-Marin et al. (2025). Image resolution in Naqvi et al. (2022) was higher, suggesting the Bushnell NatureView HD model 119740 cameras used in their study may be more useful for recording plant-flower visitor interactions. Yet, even in Naqvi et al. (2022), some flower visitor identifications, such as ants, are questionable. Moreover, the use of cameras by Naqvi et al. (2022) resulted in a higher proportion of unidentifiable insects compared to human observations (11% in cameras with pre-scheduled recording periods, 6% motion activated cameras and 2% human observations), showing camera resolution is an important factor in recording insect flower visits. One study has suggested the use of smartphones to record flower visitor interactions, as advances in smartphone technology can offer affordable, widely accessible high-resolution cameras (Ştefan et al., 2025b). However, whether smartphones can out-perform human observers has not been determined, as Ştefan et al., (2025b) did not compare the two methodologies.

Another difficulty we encountered when using cameras was not having instant playback of videos in the field. The option of using cameras with instant playback can help to ensure that videos recorded properly and that flowers and their insect visitors were visible in the environmental conditions. We had a few instances where wind gusts and sun glare made it difficult to see flowers and their visitors. While environmental conditions are generally controlled for, variation in sunlight and wind can make the use of cameras difficult. In comparison, visual observations by human observers can adapt to these conditions by better positioning themselves to see all flower visitor interactions.

Aside from the difficulties of using cameras in field, the extraction of data from video recordings was time consuming. Approximately 72 hours of video recording was annotated to determine flower visits. Thus, camera methodologies have additional time constraints to the time required for field deployments. Recently, advancements in machine learning have allowed insect identification from images although, images with uniform backgrounds taken in laboratory settings yield more accurate results (Gao et al., 2024). One study used coloured platforms with

attached cameras to successfully implement machine learning that records insect visits in the field in real time (Sittinger et al., 2024). However, progress has been made in using machine learning to identify flower visits on complex floral backgrounds (Serra-Marin et al., 2025; Ştefan et al., 2025a). The YOLOv5-small model correctly classified around 80% of Hymenoptera flower visitors, although classification accuracy was lower for other insect groups (Ştefan et al., 2025a). Therefore, machine learning could be used in conjunction with manual classification to reduce the time required to identify flower visitors in videos whilst maintaining accuracy.

Future directions for camera recordings of flower visitors

Despite fewer flower visitor detections using cameras, network structures were similar when constructed from camera and visual observations. Additionally, similar patterns were revealed between the two methods in terms of the identity of the most frequent flower visitors and most visited plant. This suggests cameras can still be useful for constructing these networks and potentially be used over a longer period to achieve more detailed networks.

Results showing similar flower visitor network structures between the two methodologies were surprising considering differing taxonomic resolution of networks as well as overall number of flower visits. Serra-Marin et al. (2025) found that cameras recorded higher network connectance and specialisation, because they captured a greater number of flower visits compared to direct observations. However, in our study the use of Z-scores to calculate network indices helps to standardise networks by their size, allowing network structure to be directly compared despite differences in their overall number of interaction partners and the number of non-zeros (Renaud et al., 2020). Similarly, studies have found network indices are conserved when compared across networks of differing taxonomic resolution (Renaud et al., 2020). We recognise that we did not compare a wide range of network indices between the two methodologies, however, we chose indices that are commonly used in flower visitor network studies specific to urban environments like our study location.

Higher resolution cameras may help to overcome the low flower visitor detection by cameras in our study, thus longer-term deployment of cameras is a promising avenue in flower visitor studies. Increasing sampling time may help to capture

rarer flower visitors and reveal more realistic patterns of flower visits (Chacoff et al., 2012). Importantly, flower visitors can occupy different temporal niches across 24 hours, meaning certain flower visitors may not be captured from cross-sectional studies (Albrecht et al., 2012; Knop et al., 2018). Previous studies have used cameras in 24 hour monitoring of focal flowers and their insect visitors revealing distinct diurnal and nocturnal flower visitor communities (Blareau et al., 2025; Wonderlin, 2024). Of course, longer term camera deployments would require larger storage capacity for data collected as well as greater battery life for cameras. Moreover, studies assessing flower visits across 24 hours focus on one or a few focal plant species (Blareau et al., 2025), meaning information on flower visits to different plants cannot be determined. Therefore, using cameras to assess flower visits to multiple plant species would require more cameras, incurring greater equipment costs.

Finally, cameras offer the advantage of being a non-lethal sampling method. Whilst insect research, particularly studies involving lethal sampling, must adhere to ethical standards, the environmental and welfare risks are not always clear (Barrett and Fischer, 2024). The use of cameras in this area of insect research is still developing, and there are important trade-offs between time and equipment costs and the resolution of data collected. However, ethical considerations are a key component of cost-benefit analyses. Although cameras may be less reliable for accurately capturing flower visitor diversity, they have shown promise in our study for quantifying plant-flower visitor network structure. Their implementation may therefore be justified when determining network structure, rather than recording visitor diversity.

Conclusion

Overall, we found cameras to be an effective tool at recording plant-flower visitor networks, despite fewer flower visitor interactions being recorded. We believe cameras to be a useful tool in recording flower visitors but recognise that improvements need to be made to the methodology with greater resolution cameras and machine learning techniques for identification. However, the use of cameras does come with additional costs to studies, and the balance between time constraints and equipment costs needs to be considered when using cameras

in the field. Yet, with the need for long-term monitoring and non-lethal sampling in a time of global insect decline, cameras offer a viable option for research.

Chapter 3 Supporting pollinators in urban gardens: floral richness and abundance influence flower visitor interactions regardless of the surrounding landscape

Abstract

Private gardens contribute a large area of land within cities. Yet little is known about the value of private gardens in pollinator conservation in terms of their management and position within the urban matrix.

We investigated seasonal patterns in how environmental variables influenced plant-flower visitor interactions and the network structure in private gardens. We collected plant-flower visitor data in 18 private gardens, across Glasgow, Scotland, simultaneously recording floral abundance and richness, plant origin, garden size, land use diversity and the area of green space surrounding gardens.

We observed a decline in native plant abundance from June until September, but flower visits to native and non-native plants did not track this seasonal pattern. Flower visits to native and non-native plants differed depending on whether visits were analysed at the community or plant species level. Furthermore, increasing non-native floral abundance showed a greater increase in flower visitors compared to when native floral abundance increased.

Plant-flower visitor networks varied seasonally, becoming more specialised in June and September, but were not influenced by other environmental variables.

Overall, higher floral richness and abundance within a garden influenced flower visits, independent of the surrounding landscape.

Our results indicate that private gardens can support pollinators in cities, regardless of the urban context in which they are situated and that pollinator diversity may be improved in gardens by increasing floral diversity. We provide a list of attractive plants species to help inform floral plantings in gardens.

Introduction

Pollinators provide an important ecosystem service, in that they facilitate the reproduction of flowering plants (Ollerton et al., 2011), including 76% of global crop species (Klein et al., 2007). Thus, pollinator declines due to climate and land

use change, are concerning. The effects of urbanisation, which sees the conversion of natural landscapes to those dominated by impervious surfaces, on pollinator diversity are therefore of increasing interest due to the potential conservation value of urban green spaces. Urban environments support comparably fewer pollinator species and a more homogenised community than natural areas due to environmental pressures that select on pollinator traits such as body size and diet breadth (Ayers and Rehan, 2021; Wenzel et al., 2020). For example, the prevalence of impervious surfaces in urban areas limits nesting availability for ground-nesting bees (Geslin et al., 2016). Yet, mechanisms of selection against certain pollinator traits are more nuanced, as pollinators possess multiple traits which are influenced by multiple interacting environmental drivers acting at both local and landscape scales (Bennett and Lovell, 2019). However, compared to agricultural areas, urban areas can be strongholds for certain pollinator species due to the comparatively heterogeneous landscape and higher floral richness in cities (Theodorou et al., 2017).

Urban green spaces vary in their habitat suitability for pollinators (Baldock et al., 2019; Daniels et al., 2020; Dylewski et al., 2019). Few comprehensive studies of urban green spaces have been conducted, yet private, residential gardens have been cited as one of the best habitats for pollinators within the urban matrix (Baldock et al., 2019). Despite being small, private gardens collectively contribute to a large area of pollinator habitat (Baldock et al., 2019). Gardens often have high floral abundance, yet many of the floral species in gardens are non-native (Erickson et al., 2020), which are often unsuitable for specialist pollinator species (Chrobok et al., 2013; Salisbury et al., 2015). Nonetheless, some non-native plant species are highly attractive to pollinators (Salisbury et al., 2015). Many studies have investigated how the characteristics of urban green space habitats influence pollinator diversity (Baldock et al., 2019; Daniels et al., 2020; Dylewski et al., 2019; Tassin de Montaigu and Goulson, 2024), but thus far, there has been comparatively little focus on plant-pollinator networks in private green spaces.

Plant-pollinator networks are mutualistic interaction networks which form the basis of biodiversity preservation as their structure relates to the stability and functioning of ecosystems (Elle et al., 2012; Ferreira et al., 2013). Thus, the study of interaction networks can uncover valuable information for conservation (Elle et

al., 2012). Within gardens, the local habitat varies significantly, with differences in their floral diversity, composition and garden size; all of which may influence plant-pollinator networks. For example, increased floral richness allows niche segregation within pollinator species by reducing competition for floral resources (Gómez-Martínez et al., 2022). Consequently, specialisation increases with floral richness. Recently, studies have focused on the roles of non-native plants in structuring plant-pollinator networks (Staab et al., 2020; Zaninotto et al., 2023b). Pollinators show preferences for native plants (Chrobock et al., 2013; Lowenstein et al., 2019; Salisbury et al., 2015), and many specialist pollinators are unable to forage on non-native plants, leading to a loss of specialists from the environment (Seitz et al., 2020). However, some studies have shown that certain non-native plants are attractive to pollinators later in the flowering season when native plants are scarce (Staab et al., 2020; Zaninotto et al., 2023b). These late-season non-native plants either substitute for native plants, having little effect on the network (Staab et al., 2020) or decrease network specialisation by attracting generalist pollinators (Zaninotto et al., 2023b). Finally, garden size may influence network structure as smaller, specialist pollinators rely on larger patches in fragmented habitats (Bommarco et al., 2010). As size restricts foraging range, and specialism restricts pollinator diet, smaller gardens may result in fewer specialist pollinators (Bommarco et al., 2010; Herrmann et al., 2023).

Additional to the local characteristics of gardens, the context in which a green space is situated within the urban matrix may influence plant-pollinator networks (Herrmann et al., 2023). Studies on urban-rural gradients, or those that compare different land uses, have found urbanisation to positively influence network specialisation (Baldock et al., 2015; Proesmans et al., 2024; Theodorou et al., 2017). Moreover, grasslands surrounded by more impervious surfaces have higher species specialisation (Herrmann et al., 2023). However, these studies suggest that increased specialisation is due to abundant non-native plant species rather than a consequence of the impervious surface around a site. Furthermore, how the surrounding urban matrix is categorised may affect the results on plant-pollinator networks. For example, landscape diversity positively influenced network specialisation and nestedness (the extent to which specialists interact with a subset of species that generalists also interact with), whereas the abundance of green space had no effect (Graf et al., 2024). Here, landscape

diversity is thought to increase both nesting and floral resources surrounding a site (Graf et al., 2024). Overall, the effect of the surrounding landscape on plant-pollinator networks remains unclear.

Studies on plant-pollinator networks in urban green spaces often consider local and landscape variables or plant origin in isolation, despite these environmental drivers likely interacting to influence plant-pollinator networks. In this study, we therefore examined which of the following environmental variables in private gardens influenced pollinator interactions across the season; floral abundance, richness, plant origin, garden size and surrounding landscape. The aims and hypotheses tested in this study are as follows: 1) To assess the effect of garden and landscape level environmental drivers, including monthly variation, on flower visitation and community similarity. Increasing floral abundance and richness of native plants will increase flower visits (H1). Native plants will receive more flower visits than non-native plants when tested at the plant community and species level (H2). Flower visitor community composition will differ between gardens with different floral abundance and richness, and across months (H3). 2) Determine the influence of garden and landscape characteristics on plant-pollinator network structure, including monthly variation. Network specialisation will increase with floral richness due to niche partitioning (H4). Networks will become less specialised, more nested and with higher interaction evenness in September compared to June due to increased abundances of non-native plants (H5). 3) Examine whether patterns in flower visits and network structure are driven by a single dominant species. Environmental variables will still significantly affect network structure and flower visitor interactions when the most dominant species is excluded (H6). Finally, to promote pollinator-friendly gardening and guide floral plantings, we identified plant species preferred by pollinators using null networks.

Methods

A total of 18 gardens were sampled across the City of Glasgow, Scotland, extending to a 5km buffer from the city boundary (Appendix C: Figure C.1), with individual gardens sampled on separate days once a month from the 1st of June 2023 until the 30th of September 2023. Due to the difficulty in recruiting garden

owners, spring was not sampled in this study. Gardens were recruited via social media advertisement and chosen on a first-come, first-selected basis, provided they were located over 1km away from other chosen gardens. While this method of recruitment may have introduced a selection bias of sample sites towards pollinator friendly management in gardens, the gardens were visited before sampling commenced to ensure a range of management styles was included in the study. Variation in garden management is demonstrated by the range of mean floral abundances (15.38 ± 13.69 to 159.38 ± 222.48) and richness (1.38 ± 1.51 to 6 ± 5.22) across the four study months present at sites. A minimum of 1km was left between sites, as this is greater than the average foraging range of most flower visitors (Kendall et al., 2022), thus ensuring sites were independent. However, some studies have found maximum foraging ranges to be greater than 1km (Kendall et al., 2022), thus we tested for spatial autocorrelation during data analysis.

Floral resources

At the start of each sampling day, floral resources were inventoried. Transects (0.25m width) were used to record a floral inventory. Due to differences in the shape and size of gardens, transects were made equal to the length of the garden and were stratified to use one transect per 5m width of each vegetation type (grassy areas, floral borders and vegetable patches). Transects lengths ranged from 10m to 60m (mean $\pm$ SD: 25.44 ± 14.60). Plants that fell within the transect were identified to genus or species, and the number of floral units (individual flowers) on each plant was counted. Apiaceae umbels and Asteraceae flower heads were counted as one floral unit. Shrubs and trees (up to a height of 1.5m) were included in the count, with the number of flowers on one branch counted and multiplied by an estimate of the number of branches within the transect. One observer, (E.P), carried out the plant recording and identifying using botanical keys (Rose and O'Reilly, 2006). Garden owners would provide information where possible on the identification of non-native ornamental species which would be corroborated using pictures of the plants taken in the field and online resources. Where possible plants were identified to the lowest possible taxonomic level following the International Code of Nomenclature for algae, fungi and plants. Plant origin was classified using the BSBI atlas (Stroh et al., 2023), in which the

GB status of the plant was used, and neophytes and aliens were grouped as non-native and archaeotypes as native. Two plant species were not categorised into these groups by the BSBI atlas and were classified as unknown.

Plant-flower visitor network

After creating floral inventories, floral resources were identified and counted. Flower visitor sampling was carried out between 0930 and 1130 (morning) and 1230 and 1700 (afternoon), provided the temperature was above 10 degrees, on clear days with wind speed below 15km/h. One flower of each species was randomly chosen to be observed for its flower visitor interactions and randomly assigned to morning or afternoon recording. Flowers were observed by a single observer (E.P.), for 20 minutes after a 2-minute settling period in which the observer had positioned themselves nearby the flower. Any Syrphidae, Papilionoidea or Anthophila observed to touch the reproductive part of the flower were recorded. Any flower visitors that were not identifiable in the field were euthanised using ethyl acetate vapours or by freezing within 30 minutes of collection. Flower visitors were identified by E.P using the Field Guide to Bees of Great Britain and Ireland (Falk and Lewington, 2018) and British Hoverflies (Stubbs and Falk, 2002). We recognise these observations only consider flower visits, meaning actual pollination may not have occurred in these flower visits. The maximum number of plant species observed in one day, in one garden, was 17 (mean $\pm$ SD = 4.09 ± 2.40). As sampling in an individual garden was limited to one day a month, plant observations could not be longer than 20 minutes each, with 340 minutes being the maximum total observation time in one garden. Finally, sampling events were separated by at least three weeks to ensure insect populations recovered and to maintain temporal independence of sampling events.

Quantitative plant-flower visitor networks were built using the Bipartite package in R (Dormann et al., 2008). We removed networks with fewer than two species per level to calculate network-level indices, as this is the smallest possible network size that allows network indices to be calculated. For species indices, flower visitors observed once in the sampling period were removed. For each network (per site, per month), we calculated the following indices:

- H_2' -The specialisation of the whole network describes the level of selectivity within the network. This index ranges from 0 (no specialisation) to 1 (complete specialisation) (Blüthgen et al., 2008).
- Interaction evenness- The spread of interactions within the network. Higher interaction evenness equates to an even spread of interactions throughout the network. Ranging from 0 to 1, a network with fewer interactions that occur in high frequency will have lower interaction evenness (Blüthgen et al., 2008).
- Weighted Niche Overlap based on Decreasing Fill (WNODF)- a measure of nestedness, the extent to which specialists interact with a subset of species, which generalists also interact with (Blüthgen et al., 2008).
- d' - Species specialisation, the level of selectivity of a species, ranging from 0 to 1 (Blüthgen et al., 2006).
- Network size: the number of species in each level of the network (number of plant species plus the number of flower visitor species). This was calculated to use as a control when modelling network indices, as quantitative network metrics are sensitive to network size.

Environmental variables

The total area of the garden was measured in m^2 using QGIS v3.32.1 (Herrmann et al., 2023; Stewart et al., 2018). The Urban Atlas data set from Copernicus (European Union, 2020) was used to describe land use types surrounding sites (resolution 0.25ha). We quantified the total percentage cover of sports and leisure facilities, pastures, permanent crops, artificial non-agricultural vegetated areas, shrubs and herbaceous vegetation, arable land, forest and herbaceous vegetation association within buffers of 100m, 200m, 400m, 600m, 800m and 1000m to measure surrounding green space. We used the area of each land use category within the same buffers and the Shannon-Weiner index to calculate land use

diversity around gardens. While these green space types may vary in their quality as flower visitor habitat in terms of their floral resources, there are no data that quantifies the quality of these spaces in Glasgow.

Data analysis

All analysis was carried out in R version 4.4.2. All continuous explanatory variables were standardised using R's scale function, which centres variables by subtracting their mean and dividing by the standard deviation. In all models described below, the significance of variables was tested using a backwards stepwise model selection and likelihood ratio tests (Zuur et al., 2009). Models were checked for uniformity and homoscedasticity of residuals using the DHARMA package (Hartig, 2024). Collinearity, zero inflation and overdispersion of models were checked using the performance package (Lüdtke et al., 2021). We tested for spatial autocorrelation by computing Moran's I values on the residuals of each model using the DHARMA package. No spatial autocorrelation was detected in any of the models. Finally, we fitted models for each of our response variables described below with fixed explanatory landscape variables (land use diversity and area of green space), at different landscape scales (100m, 200m, 400m, 600m, 800m and 1000m). We then compared model AIC values (Bozdogan, 1987) to test the best landscape scale to use in models. For flower visitor richness at the community level the 400m buffer had the lowest AIC (AIC=520.00). In contrast, models for the other response variables did not show differences in AIC scores when comparing landscape scales, therefore 400m was chosen as the landscape scale to be included in all models. All P values reported in the results section were adjusted using the false discovery rate (FDR) method.

Floral resources

Differences in floral abundance and richness were tested using Generalised Linear Mixed Models (GLMMs). Floral abundance was modelled using a negative binomial distribution in the R package glmmTMB (Brooks et al., 2017) and floral richness using a Poisson distribution in the R package lme4 (Bates et al., 2015). Fixed explanatory variables included land use diversity, area of green space, month as a linear and quadratic effect, and plant origin. Garden size was included to control

for larger gardens having higher floral abundances. Site was included in models as a random effect.

Flower visitor interactions

Firstly, we assessed how predictor variables influenced flower visitor interactions in the whole community using GLMMs with a negative binomial distribution. Here, we used the total number of interactions and the species richness of flower visitors to all native or non-native plants as response variables. We used the continuous explanatory variables: floral richness, garden size, percentage green space, land use diversity and month as a linear and quadratic term, as well as the categorical variable plant origin as fixed effects. Interactions among month and plant origin and floral richness and between month and plant origin were also included. As floral abundance per m² introduced collinearity, we separately modelled floral abundance per m² and its interaction with plant origin as fixed effects. Site was included as a random effect. Due to the high number of interactions from *Bombus pascuorum* (~25% of interactions), we analysed the number and richness of floral visits without *B. pascuorum*. *B. pascuorum* is a known generalist species that is capable of foraging on a range of plants (Fisogni et al., 2022), thus we wanted to assess whether the patterns in flower visitor interactions were driven by *B. pascuorum*.

Secondly, we tested floral visits at the plant species level, in that response variables were the number and richness of floral visits per plant species. Floral visits at the plant species level were modelled using negative binomial distributions, and flower visitor richness at the plant species level was modelled using Poisson distributions with a zero-inflation factor. Fixed explanatory variables included garden size, area of green space, land use diversity, month as a linear and quadratic effect, plant origin and an interaction between month and plant origin. These models also included the floral abundance of plant species as a fixed effect to control for the fact that plants with higher floral abundance are more likely to attract pollinators. Site and plant species were included as random effects.

Next, we assessed the percentage of native and non-native plant species within networks that received interactions using GLMMs with a binomial distribution. Here, we divided the number of native or non-native plant species that received flower visits by the total number of native or non-native plant species in the network. Plant origin, floral abundance per m², floral richness, garden size, percentage green space and land use diversity were linear fixed effects, and month was included as both a linear and quadratic fixed effect. Interactions among month, plant origin, floral abundance and floral richness were also included. Site was a random effect.

Finally, we assessed the similarities of flower visitor communities at different sites using Hellinger-transformed species abundances. Hellinger transformations reduce the influence of highly abundant species whilst preserving ecological distances. A PERMANOVA was used to test for the significance of environmental variables (floral richness, floral abundance per m², plant origin, garden size, land use diversity, area of green space around a site and month) in influencing community differences. Here we used the `Adonis2` function in the R package `vegan` (Oksanen et al., 2024). For visualisation, NMDS plots were made using the `metaMDS` function in `vegan` (Oksanen et al., 2024) and used Bray-Curtis dissimilarity values.

Network indices

We used beta distribution GLMMs in the `glmmTMB` R package (Brooks et al., 2017), to test for differences in network specialisation, interaction evenness and flower visitor specialisation, and Gaussian distribution GLMMs for nestedness. We also modelled pollinator specialisation using a zero-inflated beta distribution; however, this did not improve the model fit. Therefore, we used the original beta regression as this was a simpler model; a similar approach was used in Zaninotto et al. (2023b). The fixed explanatory variables used were plant origin, month as both a linear and quadratic effect, floral abundance per m², floral richness and their interactions. Month was modelled separately from plant origin to avoid collinearity. We included network size as a fixed effect due to its influence on

network indices. Site was included as a random effect. In addition, models for flower visitor specialisation included the abundance of individual flower visitor species as a fixed effect, and flower visitor species identity as a random effect.

Again, because *B. pascuorum* interactions were highly frequent and may shape plant-flower visitor network structure, we recalculated all network indices when *B. pascuorum* was removed from the network. Similarly, we carried out a separate analysis of species specialisation scores without *B. pascuorum* in the data set and tested *B. pascuorum* specialisation scores when all other species had been removed from the data set.

Plant preferences based on floral abundance

We used the *econullnet* package (Vaughan et al., 2018) to generate null models based on floral abundance, allowing us to test whether flower visitors interact with plant species more or less frequently than expected given plant species availability. As visit frequency is expected to be influenced by the abundance of available plant species, this approach enabled us to identify specific floral preferences of individual flower visitor species. If flower visitors interacted with a plant more than expected, it is assumed that the flower visitor had preferences for that plant species. The complete list of plant preferences is included in the supplementary material (Appendix C, Table C.3)

Results

Floral resources

Gardens varied in their floral abundance each month (June native mean $\pm$ SD = 124.93 $\pm$ 145.12 flowers, June non-native 19.2 $\pm$ 23.67 flowers, July native 107.88 $\pm$ 76.00 flowers, July non-native 44.53 $\pm$ 26.00 flowers, August native 45.25 $\pm$ 39.50 flowers, August non-native 44.13 $\pm$ 30.50 flowers, September native 25.14 $\pm$ 17.89 flowers, September non-native 33.00 $\pm$ 22.82 flowers). Similar variation was observed in floral richness (June native: mean $\pm$ SD = 5.86 $\pm$ 2.28 flower species, June non-native 1.70 $\pm$ 1.06 flower species, July native 6.18 $\pm$ 3.11, July non-native 2.65 $\pm$ 1.11 flower species, August native 4.94 $\pm$ 2.11 flower species, August non-

native 3.31 ± 1.66 flower species, September native 4.00 ± 1.52 flower species, September non-native 3.17 ± 1.64 flower species).

Final models for floral abundance and floral richness can be seen in Table 3.1. Floral abundance changed across months with higher abundances in July and August compared to June and September (Estimate=-1.08, $z=-2.4$, $p=0.024$). An interaction between plant origin and month influenced floral abundance (Estimate=0.73, $z=4.33$, $p<0.001$) (Fig. 3.1a). Overall, non-native plant abundance increased across the months, and native plants decreased. This pattern reflects the later phenology of non-native plants compared to native plants found in other studies (Zaninotto et al., 2023b). An interaction between month and plant origin on floral richness was significant (Estimate=0.32, $z=3.13$, $p=0.001$); again, native plant richness decreased whilst non-native plants increased across the months (Fig. 3.1b). Native floral richness was greater than non-native floral richness (Estimate=-0.64, $z=-6.4$, $p<0.001$).

Table 3.1: Model outputs to explain response variables of flower visits (at the community level, for *B. pascuorum* only and the percentage of plant species interacted with), floral resources (floral abundance and floral richness), network indices (H2', interaction evenness, WNODF, d' for all pollinators and d' for *B. pascuorum* only). For each significant explanatory variable included in the final models, the table reports the estimate, standard error, z value, 95% confidence interval, and p values (adjusted using the FDR method).

Response	Predictors	Estimate	Z	Standard error	Conf. low	Conf. high	Adj. P value
Flower visits							
Flower visits at the community level	Floral richness	0.27	3.89	0.07	0.110	0.403	<0.001
	Origin	-0.30	-2.32	0.13	-0.566	-0.0436	0.035
	Month	-0.26	-3.60	0.07	-0.405	-0.116	0.004
	Floral abundance/ m2	-0.04	-0.42	0.10	-0.25	0.17	0.047
	Floral abundance*Origin	0.30	0.15	2.06	0.008	0.60	0.041
Flower visitor richness at the community level	Floral richness	0.39	7.00	0.06	0.28	0.50	<0.001
	Floral abundance * Origin	0.14	1.42	0.10	-0.06	0.33	0.041
Flower visits at the plant level	Month	-0.20	-3.15	0.06	-0.33	-0.08	0.002
	Floral abundance	0.19	2.86	0.07	0.06	0.32	0.001
Flower visitor richness at the plant level	Month	-0.16	-3.51	0.05	-0.27	-0.06	0.002
	Origin	0.33	2.01	0.17	0.01	0.66	0.048
	Floral abundance	0.16	3.30	0.05	0.07	0.26	0.001
Percentage of plants to receive visits	Origin	0.45	2.10	0.19	0.60	0.76	0.042
<i>B. pascuorum</i> flower visits	Floral richness	0.02	0.48	0.05	-0.07	0.12	0.002
	Floral abundance	0.31	7.16	0.04	0.23	0.4	<0.001
	Origin	0.12	1.85	0.07	-0.008	0.25	0.027
	Month*Origin	0.48	7.72	0.06	0.36	0.60	<0.001
	Floral richness * Origin	-0.18	-3.56	0.05	-0.29	-0.08	<0.001
Flower visits excluding <i>B. pascuorum</i>	Floral abundance	0.35	3.31	0.11	0.15	0.57	0.001
	Floral richness	0.47	5.57	0.08	0.30	0.64	<0.001
	Month	-0.31	-3.79	0.08	-0.48	-0.15	<0.001
Flower visitor richness excluding <i>B. pascuorum</i>	Floral abundance	0.28	3.02	0.09	0.10	0.47	0.003
	Floral richness	0.60	8.62	0.07	0.47	0.75	<0.001
	Month	-0.17	-2.74	0.06	-0.29	-0.05	0.013
	Origin	0.31	2.16	0.15	0.03	0.61	0.036
Floral resources							
Floral abundance	Month	0.48	1.05	0.46	-0.44	1.38	<0.001
	Month^2	-1.08	-2.40	0.45	-1.97	-0.18	0.024
	Origin	-0.58	-3.43	0.17	-0.91	-0.24	0.027
	Month*Origin	0.73	4.33	0.17	0.40	1.07	<0.001

Floral richness	Origin	-0.64	-6.40	0.1	-0.84	-0.45	<0.001
	Month*Origin	0.32	3.13	0.10	0.12	0.52	0.001
Network indices							
H ₂ '	Month^2	2.55	3.86	0.66	1.25	3.84	<0.001
Interaction evenness	Month^2	-0.40	-2.64	0.15	-0.71	-0.10	0.019
WNODF	Month^2	-22.67	-2.09	10.85	-44.2	-1.16	0.038
D' for all pollinators	Month^2	0.61	2.23	0.27	0.07	1.14	0.031
D' for <i>B.pascuourm</i> only	Month^2	2.94	4.19	0.70	1.55	4.32	<0.001

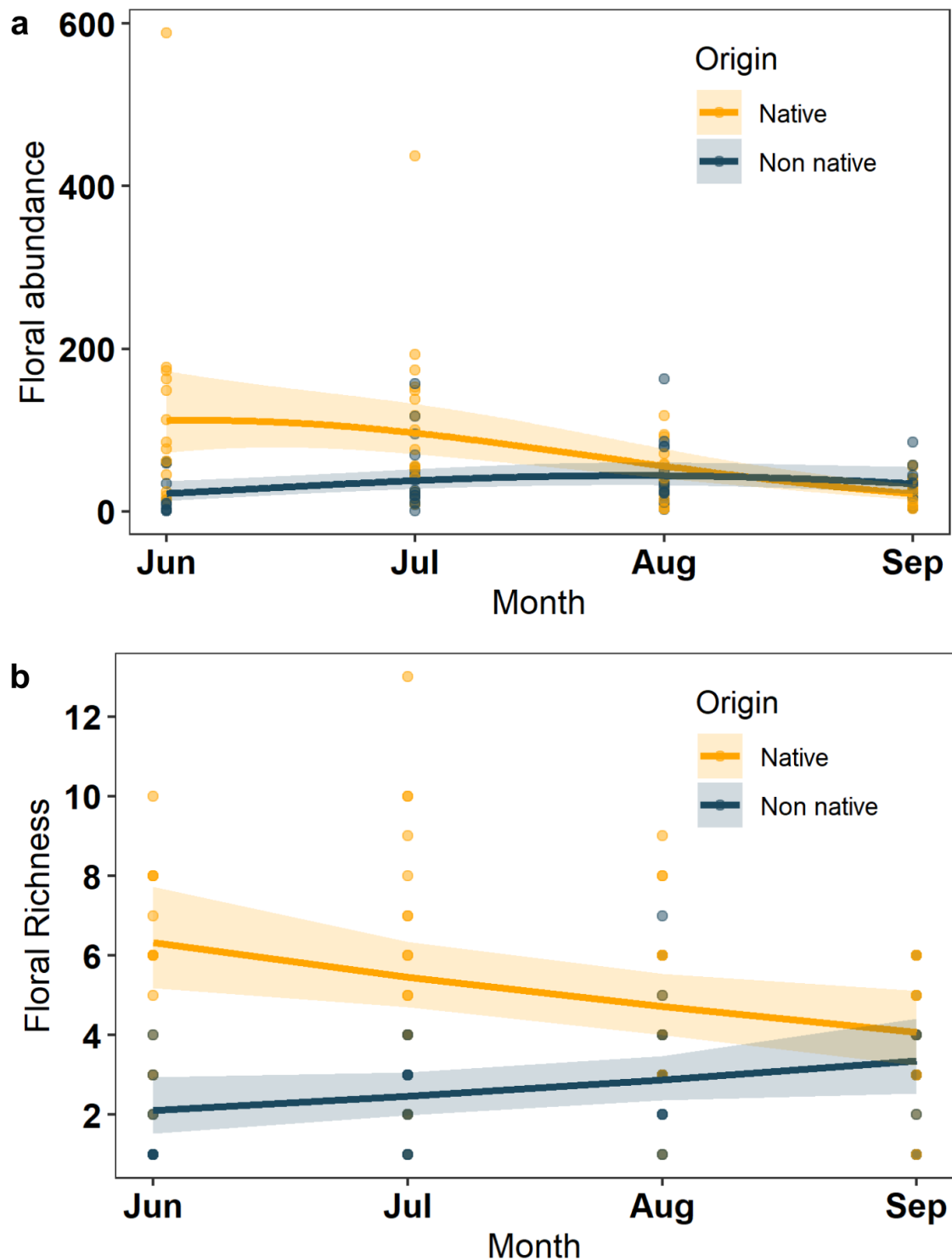


Figure 3.1: a) Floral abundance and b) floral richness of native and non-native plants across the four months of the study. Points show raw data for floral values collected in the field per site per month. The solid line shows the fitted regression with shaded areas representing the 95% confidence intervals.

Flower visitor interactions

After removing small networks, a total of 1014 flower visits were recorded in gardens, comprising 126 plant and 55 flower visitor species. *B. pascuorum*

contributed to 25% of interactions (n=256), followed by 17% from *Bombus lucorum* agg. (n=174), and 8% from *Episyrphus balteatus* (n=82). The plants that received the most visits were *Lavandula* sp. (10%, n=106), *Geranium* sp. (8%, n=76) and *Brassica rapa* (7%, n= 71). The full list of flower visitor and plant species can be found in the online resources (Appendix C, Table C. 1 and Table C. 2, respectively).

Final models for flower visits and flower visitor richness at the community level can be seen in Table 3.1. The total number of flower visits was influenced by floral abundance per m² depending on plant origin (floral abundance*plant origin: Estimate=0.30, z=0.15 p=0.041; Fig.2a). An increase in the abundance of non-native plants led to a greater increase in the number of floral visits than when native plant abundance increased. The number of flower visits was positively influenced by floral richness (Estimate=0.27, z=3.89, p<0.001), and floral abundance per m² (Estimate=-0.04, z=-0.42, p=0.047). Native plants received more flower visits than non-native plants at the community level (Estimate=-0.30, z=-2.32, p=0.035). Floral visits decreased from June to September (Estimate=-0.26, z=-3.60, p=0.004). Notably, the richness of floral visitors was influenced by floral abundance, depending on plant origin (Estimate=0.14, z=1.42, p=0.041) (Fig.3.2b). Here, the positive relationship between flower visitor richness and plant abundance was greater for non-native plants than native plants. Furthermore, flower visitor richness increased with floral richness (Estimate=0.39, Z=7.00, p<0.001). Neither land use diversity nor the area of green space affected flower visitor abundance or richness.

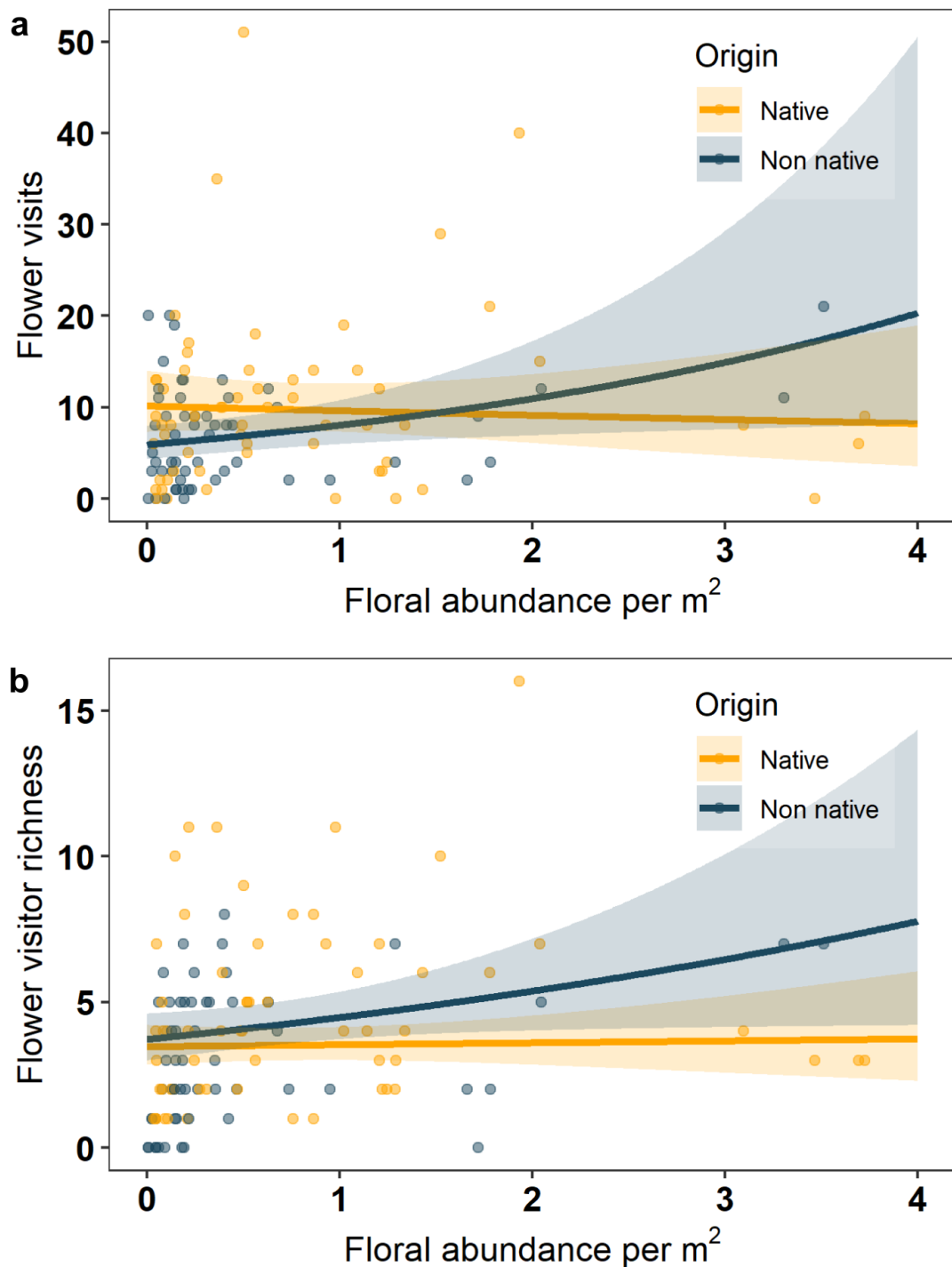


Figure 3.2: The influence of plant origin (native orange, non-native blue) on a) the total number of flower visits at the community level as floral abundance per m² increased b) the total richness of flower visitors at the community level as floral abundance per m² increased. Points show the raw values of total flower visitors to native or non-native plants per site per month. The solid line shows the fitted regression with shaded area representing the 95% confidence interval.

When removing *B. pascuorum* from flower visitor interactions, different trends were observed compared to data analysed at the whole community level. Flower visits and flower visitor richness when analysed without *B. pascuorum* were no

longer influence by floral abundance per m² depending on plant origin. Here, flower visits increased with floral abundance per m² and richness (Estimate=0.35, $z=3.31$, $p=0.001$ and Estimate=0.47, $z=5.57$, $p<0.001$ respectively), similar to their effects on flower visitor richness (Estimate=0.28, $z=3.02$, $p=0.003$ and Estimate=0.60, $z=8.62$, $p<0.001$ respectively). Both flower visits and flower visitor richness declined across the four study months when *B. pascuorum* was excluded (Estimate=-0.31, $z=-3.79$, $p<0.001$ and Estimate=-0.17, $z=-2.74$, $p=0.013$). When analysing *B. pascuorum* visits only, results showed a strong interaction between plant origin and month (Estimate=0.48, $z=7.72$, $p<0.001$) (Fig.3.3). Moreover, the flower visits of *B. pascuorum* increased with floral richness depending on plant origin (Estimate=-0.18, $z=-3.56$, $p<0.001$), where native floral richness increased flower visits more than when non-native floral richness increased. Thus, the most dominant flower visitor species appears to influence patterns of flower visitation when the whole flower visitor community was analysed.

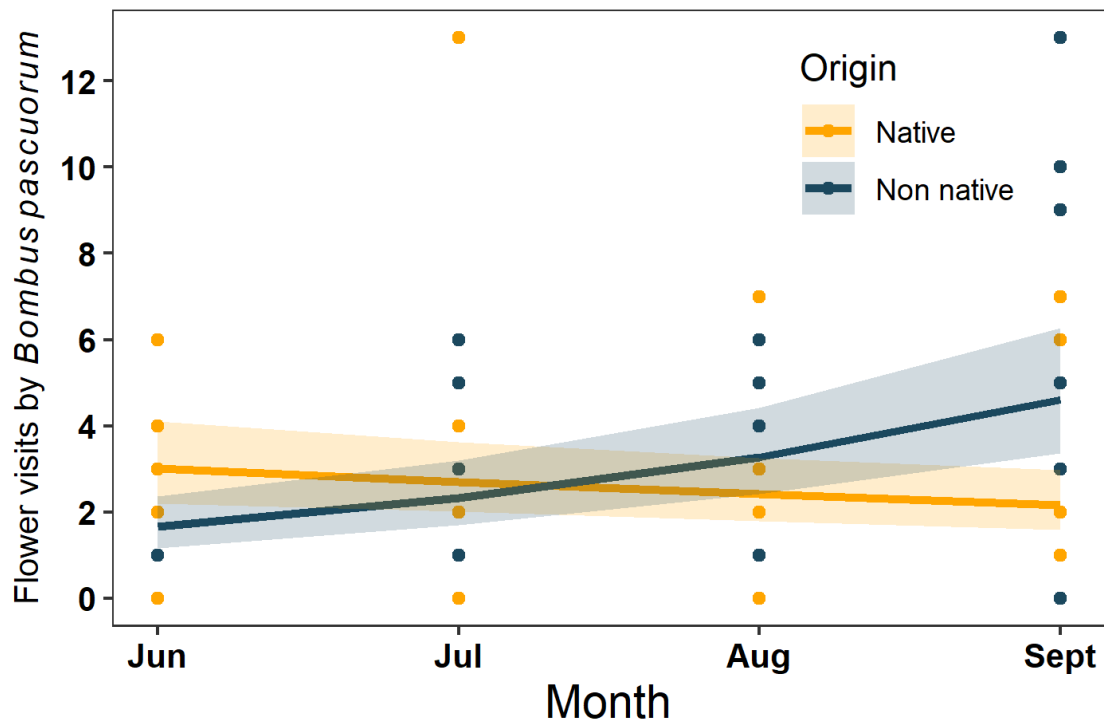


Figure 3.3: Flower visits by *Bombus pascuorum*, to native (orange) and non-native (blue) plants at the plant community level. Visits to native plants by *B. pascuorum* decreased from June to September, while visits to non-native plants increased. Points show the raw values of *B. pascuorum* visits to native and non-native plants in gardens per month. Lines show final model predictions of *B. pascuorum* visits and shaded areas represent the 95% confident intervals.

Final models for flower visits and flower visitor richness at the plant species level can be seen in Table 3.1. At the plant species level, flower visits to plants decreased from June to September (Estimate=-0.20, $z=-3.15$, $p=0.002$). Moreover, flower visits to individual plants increased with the floral abundance of plant species that were visited (Estimate=0.19, $z=2.86$, $p=0.001$). The richness of floral visitors to plant species was influenced by month (Estimate=-0.16, $z=-3.51$, $p=0.002$) and plant origin (Estimate=0.33, $z=2.01$, $p=0.048$). Non-native plants received more visitor species, and the species richness of floral visitors to plant species declined from June to September, regardless of plant origin. Finally, flower visitor richness to individual flowers increased with the floral abundance of plants species that were visited (Estimate=0.16, $z=3.30$, $p=0.001$).

Plant origin was the only determinant of the percentage of plant species that flower visitors interacted with; a higher proportion of non-native plant species received interactions, compared to native plants (Estimate=11.25, $t= 2.45$, $p=0.027$). Month did not affect the proportion of native or non-native plants within networks that received interactions.

Flower visitor communities were significantly different between months ($F=2.923$, $DF=3$, $R^2=0.127$, $p=0.001$) (Fig. 3.4) and differed with the floral richness at the site ($F=2.137$, $DF=1$, $R^2=0.028$, $p=0.044$).

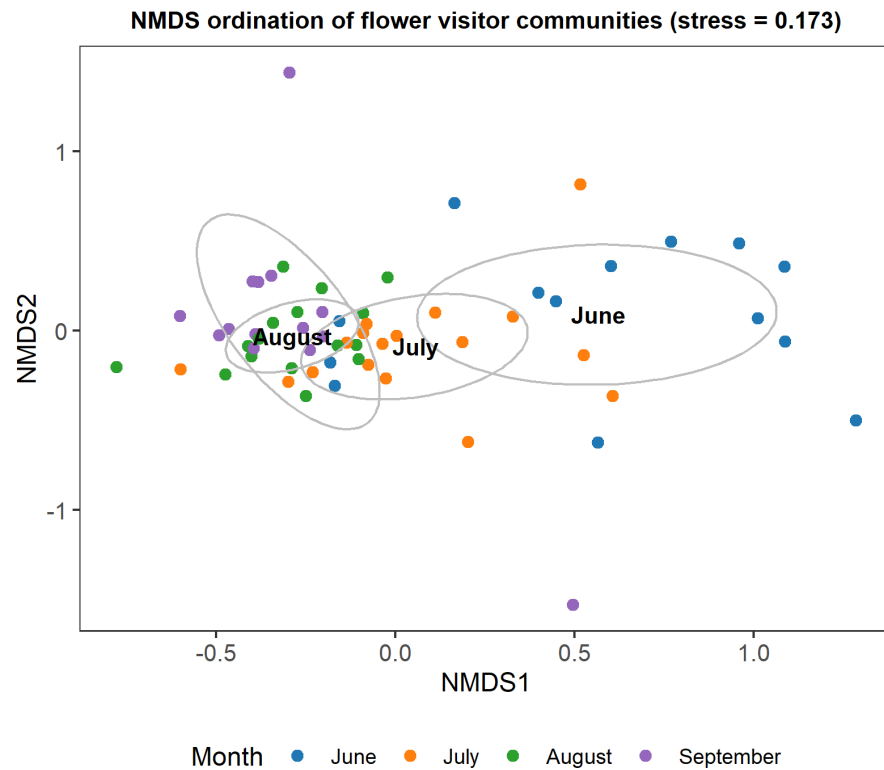


Figure 3.4: NMDS ordination plot of flower visitor communities based on Hellinger transformed species abundances and Bray-Curtis dissimilarities (stress=0.17). Points represent sites coloured by month. 95% confidence ellipses indicate monthly groupings of sites, with the centroid labelled accordingly. Month was a significant factor in structuring flower visitor community composition. NMDS axes represent the relative distance between communities at each site, in each month.

Plant-flower visitor network structure

Network sizes ranged from 4 to 25. All networks showed a mean $\pm$ SD H_2' value of 0.49 ± 0.32 , a mean WNODF value of 31.17 ± 22.21 , and a mean interaction evenness of 0.63 ± 0.08 .

Final models for network structure, with and without *B. pascuorum* can be seen in Table 3.1. All indices of network structure were influenced by month (H_2' : Estimate= 2.55, $z=3.86$, $p<0.001$; Fig. 5a, Interaction evenness: Estimate= -0.40, $z=-2.642$, $p=0.019$; WNODF: Estimate= -22.67, $z=-2.09$, $p=0.038$). No other explanatory variables influenced network structure. Similarly, month was the only predictor variable of flower visitor specialisation (d' : Estimate= 0.61, $z=2.162$, $p=0.031$).

When removing *B. pascuorum* from networks, network specialisation did not vary across the four months of the study (Fig.3.5b), nor were they influenced by any of the variables tested. However, when analysing the specialisation of *B. pascuorum* only, month had a strong influence (Estimate=2.94, $z=4.19$ $p<0.001$), with specialisation increasing in September (Fig.3.5c). Yet species specialisation values for all species excluding *B. pascuorum* showed no differences across the four months (Fig.3.5d).

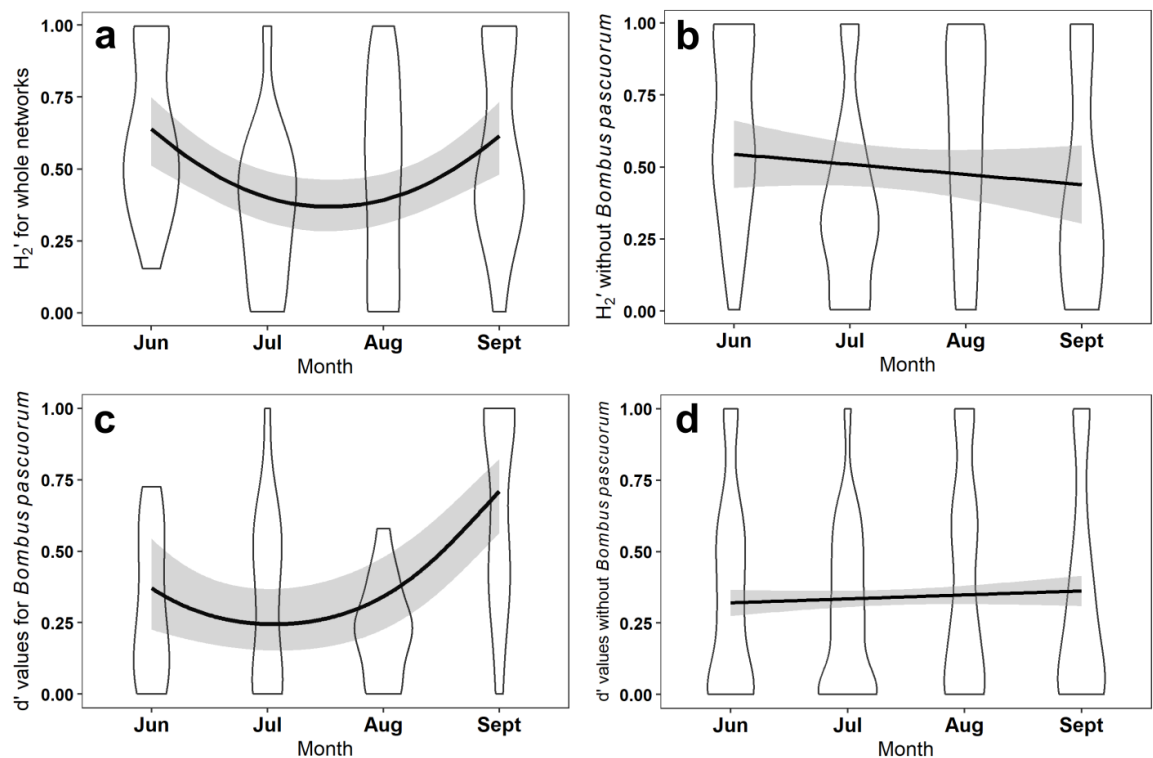


Figure 3.5: a) H_2' when calculated for whole networks including *Bombus pascuorum*, showed variation across the months of the study, increasing in June and September, and decreasing in July and August. b) H_2' when calculated without *B. pascuorum* interactions did not show any variation across the four months of the study. c) species specialisation in *B. pascuorum* showed variation between months, decreasing in July and August and increasing in September. d) Flower visitor specialisation (d') when *B. pascuorum* was filtered from the data set showed no variation across the four months of the study. Violin plots show the spread of network indices calculated in each month for each garden and duplicated across native and non-native plants. Lines in graphs a & c show predicted values from the model fit and lines in b & d show the lines of best fit to the raw data. Grey shading represents the 95% confidence intervals.

Plant preferences

The full results table for the plant preference analysis can be seen in the appendix C, Table C3. However, a summarised version of the results is shown in Table 3.2,

where plant species that were preferred by more than one pollinator species for each month are displayed. For June and July only one non-native plant species was preferred by more than one pollinator. However, in August and September then number of nonnative plants that were preferred increased to 4 and 2 plant species respectively. In contrast, there were five native plant species preferred in June and July. However, the number of native plant species preferred in August and September was 3 and 1, respectively. As such, results from the pollinator preference analysis showed more native plant species were preferred earlier in the sampling period, and more non-native species were preferred later in the sampling period.

Table 3.2: Results of the plant preference analysis performed using econullnetr. The table includes plant species that were preferred by more than one flower visitor and shows plant origin, the month in which they were preferred and the total number of pollinator species that preferred each plant.

Plants	Plant origin	Month	No. flower visitors
<i>Epilobium</i> sp.	Native	June	2
<i>Geranium</i> sp.	Native	June	2
<i>Papaver</i> sp.	Native	June	2
<i>Rubus</i> sp.	Native	June	2
<i>Salvia</i> sp.	Native	June	2
<i>Rhododendron</i> sp.	Non native	June	3
<i>Aquilegia</i> sp.	Native	July	2
<i>Epilobium</i> sp.	Native	July	2
<i>Geranium</i> sp.	Native	July	2
<i>Papaver</i> sp.	Native	July	2
<i>Rubus</i> sp.	Native	July	2
<i>Rhododendron</i> sp.	Non native	July	3
<i>Chamaenerion</i> sp.	Native	August	2
<i>Mentha</i> sp.	Native	August	2
<i>Solidago</i> sp.	Native	August	2
<i>Bistorta</i> sp.	Non native	August	2
<i>Echinops</i> sp.	Non native	August	3
<i>Lavandula</i> sp.	Non native	August	3
<i>Reynoutria</i> sp.	Non native	August	2
<i>Papaver</i> sp.	Native	September	2
<i>Reynoutria</i> sp.	Non native	September	3
<i>Symphyotrichum</i> sp.	Non native	September	2

Discussion

Private residential gardens contribute to a large proportion of land within a city. Small enhancements to floral plantings, such as increasing floral abundance and richness may help to increase pollinator diversity, as our study found greater floral richness and abundance were associated with more flower visits. Importantly, our results suggest that such measures could be effective in any garden, regardless of its position within the urban matrix. Finally, plant-flower visitor network structure varied seasonally which appeared to be driven largely by the increasing abundance of a dominant species and its interactions with native and non-native plants. We discuss the implications for garden management below.

Native and non-native plants increase flower visits

Our study showed the importance of native plants within private gardens, as at the community level, native flowers were associated with more floral visits than non-native flowers. Other studies have found that increasing floral resources within a green space can increase flower visits, and that native plants receive more flower visits (Chrobock et al., 2013; Zaninotto et al., 2023b). Despite this, non-native plants still provided resources for flower visitors in our study. We found that increasing the abundance of non-natives was linked to a higher number of flower visits. Our results are consistent with other studies where certain non-native plant species received a high proportion of flower visits (Kovács-Hostyánszki et al., 2022; Salisbury et al., 2015), as 10% of flower visits were to *Lavandula sp.*, a non-native plant. Furthermore, at the plant species level, non-native plant species received a higher richness of floral visitors than native plants. However, this was not observed when assessing the richness of floral visitors in the whole community. This indicates that certain non-native species are attractive to pollinators, as the difference in flower visitor richness was only evident at the plant species level. In our study, it is likely pollinators foraged on non-native plants due to the large proportion of generalist flower visitors; for example, *B. pascuorum* accounted for 25% of all floral visits. Generalist pollinators can utilise a range of plant species; thus, increasing the abundance of non-native plants may provide additional foraging opportunities for pollinators which can reduce competition and allow more generalist species to forage on these resources.

However, whether increased floral abundance alleviates competition for floral resources also depends on resources quality (pollen and nectar nutritional content), which was not measured in this study.

Interestingly, the percentage of plant species visited by flower visitors within networks was higher for non-native than native plants. Previously, it has been found that certain native plants, such as *Bellis perennis* and *Myosotis arvensis*, can be unsuitable for pollinators, in that they provide little nectar and pollen resources (Hicks et al., 2016). Moreover, plant origin may not be the only variable to influence flower visits, plant morphology (flower shape and colour), as well as life cycles (annual or perennial), may play important roles in attracting flower visitors (Lowenstein et al., 2019).

Overall, regardless of plant origin and the surrounding landscape, an increase in either richness or abundance was associated with greater flower visitor abundance and richness, respectively. Many studies have reported the positive associations of floral diversity with pollinator abundance (Baldock et al., 2019; Fowler et al., 2016; Salisbury et al., 2015; Seitz et al., 2020; Simao et al., 2018; Theodorou et al., 2017), with one study showing how small-scale interventions, such as sowing “mini meadows”, can boost pollinator diversity (Griffiths-Lee et al., 2022).

Seasonal changes in non-native plant abundance

Floral richness and abundance of non-native plants increased from June until September, whilst a decreasing trend was observed in native plants. Previous studies have found non-native plants with later flowering times become more dominant later in the season (Zaninotto et al., 2023b), receive similar or more flower visits (Salisbury et al., 2015; Seitz et al., 2020; Staab et al., 2020; Zaninotto et al., 2023b), and substitute the role of native plants (Staab et al., 2020). Thus, it has been argued that the later blooming period of non-native plants can be used to provide floral resources across a longer time period (Staab et al., 2020). In our study, floral visits to native and non-native plants did not match changes in the seasonal abundance of these plants. Furthermore, we found a large variation in native plant abundance across gardens in September, showing some gardens can provided high native floral resources later in the season. Thus, it may be

unnecessary to supplement gardens with large numbers of non-native plants later in the season. This is particularly important given that some invasive non-natives can harm ecosystem functioning (Aizen et al., 2008).

Seasonal changes in network structure

We highlighted seasonal variations in network structure where nestedness and interaction evenness were lower in June and September; the opposite trend was seen for network specialisation. However, these seasonal patterns disappeared when networks were calculated whilst excluding *B. pascuorum* visits. Furthermore, when *B. pascuorum* was removed from data, pollinator specialisation did not vary across the season, further supporting its role as the main driver of these dynamics. While seasonal changes in network structure are often attributed to an influx of generalist pollinators later in the season (Luder et al., 2018) or temporal changes in resource availability (Souza et al., 2018), our results suggest that a single dominant species can determine network structure. Experimental studies have shown that the removal or addition of dominant species can influence network structure (Brosi et al., 2017; Worthy et al., 2023). For example, Worthy et al. (2023), highlights how increased dominance of honeybees in plant-pollinator networks can change network structure. This change in network structure occurred through the addition of honeybee interactions rather than by altering wild bee interactions with plants. However, it is important to note that in our study, the removal of *B.pascuorum* from networks was simulated and networks excluding this species were still observed in the field where *B.pascuorum* was present.

Moreover, closer inspection of *B.pascuorum*'s foraging behaviour showed a marked increase in visits to non-native plants in September, which coincided with higher specialisation values for *B. pascuorum*. Several mechanisms have been proposed to drive short term specialisation of generalist pollinators. Firstly, optimal diet theory suggests that abundant plant species can result in pollinator specialisation due to the cost effectiveness of foraging on these plants (Sunj et al., 2022). A high floral abundance of plant species in urban areas has been shown to influence the short-term specialisation of pollinators, as urban pollinators carry more conspecific pollen than rural pollinators despite similar pollinator diversity (Sunj

et al., 2022). Secondly, interspecific competition can drive specialisation through niche partitioning. Studies have found that *B. pascuorum* is a central, generalist species, yet may reconfigure its interactions with plants in the presence of high floral diversity (Fisogni et al., 2022). Furthermore, as the most abundant pollinator in the community, *B. pascuorum* may displace other species from floral resources (Wignall et al., 2020), thereby reinforcing its own interactions with a narrower subset of plants. Alternatively, this pattern may reflect phenological matching (Glaum et al., 2021), since the non-native species it visited most frequently were abundant in September.

Network structure is thought to be strongly related to the robustness of a network (Proesmans et al., 2024; Theodorou et al., 2017). Increasing link density increases network robustness (Proesmans et al., 2024; Theodorou et al., 2017), whilst nestedness buffers networks against extinction cascades (Proesmans et al., 2024). Therefore, the seasonal changes to network structure found here may translate to more vulnerable networks in June and September. Thus, we suggest that a higher abundance of floral resources should be provided for pollinators at the end of the season, to buffer against negative effects on network structure.

Management recommendations and conservation context

To support pollinator diversity in gardens, we recommend maintaining high floral richness of native plants throughout the season. Although our study found that non-native floral abundance increased visitation more than native abundance, this effect was not evident for floral richness. Moreover, several non-native species were highly preferred by pollinators, but the invasive potential of non-native plants makes them unsuitable for broad recommendation. Instead, we suggest prioritizing native species that attract diverse pollinators, including later-flowering taxa such as *Geranium sp.*, *Allium sp.*, and *Fragaria sp.* While we did not compare gardens to other urban green spaces, previous work shows that private gardens collectively cover large areas and exceed other habitats in supporting pollinator diversity at the city scale (Baldock et al., 2019). Our findings complement these studies by demonstrating how increasing floral richness can enhance the contribution of gardens across a city to urban pollinator conservation.

Limitations

Our study contributes to understanding plant-flower visitor interactions in urban green spaces, particularly private residential gardens, where research is limited. Although restricted to one city and year, we believe our findings are transferable to other European cities with extensive green spaces, such as Glasgow. The absence of an effect of surrounding green space on flower visits may be more pronounced in cities with little green cover.

Sampling was constrained to June-September and to 20-minute observation periods per flower. Short observation times can bias results toward the most abundant species, but total sampling time per garden was relatively long compared to similar timed studies (e.g., Sirohi et al., 2022). Furthermore, within the study period, we observed clear monthly differences in network structure, suggesting greater seasonal variation had spring been included. Recruitment through volunteer participation may also have introduced bias, though our gardens ranged from pollinator-friendly habitats to intensively managed lawns, capturing useful variation.

Finally, to identify visitors to species level, individuals were removed from the system. While this may alter interactions by removing cues or reducing subsequent visits, it is standard in network studies and ensures our results remain comparable with others (Baldock et al., 2019; Herrmann et al., 2023; Sirohi et al., 2022; Staab et al., 2020; Zaninotto et al., 2023b).

Conclusions

Our study shows that increasing floral richness in gardens is a key driver of pollinator diversity. Importantly, this effect is maintained regardless of where gardens are located within the urban landscape. Both native and non-native plants can contribute to floral richness, with some non-native plants being particularly attractive to several pollinator species. However, the predominance of generalist species in our study suggests that more native plants may be required to support specialist pollinators across the season. Overall, given that private gardens make up around 30% of urban green space in Great Britain (Office for National Statistics

(ONS, 2023), even small increases in floral richness could enhance pollinator diversity at the city scale.

Chapter 4 Floral richness drives flower-insect networks in city gardens and allotments

Abstract

Urban-rural studies have largely found a negative effect of urbanisation on pollinator diversity. However, within cities different types of green spaces may vary in their environmental characteristics, thus influencing their quality as pollinator habitat. Private green spaces in urban areas, such as residential gardens, can contribute to a large proportion of land. Yet little is known about how the environmental drivers influence pollinator diversity within these spaces.

Here, we compare nine gardens and eight allotments (defined as plots of land privately leased and typically used for horticulture), in Glasgow, Scotland, to assess which environmental drivers influence, insect diversity, flower visitor diversity and plant-flower visitor network structure. Furthermore, we investigate the effectiveness of companion planting in increasing flower visits to crop plants in allotments.

Our study revealed that gardens and allotments supported similar flower-visitor and insect diversity, showing they are equitable habitat for pollinators within cities. This is likely because no differences in floral diversity were found between gardens and allotments. In fact, floral richness was the main driver of flower visits within spaces, and the area of surrounding green space influenced flower visits by amplifying the effects of floral richness. Thus, the urban landscape may influence flower visits, yet pollinator diversity can still be supported by providing a higher floral richness at sites in dense urban areas.

Floral richness was also associated with changes to plant-flower visitor network structure. Most notably, specialisation increased with floral richness.

Finally, crop plant visits were not influenced by ornamental floral availability specifically, but more crop visits were related to higher spontaneous plant richness.

Overall, our study indicates that gardens and allotments support pollinators equally, and greater floral richness in these sites can help increase pollinator diversity. Private green spaces therefore have an important role in supporting pollinators within cities and these habitats should be considered in urban planning.

Introduction

The growing recognition of cities as important pollinator habitats has prompted national pollinator strategies to include urban green spaces (Department for Environment, Food & Rural Affairs (Defra), 2014). Thus, local authorities often implement management practices for pollinators in urban green spaces, many of which are carried out in public parks or along road verges. However, little is known about how private green spaces support pollinator diversity and plant-pollinator interactions.

Gardens are private green spaces which typically take one of two forms. Firstly, private residential gardens are green spaces adjacent to housing, constituted by a variety of forms, such as lawns, vegetable plots, ponds, flower patches and hedgerows (Loram et al., 2007). As such they can contribute to a large proportion of urban green space. For instance, residential gardens in Great Britain cover approximately 30% of land within cities (Office for National Statistics (ONS), 2023). Second, allotment or community gardens are larger green spaces made up of plots of land that are privately leased by individuals, or a local community and are typically used for horticultural purposes (Haase and Gaeva, 2023; Kwartnik-Pruc and Droj, 2023). In Great Britain, allotments and community gardens together represent less than 1% of land in cities (Office for National Statistics (ONS), 2023).

Local habitat variables differ between gardens and allotments, which may be influencing their suitability as pollinator habitats. For example, gardens with extensive lawn cover will support low floral diversity compared to allotment plots planted with various crop and ornamental plant species (Baldock et al., 2019). Within allotments, the addition of ornamental plants alongside crop plants is often implemented to enhance crop pollination (known as companion planting) (Griffiths-Lee et al., 2020). Floral abundance and richness are key drivers of pollinator diversity (Gerner and Sargent, 2022; Gómez-Martínez et al., 2022; Neumann et al., 2024; Plant et al., 2025), as well as network specialisation within green spaces (Gómez-Martínez et al., 2022). In fact, floral diversity can buffer the negative effects of urbanisation on pollinator diversity (Birdshire et al., 2020). However, these green spaces often host a large abundance of non-native plants as gardeners favour non-native ornamental species. Non-native plants can exclude specialist pollinators and reduce overall diversity within green spaces (Baldock et

al., 2015; Fukase, 2016; Pardee and Philpott, 2014). Network structure can also be altered by non-native plants through their role in attracting generalist pollinators (Zaninotto et al., 2023b). However, the role of plant origin in influencing the effectiveness of companion plants in increasing crop-pollinator interactions remains largely unexplored. Moreover, green space size may also drive pollinator diversity. Garden sizes vary greatly between individual houses (3.6m² to 2290m², when measured across five UK cities) (Loram et al., 2007). In contrast, allotment plots within the UK are typically split into three size categories. In Glasgow, Scotland for example, they are classified as small plots (under 50m²), half plots (50m²-124m²) or full plots (over 124m²) (Glasgow City Council, n.d.). Smaller, less mobile pollinators rely on larger habitat patches in order to meet their resource requirements as they are unable to travel between green spaces (Bommarco et al., 2010). In turn, small habitat patches can influence network structure by limiting specialist pollinators, which require specific foraging resources that may be sparsely distributed (Bommarco et al., 2010; Herrmann et al., 2023).

Landscape-scale environmental factors can also influence pollinator diversity and interact with local environmental drivers. Urban landscape features such as impervious surfaces fragment pollinator habitat, making floral and nesting resources harder to find (Geslin et al., 2016). Furthermore, urbanisation reduces habitat availability, and pollinator diversity has been found to be positively influenced by the amount of natural habitat within a city (Ulrich and Sargent, 2025). However, urbanisation has been associated with higher land use diversity (Baldock, 2020), which is linked to higher pollinator abundance (Gómez-Martínez et al., 2022), and increased network specialisation (Graf et al., 2024).

Comparisons of green space types in terms of their suitability as pollinator habitat are lacking, with most studies focusing on one green space type. Moreover, surveys of pollinator diversity and plant-pollinator interactions in allotments are also rare (Silva et al., 2023), highlighting the need for further research in these spaces. Here, we combined allotments and community gardens, hereafter allotments, to contrast with residential gardens in Glasgow, Scotland. As allotment plots (within allotment sites) are individually managed, we compared gardens to allotments at the plot level. Specifically, we aim to:

- 1) Evaluate how floral abundance and richness in gardens and allotments is influenced by environmental drivers, including site type and seasonal variation. We predicted higher floral abundance and richness in allotments due to crop cultivation (H1), and that non-native floral abundance would increase whereas native floral abundance would decrease across the season owing to later non-native phenology (H2).
- 2) Examine environmental drivers of insect abundance, plant-pollinator interactions and network structure in gardens and allotments including any seasonal variation. We predicted higher insect abundance and flower visitor diversities within allotments, and sites with higher floral richness (H3), and that that greater floral richness within sites would increase network specialisation (H4).
- 3) Test whether greater ornamental floral diversity is associated with increases in pollinator visits to crop plants. We expected ornamental plant diversity to increase flower visits to crop plants (H5).

As plant-pollinator networks underpin the maintenance of diversity within an ecosystem (Elle et al., 2012), understanding drivers that affect pollinators and their interactions can help guide effective urban planning and habitat management.

Methods

Located in West Central Scotland, the Glasgow City Council area covers ~175km², with a total green space area of ~96 km² (NatureScot., 2022). Publicly accessible parks in Glasgow City Council makes up around 10% of the total green space area in comparison to private gardens, which amount to 30%, and allotments which cover less than 1% of the total green space area (NatureScot, 2022).

A total of nine private residential gardens and eight allotments (Fig.4.1) were sampled for their plant and flower visitors, once a month from the 1st of April 2024 until the 30th of September 2024. Within gardens, the entire area was surveyed during each sampling visit. Within allotments, sampling was conducted within individual plots. Consequently, between 7 and 13 plots (mean±SD 7.1±4.2 plots), were sampled in each allotment to capture variation in management practices across plots. Plot selection within allotments was determined by plot holder

permission; however, plots were distributed throughout allotment sites where possible. Two allotment sites were community-owned, for which the whole site was sampled. Mean sampled area across all allotment plots was $170.2 \pm 242.4 \text{ m}^2$, compared to $122.2 \pm 63.1 \text{ m}^2$ for whole garden surveys. Appendix D, Table D.1 details the sample sites for gardens and allotment plots. Gardens and allotments were recruited via social media and selected for the study if they were at least 1km from other sites, as this is larger than the average foraging distance of most bees (Kendall et al., 2022). Prior to sampling, sites were visited to ensure a range of floral availability (i.e. sites included those managed in a pollinator friendly way as well as those that were mostly lawn cover or had small floral borders), thus we believe that the study sites were not biased by the selection process.

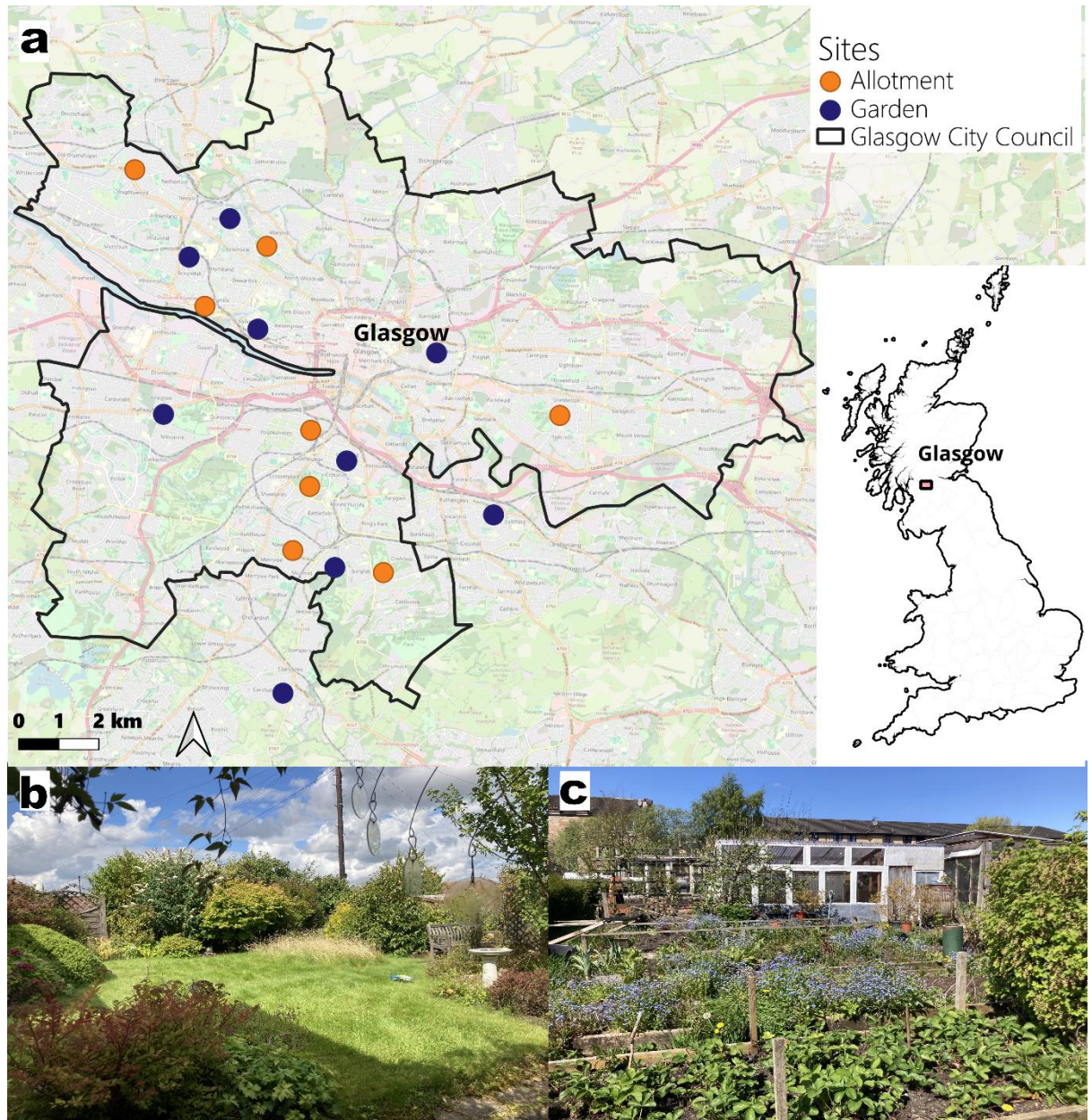


Figure 4.1: a) The map shows the position of Glasgow in the UK and the location of sample sites across Glasgow City Council (black line) and the surrounding area. Allotment sites are plotted in orange and garden sites in blue. Below images show b) garden site and c) allotment plot.

Flower visitor sampling

Plant-pollinator visitor observations were carried out using timed transects, in which all flowers at a site were observed within a 30-minute sampling period for their flower visitors. Either a whole garden, or an individual allotment plot, would be sampled for 30 minutes. As flower visits may not equate to active pollination we use the term flower visitors instead of pollinators throughout the manuscript. Flower visitor observations were instantaneous counts at each flower, recording

the Syrphidae, Anthophila and Papilionoidea that were actively foraging on the flower. These taxa were chosen as they are known to be effective pollinators and could be confidently identified. Flower visitor observations were carried out on days with no rain and with air temperatures above 10°C. Allotment sampling would always start in the morning, and plots would be randomised between morning (between 0900 and 1130) and afternoon (between 1230 and 1730), ensuring all plots from one allotment were sampled on the same day. Garden sampling was also randomised between morning and afternoon. All flower visitor observations were carried out by E.P. Flower visitors that were unable to be identified in the field were collected and euthanised by freezing at -20°C. Specimens were identified to species level by E.P. Removal of flower visitors for identification is a common practice in other studies (Baldock et al., 2019; Herrmann et al., 2023; Sirohi et al., 2022; Zaninotto et al., 2023b), however we recognise that this process can potentially alter the subsequent flower visitor interactions.

Floral inventory

Floral inventories were recorded at each site, following (Nicholls et al., 2023). Here, each plant species was recorded, along with the approximate number of individual plants, grouped into categories (0-10, 11-20, 21-30, 31-40, 41-60, 61-80, 81-100, 100+). For each plant species, two individuals were randomly chosen to record their floral abundance (number of individual flowers). Asteraceae sp. flower heads and Apiaceae sp. umbels were counted as one floral unit. Shrubs and trees (up to a height of 1.5m) were included in the count, with the number of flowers on one branch counted and multiplied by an estimate of the number of branches within the transect. The floral abundance for plant species was then averaged and multiplied by the number of individual plants per species to calculate a total floral abundance per garden or allotment plot. Two trained recorders (E.P. and W.M.) inventoried plant abundance and compared the recorded floral abundance for plant species within sites to ensure no recorded bias was introduced. Plant origin was determined as native or non-native in Great Britain using the Botanical Society of Britain and Ireland (BSBI's) online database <https://bsbi.org/taxon-lists>, and plants were recorded as either spontaneous (not

deliberately planted), ornamental (deliberately planted) or crops (harvestable) (Appendix D, Table D.2).

Local environmental variables

In addition to the floral inventory, green space size was measured using QGIS (version 3.44.0). Green space size refers to the size of the sampled area (total garden area or allotment plot area) and was measured in m².

Landscape environmental variables

Several variables were used to describe the urban matrix around the sample site, including land-use diversity (LUD) and green-space area. These values were calculated in 250m, 500m and 1000m buffers from the centre of each site. As bees are central place foragers, the 1000m buffer was chosen to cover the average foraging range of most bee species (Kendall et al., 2022), whilst the smaller buffers were used to account for the fact that some smaller bee species forage over shorter distances (Greenleaf et al., 2007). The area of each land use category within buffers around the site was used in calculating LUD. The Shannon-Wiener diversity index in the R package Vegan (Oksanen et al., 2001), was used to calculate LUD values. The area of surrounding green space was quantified as the total area of green land use in buffers surrounding the site. Land use was classified by the Copernicus urban atlas data set (European Union, 2020) and green land use included the categories: urban green space, sports and leisure facilities, pastures, arable land, wetlands and forests.

Pan traps and corresponding environmental variables

Pan traps were used as an additional method to collect insects at each site once a month, excluding April. In contrast to flower visitor observations, pan trapping is a passive sampling method that allows insects to be collected over a longer time period without the presence of an observer. This may allow the capture of insects that are less likely to be detected during active flower visitor observations, including those that are disturbed by observer presence. One pan trap consisted of three coloured bowls (blue, white and yellow), filled with a soapy water solution (5ml of odourless soap per 100ml water). Pan trap height was set to the average height of the surrounding vegetation. One pan trap was left at each site

for 72 hours, starting at 0900. Pan trap sampling was carried out at half the sites at one period and at the remaining sites the following week, providing there were 72 hours of appropriate weather conditions (dry days with temperatures above 10°C). Pan trap sampling would be conducted on different days to the flower visitor observations to ensure collecting visitors in one method did not affect the results of the other. We preserved specimens of order Insecta in 70% ethanol. Due to the low catch rate of Syrphidae, Papilionidae and Anthophila within pan traps, all insects were identified to family level by E.P. to be used in data analysis.

Environmental variables were recorded as previously mentioned. However, for allotments, we calculated the mean floral abundance per m² and mean floral richness across all sampled plots. Site size was measured as the total area of the allotment, rather than individual plots. Finally, the surrounding green spaces and land use diversity were quantified in 250m, 500m and 1000m buffers from the centre of allotment sites.

Network indices calculations

Data obtained from plant-flower visitor observations were used to calculate network indices using the R package Bipartite (Dormann et al., 2008). Network specialisation (H_2') describes the selectiveness of all interaction partners in the network (0= no specialisation, 1= complete specialisation). Nestedness, measured as niche overlap based on decreasing fill (hereafter NODF), is the extent to which a specialist interacts with a subset of partners that generalists also interact with. Interaction evenness is a measure of the spread of interactions within the network (bounded between 0 and 1, with one showing an even spread of interactions). For each network index, Z-scores were calculated to standardise indices. To do this, 1000 null networks were generated for each observed network using the r2d method in the Bipartite package. The mean and standard deviation of each network index across the null networks were used to calculate Z-scores as $Z = (\text{observed} - \text{mean}(\text{null})) / \text{standard deviation}(\text{null})$. Z-scores have been commonly used in previous studies that compared network structures across different networks (Philpott et al., 2025). Finally, species specialisation (d') was calculated for flower visitors, which represents how selective they are over their plant partners (0= no specialisation, 1= complete specialisation).

Data analysis

All data analysis was carried out in R (“R version 4.5.2,” 2025). The significance of variables was tested using a backwards stepwise model selection and likelihood ratio tests (Zuur et al., 2009). For all models, QQ plots were used to assess the fit of model distributions and collinearity was checked using Variance Inflation Factors in the package Performance (Lüdecke et al., 2021), as well as uniformity of residuals, overdispersion and zero inflation. We tested for spatial autocorrelation by computing Moran’s I values on the residuals of each model when site and plot were included as random effects using the DHARMA package (Hartig, 2024). No spatial autocorrelation was detected in any of the models. To inform which random effects to use we compared AIC values (Bozdogan, 1987) of models with either the random effects plot nested in site, or the random effect site, or the random effect plot (Appendix D, Table D.5). The best spatial scale for describing the surrounding urban landscape was first selected by comparing full models with land use diversity and area of surrounding green space in buffer zones of either 1000m, 500m, or 250m. Both models that represented 1000m and 500m spatial scales had similar AIC values, whereas 250m had higher AIC values (Appendix D, Table D.5). Therefore, it was decided to use 500m spatial scales in all models, to ensure no overlap between sites. This scale has commonly been used in previous studies (Herrmann et al., 2023; Schmack and Egerer, 2023).

Environmental drivers of floral diversity

To test H1 and H2, generalised linear mixed models (GLMMs) with negative binomial distributions modelled the response of floral abundance and richness to environmental variables using the glmmTMB package (Brooks et al., 2017). As floral abundance was calculated as an average value per plant species, we rounded all total floral abundance values for sites to the nearest whole number to conform to a negative binomial distribution. Fixed effects were plant origin, green space size, LUD, surrounding green space area and month as a continuous value. Seasonal, non-linear patterns of floral diversity were included as a quadratic term of the variable month. Two-way interactions were included between month and plant origin and between site type with plant origin. The plot nested within site was a random effect.

Environmental drivers of flower visits and insect diversity

H3 was tested with GLMMs with zero-inflated negative binomial distributions which modelled differences in the number and richness of flower visits. Here, response variables were the total number of flower visits and total richness of flower visitors to native and non-native plants per site, per month. Fixed effects included floral abundance per m², floral richness, plant origin, green space size, LUD, area of green space and site type. Month was included as both a linear and quadratic effect. Two-way interactions included those between plant origin and floral abundance per m², floral richness and month; and between both floral abundance and richness with LUD and green space. Plot was a random effect.

We further tested H3 using data on insect abundance and richness from pan traps and GLMMs with zero inflation negative binomial distributions. Fixed explanatory effects included LUD, green space, site size, average floral abundance per m², average floral richness per month as both a linear and quadratic effect and site type. Two-way interactions were included between site type with floral abundance and richness and month. Site and pan trap colour were included as random effects.

Environmental drivers of plant-flower visitor network structure

When testing hypothesis H4, we modelled variation in network structure using Z-scores for network specialisation, interaction evenness, and nestedness per site, per month as response variables. All models were fitted with a Gaussian distribution. Furthermore, flower visitor specialisation, per species per month, was modelled with a beta distribution. Only species with more than six interactions for each sampling effort were included to ensure model residuals were uniform. Fixed explanatory variables included site size, site type, floral abundance per m², floral richness, month as both a linear and quadratic effect and the percentage of native floral abundance and richness at sites. Two-way interactions were included between floral variables and month, and floral variables with LUD and area of surrounding green space. Plot was a random effect and for pollinator specialisation models, species was also included as a random effect.

Preferred plants

To better inform management of green spaces we assessed the plant preferences of flower visitors using the `econullnet` package in R (Vaughan et al., 2018). This package allows the resource preferences of consumers to be analysed based on the abundance of resources in the environment. To do this, null models are employed, wherein interactions between consumers and resources are randomly shuffled within networks. The resulting null models are used to compare interaction frequencies with the observed networks, allowing the determination of whether a consumer interacts with a resource more or less than expected based on the availability of that resource. Here we analyse plant preferences in networks collected in each garden, each month, using the floral abundance to inform the availability of resources in models.

Crop-plant analysis

When evaluating the effectiveness of companion plants (H5), the number and the richness of flower visits to crop plants per plot, per month was assessed using only the allotment data. This analysis was conducted using zero-inflated negative binomial GLMMs. The explanatory variables included the richness, abundance and origin of ornamental plant species and their interactions, as well as control variables for the abundance and richness of spontaneous plant species and the crop plants themselves. Green space size and type, LUD and surrounding green space area were also included as fixed variables, and plot as random effect.

Results

Environmental variables were similar between gardens and allotments, however individual sites showed substantial variation from the mean in their environmental variables (Table 4.1).

Table 4.1: Mean $\pm$ SD of the environmental variables in gardens and allotment plots across the 6-month sampling period.

Environmental variable	Allotment plot mean $\pm$ SD	Garden mean $\pm$ SD
Size m ²	169.82 $\pm$ 228.61	123.50 $\pm$ 60.64
Floral richness	7.35 $\pm$ 5.15	7.65 $\pm$ 5.58
Floral abundance per m ²	5.67 $\pm$ 6.09	6.53 $\pm$ 6.00

Green space area m ² (500m buffer)	204940.2 ± 124834.0	119483.9 ± 69577.9
Land use diversity (500m buffer)	1.61 ± 0.14	1.58 ± 0.13

Environmental drivers of floral diversity

Across all sites, 374 plant taxa were recorded (Appendix D, Table D.2). Mean $\pm$ SD floral abundance was lowest in September, 590.36 ± 610.02 flowers, and highest in August, 964.97 ± 1150.82 flowers. When separated by plant origin, April had the highest mean native plant abundance, 1365.60 ± 1544.61 flowers and the lowest non-native plant abundance, 280.26 ± 392.68 flowers. September had the lowest mean native plant abundance, 504.51 ± 603.92 flowers and August had the highest mean non-native plant abundance, 873.88 ± 837.86 flowers.

Mean ($\pm$ SD) floral richness was lowest in April, with 4.08 ± 2.59 flower species, and highest in July, with 9.32 ± 6.05 flower species. The greatest mean floral richness of native plants occurred in July 11.38 ± 6.39 flower species, and the lowest occurred in April 5.17 ± 2.75 flower species. The highest mean floral richness of non-native plants occurred in August with 9.18 ± 6.12 flower species, and the lowest mean non-native floral richness occurred in April with 2.67 ± 1.49 flower species.

A relationship was found between month and floral abundance, depending on plant origin (Month*Origin: Estimate=0.65, $Z=9.84$, $P<0.001$) (Fig. 4.2a), with native floral abundance decreasing and non-native floral abundance increasing from April to September. A non-linear relationship was found between floral abundance and month, with lower abundances in April and September (Estimate=0.53, $Z=-3.23$, $P=0.004$). Finally, higher floral abundances were recorded for native than non-native plants (Estimate=-0.55 $Z=-8.28$ $P<0.001$) and larger sites had higher floral abundances (Estimate=0.29, $Z=3.83$, $P<0.001$).

Floral richness in each month depended on plant origin (Estimate=0.38 $Z=2.45$, $p=0.014$) (Fig. 4.2.b), native plant richness was highest in July; in contrast, non-native floral richness increased from April to September. Differences in floral richness between gardens and allotments depended on the plant origin (Estimate=-0.20, $Z=-2.49$, $p=0.044$). Here, gardens showed a greater difference in the richness of native and non-native plants than allotment plots. Floral richness

followed non-linear seasonal patterns, peaking in July and August (Estimate=-1.09, $Z=-11.67$, $P<0.001$), with a higher overall floral richness for native compared to non-native plants (Estimate=-0.44, $Z=-13.40$, $P<0.001$). Finally, floral richness increased with site size (Estimate=0.19, $Z=3.91$, $p<0.001$).

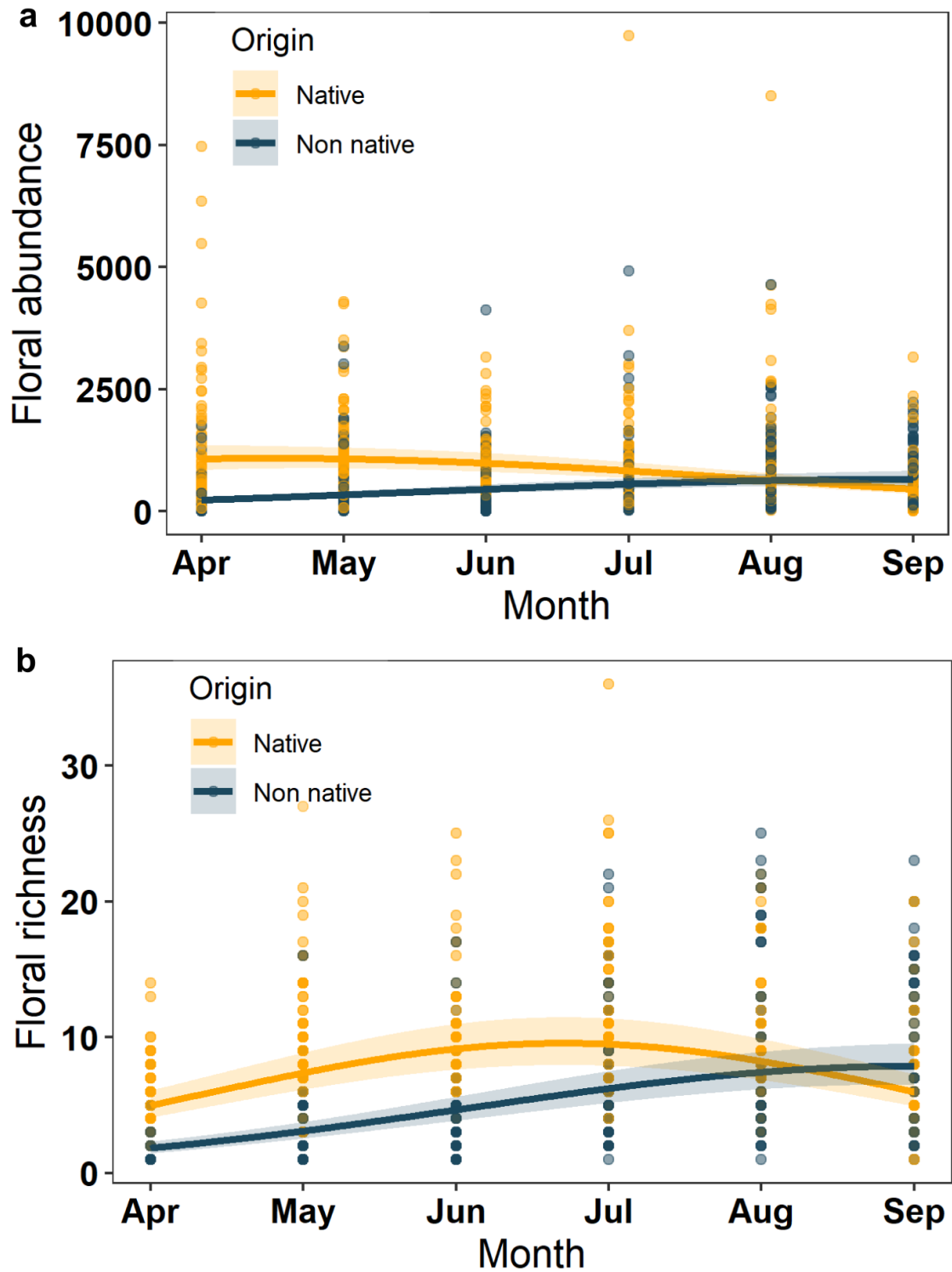


Figure 4.2: a) Floral abundance and b) floral richness followed seasonal trends depending on plant origin. Native floral abundance decreased from April to September, whereas non-native floral abundance increased. Native floral richness peaked in June and July, whereas non-

native floral richness peaked in September. Points show floral values for each site sampled each month and lines show model predictions with shading representing 95% confidence intervals.

Environmental drivers of flower visitor diversity

A total of 6943 plant-flower visitor interactions were recorded, comprising 87 species (Appendix D, Table D.3). The most common flower visitors were *Bombus pascuorum* (24% n=1681), *Bombus terrestris/lucorum* agg. (13% n=920), and *Apis mellifera* (10%, n=660). The mean ($\pm$ SD) number of flower visits ranged from 3.77 flower visits $\pm$ 3.74 in April to 15.74 flower visits $\pm$ 14.99 in August. The mean species richness of flower visitors ranged from 2.36 flower visitors $\pm$ 1.94 in April to 6.13 flower visitors $\pm$ 4.16 in August.

Flower visits increased with increasing floral abundance per m² and richness depending on plant origin (Floral abundance per m² *Origin: Estimate=0.23, Z=3.57, P<0.001, Floral richness*Origin: Estimate=0.12, Z=2.06, p=0.003). Here, both non-native floral abundance and richness (Fig.4.3a), resulted in a greater number of flower visits than for native plants. However, the number of visits to native and non-native flowers depended on month (Estimate=0.23, Z=3.78, P<0.001), with more visits to native plants from April until July and more visits to non-native plants in September. Flower visits also increased with floral richness depending on the amount of surrounding green space (Estimate=0.08, Z=2.79, p=0.001). Here, flower visits showed a greater increase with floral richness in areas with more surrounding green space (Fig.4.3b). Overall, flower visits increased with both floral abundance per m² and richness (Estimate=0.14, Z= 4.17 p<0.001 and Estimate=0.46, Z=10.70, p<0.001, respectively). Flower visits increased with month (Estimate=0.13, Z=3.69, p<0.001), and native plants received more visits than non-native plants (Estimate=-0.28, Z=-4.87, p=0.002).

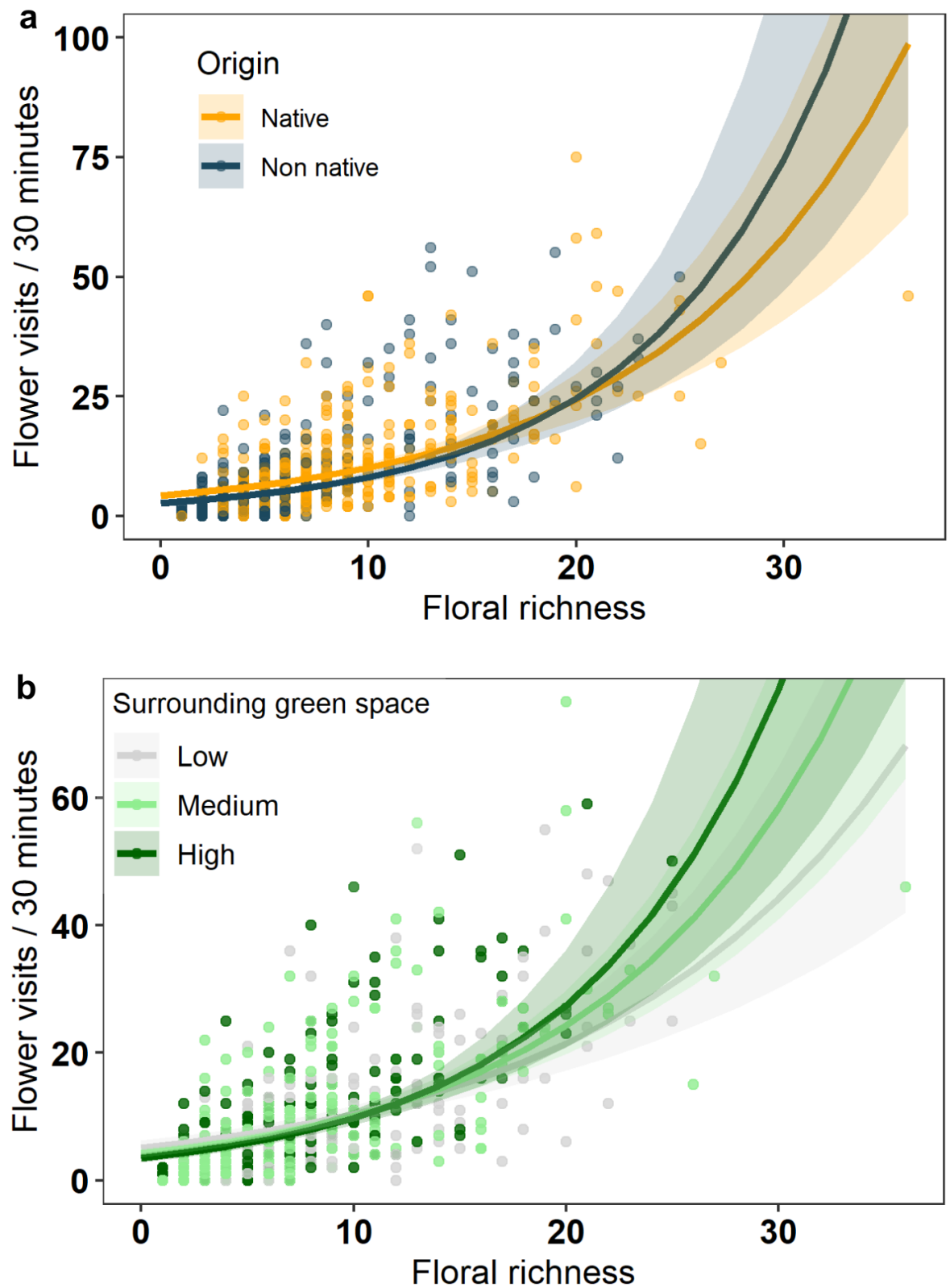


Figure 4.3: The graphs show the environmental drivers of flower visits, with each point representing the total flower visits per site per month. All graphs show observed data as points and model predictions of flower visits from final models as lines, with shading representing the 95% confidence intervals. a) Flower visits showed a greater increase with floral richness for native plants (orange) compared to non-native plants (blue). b) Flower visits increased with floral richness more in sites surrounded by more green space (dark green) compared to sites with less green space (grey). Surrounding green space was categorised as high (mean+1SD), medium (mean) and low (mean-1SD) for plotting purposes.

An increase in the floral abundance per m² and richness of non-native plants was associated with a greater increase in flower visitor richness than equivalent increases in native plants (Floral abundance per m²*Origin: Estimate=0.15, Z=3.83 P<0.001; Floral richness*Origin: Estimate=0.09, Z=2.76, p=0.018). At lower floral abundances, flower visitor richness was greater on native plants, however the model predicted a greater increase in flower visitor richness with increasing floral abundance of non-native plants (Fig.4.4b). Although, there was greater uncertainty around these predictions at higher floral abundances. the richness of floral visitors to native and non-native plants depended on month (Estimate=0.21, Z=4.35 p=0.03) (Fig.4.4a), with a greater richness of flower visitors to native plants from April to August and visits to native and non-native plants becoming even in September. A two-way interaction between floral richness and surrounding green space area (Estimate=0.06, Z=2.76, p=0.002), influenced flower visitor richness. Here, a greater increase in flower visitor richness was associated with increased floral richness in sites surrounded by a greater area of green space. Flower visitor richness increased with floral abundance per m² (Estimate=0.11, Z=4.65, p<0.001), floral richness (Estimate=0.29, Z=10.17 p<0.001), and month (Estimate=0.09, Z=3.23, p<0.001). Native plants received a higher richness of floral visitors than non-native plants (Estimate=-0.30, Z=-6.42, p=0.013).

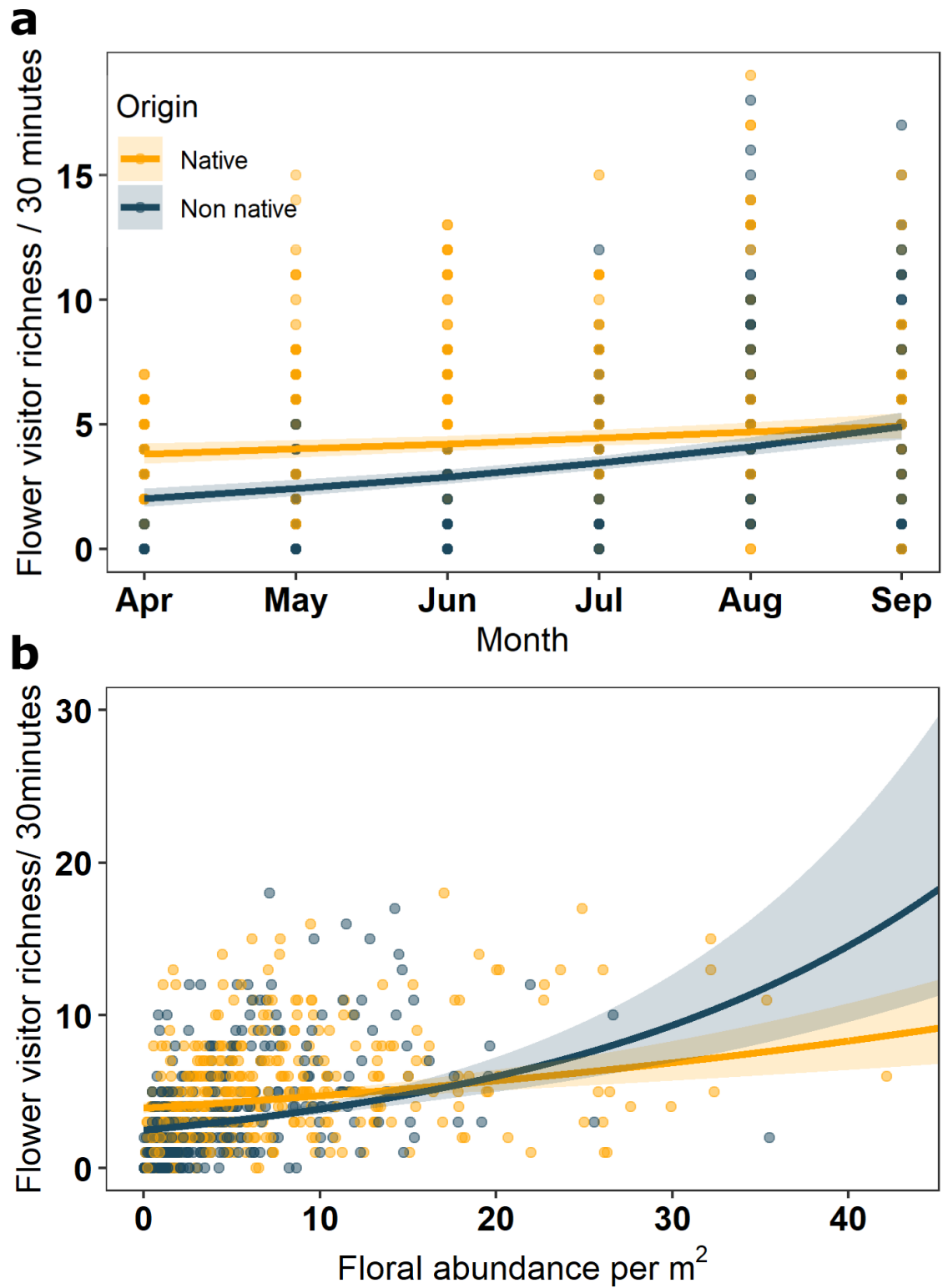


Figure 4.4: The graphs show the environmental drivers of flower visitor richness per site per month. Each point shows the observed flower visitor richness. Lines show the model predictions with grey shading representing the 95% confidence intervals. a) Flower visitor richness to native (orange) and non-native plants (blue) from April until September. From April until August, native plants received more flower visitors. b) Flower visitor richness showed a greater increase with floral abundance per m^2 for native plants (orange) compared to non-native plants (blue).

Insect abundance and richness in pan traps

2593 individual insects and 85 insect families were present in pan traps. The most abundant families were Dolichopodidae (n=283), Aphididae (n=255), Sciaridae (n=219) and Anthomyiidae (n=159).

Insect abundance and richness in pan traps were positively associated with average floral abundance per m² (Estimate=0.12, Z=2.07, p=0.037; Estimate=0.12, Z=3.03, p=0.002, respectively), and average floral richness (Estimate=0.09, Z=1.00, p=0.04; Estimate=0.03, Z=0.54, p=0.02, respectively) at sites. Moreover, insect abundance and richness followed non-linear seasonal patterns (Estimate=-1.04, Z=-3.82, p<0.001; Estimate=-0.73, Z=-4.05, p<0.001, respectively). Here, insect abundance and richness peaked in July, being comparatively lower in May and September. Finally, insect richness was also positively associated with site size (Estimate=0.18, Z=2.45, p=0.02).

Environmental drivers of plant-flower visitor network structure

Network specialisation increased with both floral richness (Estimate=0.97, Z=9.05, p<0.001) (Fig.4.5b), and abundance (Estimate=0.27, Z=2.75, p<0.001), whereas interaction evenness and nestedness decreased with floral richness (Interaction evenness: Estimate=-0.97, Z=-9.10, p<0.001, nestedness: Estimate=-0.97, Z=-9.10, p<0.001) and abundance (Interaction evenness: Estimate=-0.29, Z=-2.76, p<0.001, nestedness: Estimate=-0.29, Z=-2.76, p<0.001, Fig.4.5a). Increasing the percentage of native plants at sites increased network specialisation (Estimate=0.28, Z=2.55, p=0.01), whereas the opposite trend was observed in interaction evenness (Estimate=-0.28, Z=-2.55, p=0.01), and nestedness (Estimate=-0.28, Z=-2.55, p=0.01). Pollinator specialisation showed an increase with floral richness depending on LUD (Estimate=0.30, Z=3.17, p=0.003), with higher LUD sites showing a decrease in pollinator specialisation with increased floral richness (Fig.4.5c). Finally, month influenced pollinator specialisation depending on the percentage of native floral richness at a site (Estimate=-0.25, Z=-2.20, p<0.015). High percentages of native floral richness showed an increase in pollinator specialisation from April until September. The opposite trend was found for low percentages of native floral richness, which showed decreases in

specialisation from April until September (Fig.4.5d). Full summaries of model outputs can be seen in Appendix D, Table D.4.

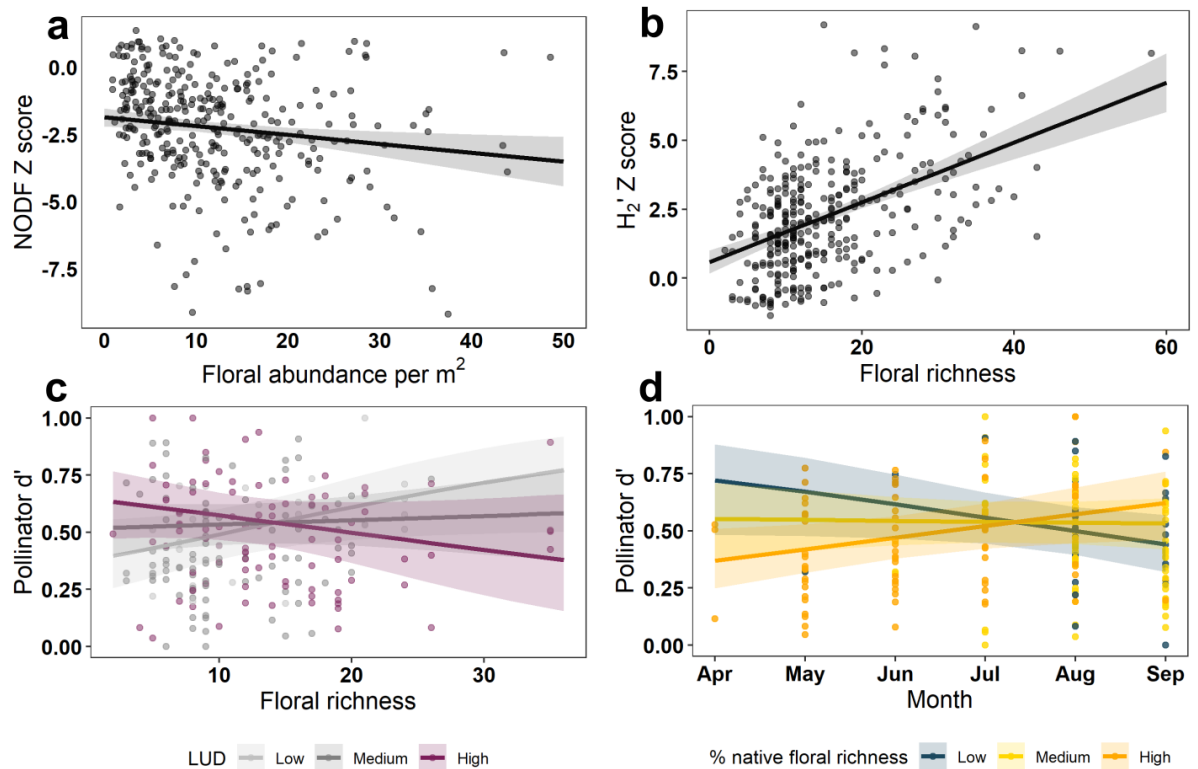


Figure 4.5: Changes in the z-scores of H₂' values and species specialisation. a) Nestedness (NODF) decreased with increasing floral abundance per m². b) Network specialisation increases with floral richness. c) Pollinator specialisation (d'), decreased with floral richness in sites that were surrounded by higher land use diversity within a 500m buffer around the site, yet sites with lower land use diversity showed an increase in pollinator specialisation with increased floral richness. d) Pollinator specialisation increased from April to September in sites with a higher percentage of native floral richness, whereas sites with a lower percentage of native floral richness showed a decrease in pollinator specialisation. Lines show model predictions, and the shading represents the 95% confidence intervals. Points in graphs a&b represent one network sampled per month per site, and points in graphs c&d represent pollinator species with more than six interactions sampled per month per site.

Preferred plant species

Table 4.2 summarises results of the plant preference analysis, showing plant species that were strongly preferred by more than 5 flower visitors. Until August, only native species were found to be significantly preferred by more than 5 flower visitor species. In August, five native and three non-native plants species were preferred. September was the only month where the number of non-native plants preferred (n=3) was greater than the number of native plants preferred (n=2). A full list of plant species that were preferred by at least one pollinator species is shown in Appendix D, Table D.6.

Table 4.2: Plant species that were preferred by more than five flower visitors calculated using the econullnetr package. Each preferred plant species is presented with plant origin, the month it was preferred by pollinators and the total number of flower visitor species which preferred the plant.

Plant	Month	Plant origin	No. of flower visitors
<i>Taraxacum</i> agg.	April	Native	9
<i>Allium</i> sp.	May	Native	6
<i>Allium schoenoprasum</i>	May	Native	9
<i>Ranunculus</i> sp.	May	Native	9
<i>Cirsium</i> sp.	May	Native	6
<i>Taraxacum</i> agg.	May	Native	11
<i>Geranium</i> sp.	June	Native	14
<i>Ranunculus</i> sp.	June	Native	6
<i>Ranunculus</i> sp.	July	Native	8
<i>Hieracium</i> sp.	July	Native	7
<i>Cirsium arvense</i>	August	Native	6
<i>Succisa pratensis</i>	August	Native	6
<i>Brassica rapa</i>	August	Native	8
<i>Lapsana communis</i>	August	Native	6
<i>Leucanthemum</i> sp.	August	Native	6
<i>Calendula officinalis</i>	August	Non native	9
<i>Cosmos bipinnatus</i>	August	Non native	6
<i>Foeniculum vulgare</i>	August	Non native	7
<i>Hieracium</i> sp.	September	Native	6
<i>Brassica rapa</i>	September	Native	6
<i>Calendula officinalis</i>	September	Non native	7
<i>Cosmos bipinnatus</i>	September	Non native	9
<i>Eruca</i> sp.	September	Non native	6

Floral visits to crop plants

The crop plant that received the highest number of flower visits was *Rubus* sp. (324) and the crop plant with the highest richness of floral visitors was *Brassica rapa* (18 species). Three crop plant species received no flower visits: *Pastinaca sativa*, *Lactuca sativa* and *Armoracia rusticana*.

Our results found that an increase in non-native ornamental floral abundance increased the flower visits to crops more than when native ornamental floral abundance increased (Estimate=0.42, $Z=4.13$, $p<0.001$) (Fig.4.6). A similar relationship was found for flower visitor richness to crop plants (Estimate=0.37, $Z=4.55$, $p<0.001$). Both flower visits and flower visitor richness to crop plants were influenced by month, depending on crop plant origin (Estimate=0.64, $Z=5.04$, $p<0.001$, Estimate=0.58, $Z=5.41$, $p<0.001$ respectively). Flower visits and flower

visitor richness decreased with increasing richness of spontaneous plants (Estimate=-0.10, $Z=-2.60$, $p<0.001$, Estimate=-0.10, $Z=-2.21$, $p<0.001$ respectively), but increased with the floral abundance per m^2 (Estimate=0.23, $Z=4.11$, $p<0.001$, Estimate=1.25, $Z=4.59$, $p<0.001$ respectively) and floral richness of crop plants themselves (Estimate=0.95, $Z=17.16$, $p<0.001$, Estimate=0.58, $Z=16.92$, $p<0.001$ respectively). Finally, native crop plants received more flower visits (Estimate=-1.79, $Z=-12.57$, $p<0.001$) and a higher richness of flower visitors (Estimate=-1.41, $Z=-11.27$, $p<0.001$) than non-native plants.

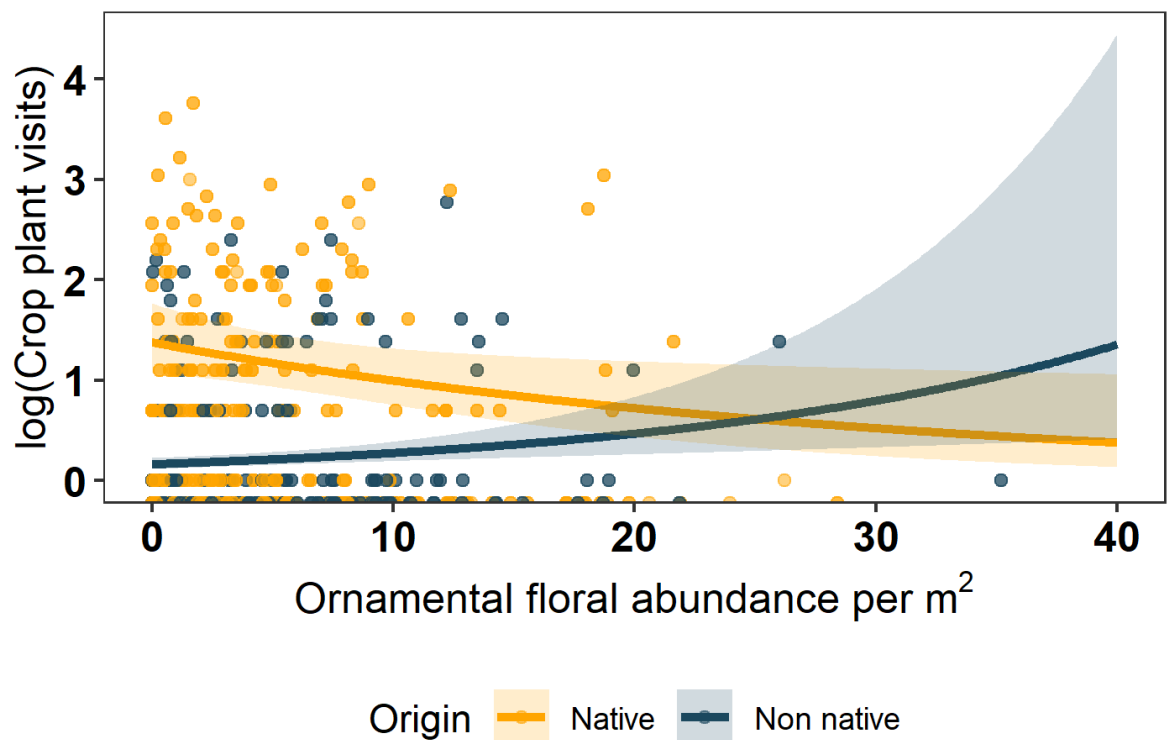


Figure 4.6: Ornamental abundance per m^2 at sites increased the number of flower visits to crops, depending on ornamental plant origin. Increased abundance of non-native ornamental plants increased visits to crops more than native ornamental plants. Each point represents the observed number of visits or visitors to crops per site, per month. Lines show the model predictions and shading represents 95% confidence intervals.

Discussion

Our study showed that gardens and allotments are equitable pollinator habitats within a city, with flower visitor observations revealing similar flower-visitor abundance and richness and pan traps showing similar insect diversity between the two site types. This is likely due to the lack of differences in the measured floral variables between gardens and allotments, which were the main drivers of flower visits within these green spaces. The area of surrounding green space

influenced flower visits by amplifying the effects of floral richness. This suggests that while the urban context may influence flower visits, the most effective way to support flower visitors is to actively manage green spaces to promote high floral richness. The association between floral variables and flower visits also translated to changes in network structure, most notably with floral abundance and richness increasing network specialisation. Finally, crop plant visits were not influenced by total ornamental floral availability, yet there was some effect of the origin of ornamental plant species abundance.

Gardens and allotments as pollinator habitat

Visual surveys and pan trap samples both indicated no differences in either flower visitor nor insect abundance and richness, between gardens and allotments. Consistent with our results, pollinator abundance and richness did not differ between gardens and allotments when measured across four other UK cities (Baldock et al., 2019). This result was found despite these green spaces having different primary uses. Allotments are primarily used for crop growing; however, in our study, some plots contained a large proportion of ornamental plants, while others were dominated by only a few crop plant species. In the UK, gardens are mostly used for leisure, attributing to the high lawn coverage and little floral diversity, yet some gardens in our study were actively managed for pollinators through the sowing of wildflower plants. Thus, variation in management styles, in terms of floral plantings within gardens and allotments, may indicate that these spaces support similar pollinator diversity across Glasgow.

Floral diversity as a key environmental driver

The main drivers of flower visits were floral abundance per m², floral richness and plant origin. Native plants were the predominant floral resources at sites, with non-native plants only becoming more abundant in September. Interestingly, allotments had lower native floral richness than gardens, which may have been due to the greater number of non-native crop plant species at the former sites.

Overall, increasing floral abundance and richness was positively associated with floral visits and insect diversity at sites. However, increasing non-native plant abundance and richness was related to a greater increase in floral visits than native plant abundance and richness increased. While many studies have found

positive effects of increased floral diversity on flower visits (Fowler et al., 2016; Herrmann et al., 2023; Plant et al., 2025; Seitz et al., 2020; Simao et al., 2018; Theodorou et al., 2017), most studies show native plants to be preferred by flower visitors (Chrobock et al., 2013; Lowenstein et al., 2019; Pardee and Philpott, 2014; Salisbury et al., 2015; Zaninotto et al., 2023b). However, certain non-native species are highly attractive to flower visitors (Kovács-Hostyánszki et al., 2022; Plant et al., 2025; Salisbury et al., 2015; Seitz et al., 2020; Turo et al., 2021), which may explain the observed increase in flower visits as the availability of non-native plants increases. Moreover, recent studies have substantiated the role of non-native plants in providing floral resources later in the season (Poole et al., 2025; Seitz et al., 2020; Zaninotto et al., 2023b); this is shown in our study as floral visits tracked seasonal changes in native and non-native floral availability.

Our pan trap results support the positive association among floral abundance and richness and insect diversity. However, pan traps did not capture many of the taxa observed during flower visitor surveys, highlighting the difference in the insect community sampled by these two methods. Pan traps are a passive sampling protocol, and their effectiveness can vary among taxa according to factors such as visual attraction to trap colours and floral abundance surrounding traps. Consequently, some flower visiting taxa may be unrepresented or absent from pan trap samples. Conversely, pan trap samples included taxa that were not the focus of flower visitor observations. Because all insect families in the pan traps were included rather than just Syrphidae, Lepidoptera and Anthophila, pan trap results may not be directly comparable to flower visitor surveys with non-flower visiting insect families and other unmeasured environmental variables potentially influencing pan trap diversity. Yet, floral variables still showed a strong positive association with insect abundance and richness suggesting floral resources may influence broader insect communities in these green spaces, although this relationship should be interpreted with caution.

The influence of urban context on flower visits

Larger areas of surrounding green space amplified the effects of floral richness, leading to a stronger increase in the abundance and richness of flower visits at sites with higher floral richness. Larger areas of surrounding green space may increase flower visitor richness within sites by allowing pollinator movement into

these spaces (Graffigna et al., 2024) or by providing more floral and nesting resources directly around the site (Baldock, 2020; Turo et al., 2021).

We found no relationship between land use diversity and flower visits. As mobile organisms, pollinators may be less constrained by the surrounding landscape when meeting their resource requirements. Current literature remains unclear as to the landscape-scale effects on pollinator diversity. Many studies have found negative relationships between the amount of impervious surface and pollinator diversity (Baldock et al., 2015; Geslin et al., 2016; Gordon and Kerr, 2025), although these were conducted along urban-rural gradients (except (Herrmann et al., 2023; Zaninotto et al., 2023a)). Whereas a study on urban roadsides found a positive effect of impervious surfaces on pollinator diversity (Dietzel et al., 2023) and a study in community gardens found no effect (Schmack and Egerer, 2023). In our study, we categorised green spaces that may not directly benefit flower visitors in terms of the floral resources they provide. However, to our knowledge there are few data sets that determine the floral availability in these green spaces, highlighting a potential future research topic.

Plant flower-visitor networks are influenced by floral resources

Network specialisation increased with increasing floral abundance and richness, whereas nestedness and interaction evenness decreased. Similar changes in network structure were observed in a study of urban agro-ecosystems (such as allotments), where network specialisation increased while nestedness and interaction evenness decreased with increasing floral richness (Philpott et al., 2025). Floral richness has been associated with network specialisation in other studies (Ebeling et al., 2011; Gómez-Martínez et al., 2022; Philpott et al., 2025; Theodorou et al., 2017), likely due to niche segregation among pollinators, except (Schmack and Egerer, 2023; Suni et al., 2022). Increased floral richness can promote niche segregation by reducing competition, enabling foraging on rewarding resources and increasing foraging efficiency (Gómez-Martínez et al., 2022). We cannot infer resource quality from our study; thus, the mechanisms behind the increase in network specialisation remain unclear. Nestedness decreased with increased floral richness, yet in other studies, the opposite relationship has been recorded (Schmack and Egerer, 2023). Increased floral richness may increase network complexity, resulting in higher nestedness.

However, in our study, nestedness may have decreased because of niche segregation, meaning there was less overlap between pollinators and their foraging plants.

Network structure also changed as the percentage of native floral abundance increased across sites. As a greater proportion of the available floral resources were native, network specialisation increased, while nestedness and interaction evenness decreased. Previous studies have found that network specialisation decreases with higher proportions of non-native plants, as these often attract generalist pollinators (Seitz et al., 2020; Zaninotto et al., 2023b). Therefore, the higher percentages of native plants in our study may have supported a greater number of specialist pollinators. Indeed, we found that pollinator specialisation increased with month in site with high proportions of native plants. Native plants were visited more often throughout the study than non-native plants. Increased pollinator specialisation was observed with higher percentages of native plants, particularly when non-native plants were the dominant resource. This may reflect pollinator preferences for native species, leading to greater specialisation when native resources are less available.

Low land-use diversity was associated with increased pollinator specialisation and floral richness, whereas high land-use diversity corresponded to decreased specialisation. Greater land-use diversity can enhance resource heterogeneity in the urban landscape (Ayers and Rehan, 2021; Liang et al., 2023), while higher floral richness at sites promotes niche segregation among pollinators. In landscapes with low land use diversity, limited surrounding resource availability may concentrate pollinators within sites, leading to greater specialisation as floral richness increases. Conversely in landscapes with high land use diversity, broader resource availability may reduce the need for niche partitioning of pollinators within sites, resulting in lower specialisation within sites.

Crop plant visits

No relationship between ornamental plants and crop plant flower visits was recorded; however, increased richness of spontaneous flowers was associated with more crop plant visits. Many studies have found interventions of increased floral diversity, such as wildflower strips, have positive effects on floral visitation to crops (Blaauw and Isaacs, 2014; Campbell et al., 2017), although these studies

focus on agricultural settings. Even the addition of a single companion plant (*Borago officinalis*) was found to increase floral visitation to strawberry plants by flies, in turn increasing strawberry yield (Griffiths-Lee et al., 2020). We found that non-native ornamental plant abundance increased the richness of visits to crop plants more than non-native ornamental plants. This may be due to certain native plants being highly attractive to pollinators, potentially diversity flower visitors away from crop plants. However, there were relatively few data points at higher floral abundances, resulting in greater uncertainty around the model predictions. Therefore, although the model predicted a greater increase in visits to crop plants was associated with increasing non-native ornamental plant abundance, this result should be interpreted with caution. Additional data at higher floral abundances may have resulted in a greater positive association between native ornamental plant abundance and visits to crop plants. To our knowledge, there have been no previous studies on the utility of native and non-native plants as companion plants and future studies would benefit from a controlled experimental design to test this. Overall, maintaining a high floral diversity at sites can be a beneficial management practice for both pollinators and land managers, as it is associated with greater flower visitor diversity and crop visits. However, further research is needed to establish whether these associations are consistent across a wider range of floral abundances.

Conclusion

We conclude that both gardens and allotments provide valuable habitat to support pollinators within cities, and even small-scale management interventions such as increasing floral resources can boost pollinator diversity irrespective of site type. Whilst non-native floral resources had a greater impact on increasing pollinator diversity, we advocate for the prioritising of native floral resources by gardeners. Native plants consistently received more visits, and a higher proportion of native plants increased network specialisation, indicating native plants may facilitate more specialist pollinators within green spaces. However, non-native plants can be used to supplement the floral resources later in the year, providing a high availability of plants throughout the main pollinator season. Yet caution is required when selecting non-native plantings, as invasive non-native species can have negative effects on ecosystems (Aizen et al., 2008). We have provided a list

of plants that were preferred by more than five pollinator species for each month of the study, to help guide floral plantings (Table 4.2 and Appendix D, Table D.6). Finally, surrounding green space area had a small, positive impact on flower visitor diversity through increasing the effect of floral richness. Yet even in dense urban areas, increasing the floral richness within sites still had positive effects on flower visitor diversity, and thus can be used as a management intervention in any green space. In other cities, with dense urban layouts, landscape-level green space may become a more important factor in shaping flower visitor diversity in gardens and allotments. However, our results remain relevant to cities with large areas of green space, such as our study location.

Overall, gardens and allotments with high floral richness play a crucial role in supporting pollinator diversity in urban environments. National pollinator strategies have helped local authorities to implement positive management in public parks (NatureScot, 2017). However, private gardens are not necessarily managed for pollinator diversity, yet these spaces make up substantially more urban land than publicly managed parks. Therefore, encouraging pollinator friendly gardening practices within local communities is especially important. Although allotments occupy less than 1% of land use within cities, they provide important pollinator habitat as well as valuable spaces for people. As such, allotments should be considered more in urban planning and recognised as key green spaces for resilient and biodiverse cities.

Chapter 5 Pollinator community assembly in urban green spaces is shaped by trait filtering at broader spatial scales.

Abstract

Urban pollinator diversity is generally lower than in natural areas, but green spaces such as gardens and allotments can help to maintain substantial pollinator diversity. Thus, understanding the processes shaping community assembly in urban green spaces is vital for informing pollinator conservation. While previous studies have assessed trait-environment relationships, primarily within single green space types, less is known about how pollinator communities assemble across different urban habitats.

Here, we used Hierarchical Modelling of Species Communities (HMSC), a joint species distribution modelling approach, to investigate community assembly of bees and hoverflies in two green space types: private residential gardens and allotments in Glasgow, Scotland. Specifically, we aimed to 1) evaluate how environmental variables structure community composition, 2) determine whether environmental gradients shape pollinator communities through trait filtering, and 3) whether species co-occurrence patterns influence pollinator community assembly. Finally, we 4) assessed whether urban pollinator traits are filtered relative to the regional trait pool.

Species generally responded in similar directions to environmental drivers, although response magnitudes varied. In bees, floral richness on average explained the largest proportion of variance (32.4%) and was positively related to species occurrence. In hoverflies, month explained largest proportion of variance (28.5%) and was predominantly positively related to species occurrence.

At the local scale, we found little evidence that environmental variables structured communities through trait-environmental relationships. However, at the regional-city interface, trait filtering was evident. Bee communities were filtered towards above-ground nesting species that emerged earlier in the season, and hoverfly communities towards early emerging species.

Together, these findings suggest that within gardens and allotments, community assembly is primarily driven by species level responses to local environmental

variables, while trait filtering operates at broader spatial scales. Such large spatial scale of trait filtering may limit the effectiveness of conservation efforts to increase functional diversity within these urban green spaces. Small scale interventions, such as increasing floral richness, may support greater taxonomic diversity in green spaces. However, these interventions may need to be applied at larger scales, to help increase the permeability of cities and promote the movement of pollinators from regional areas into urban green spaces. Moreover, we recommend providing greater bare soil availability to support ground nesting bees in urban areas.

Introduction

Urbanisation is a significant driver of land use change (Nuisl and Siedentop, 2021) and a recognised threat to biodiversity (Li et al., 2022) including for invertebrates such as pollinators (Sánchez-Bayo and Wyckhuys, 2019). This is concerning, given the high economic value of pollinators through the ecosystem services they provide (Porto et al., 2020), and the fact that urban growth is projected to increase until at least 2040 (United Nations, 2025). Pollinator diversity is reduced in cities in comparison to natural areas, due to novel environmental pressures and their interactions, such as habitat fragmentation, floral resource availability, light pollution and habitat patch size (Ayers and Rehan, 2021; Wenzel et al., 2020). Despite this, studies have shown relatively high pollinator diversity in urban areas when compared to agricultural settings (Baldock et al., 2015), leading to the implementation of conservation actions that target urban environmental drivers such as increasing floral richness (Baldock, 2020). However, inconsistencies in the relationship between urbanisation and pollinator diversity remain and can depend on location and taxonomic group (Baldock et al., 2015; Liang et al., 2023).

Taxon-specific responses of pollinators to urbanisation can be partly explained by their traits. Urbanisation acts as a strong abiotic filter on pollinator communities whereby environmental drivers select for species with certain traits (Ayers and Rehan, 2021; Fournier et al., 2020; Wenzel et al., 2020). Indeed, studies have shown an increased abundance of non-native, above ground nesting and solitary bees (Wilson and Jamieson, 2019), as well as small bodied bees that are active later in the season (Banaszak-Cibicka and Żmihorski, 2012) in urban areas. For

example, ground nesting bee species richness and abundance have been found to decrease across an urbanisation gradient, and were negatively associated with impervious surface cover (Geslin et al., 2016). Additionally, fourth-corner analysis (a statistical approach testing associations between species traits and environmental variables using community composition data) has been used to address trait-environmental relationships in urban pollinator communities (Buchholz et al., 2020; Gathof et al., 2022; Theodorou et al., 2020b). However, fourth-corner results have also been inconsistent, for example in bees, body size has been positively associated with floral richness (Theodorou et al., 2020b) and proportion of impervious surface (Gathof et al., 2022), whilst another study found no relation with environmental variables (Buchholz et al., 2020).

Urban areas are inherently complex and heterogeneous environments. Cities contain a mosaic of urban green spaces which differ in their primary functions, and as a result vary in their habitat quality for pollinators (Baldock et al., 2019). From a community assembly perspective, this heterogeneity may create a matrix of local environmental filters that structure pollinator communities within cities, nested within the broader trait filtering associated with transitions from rural or natural to urban habitats. Accordingly, trait filtering within bee communities was shown to occur at two spatial scales; the urban green space and the city scale (Fournier et al., 2020). Here, gardens and allotments selected for bee species with short tongues while brownfields, parks and green roofs selected for generalists, with longer and earlier activity periods (Fournier et al., 2020). Furthermore, at the city scale bees were selected to be large, social, cavity nesting, pollen generalists that were active earlier and longer in the season (Fournier et al., 2020). However, the environmental drivers underlying these patterns of pollinator community assembly within green spaces remain poorly understood, and previous research often oversimplified the heterogeneous nature of the urban landscape. Indeed, while studies have assessed trait-environmental relationships in pollinators, it is still unclear whether these relationships vary among green space type (Brasil et al., 2024; Buchholz et al., 2020; Gathof et al., 2022; Theodorou et al., 2020b). Previous research show gardens and allotments to provide valuable habitat for pollinators (Baldock et al., 2019), however the potential for trait-environmental relationships to shape pollinator communities within these green spaces have largely been ignored. Given substantial variation in traits among

pollinator groups, there remains a critical gap in understanding how environmental variables influence trait-environmental relationships and shape pollinator communities across green spaces.

To address this gap, we used Hierarchical Modelling of Species Communities (HMSC) to model bee and hoverfly community assembly in two urban green spaces: private residential gardens and allotments. HMSC is a multivariate hierarchical modelling framework that allows the patterns in community composition to be evaluated, while accounting for multiple sources of ecological structure (Abrego and Ovaskainen, 2020). Compared to fourth-corner analysis, HMSC enables trait-environmental relationships to be evaluated while accounting for both abiotic, biotic and phylogenetic structure (Abrego and Ovaskainen, 2020). Moreover, the multivariate nature of HMSC allows species-specific variation to be retained (Abrego and Ovaskainen, 2020). Using a HMSC modelling framework, we aimed to 1) evaluate how environmental variables in two urban green space types affect the occurrence of bee and hoverfly species within the community, to 2) determine whether environmental variables influence pollinator assembly through trait filtering, and 3) whether species co-occurrence patterns influence pollinator community assembly. We predicted that pollinator occurrence would be influenced by green space type and floral richness as well as the proportion of non-native plants (H1). We expected that oligolectic bees would be negatively associated with the percentage richness and abundance of native plants, whilst body size would be positively associated with green space size but negatively associated with surrounding green space in both bees and hoverflies (H2). Moreover, if environmental drivers explained variance in species occurrence, we expected weak co-occurrence between species (H3). Finally, we used a null model approach based on bee and hoverfly occurrence data from the NBN Atlas (NBN Trust, 2026), to compare observed community-weighted means of trait values with those expected from a regional trait pool. To this end we aimed to 4) assess whether trait filtering in bee and hoverfly communities in our study occurred at the regional-city interface. We expected the urban area would select for generalist (polylectic), early emerging, above ground nesting traits and larger bees, whereas hoverfly communities were expected to be selected for early emerging and larger body sizes (H4).

Methods

Study location

We conducted our study in Glasgow, Scotland (55° 51' 46" N, 4° 15' 07" W). Glasgow is the largest Scottish City by population and is approximately 175km² in area. We sampled nine private residential gardens and eight allotments which were all situated within Glasgow, including a 5km buffer around the Glasgow City Council boundary (Fig.5.1). The 5km buffer was applied to increase the potential sampling pool, allowing the selection of sites with a minimum separation of 1km distance. Moreover, the 5km buffer still encompassed the urban core within this area. Gardens are defined as green space adjacent to domestic buildings. Allotments (or community gardens) are defined as green spaces made up of parcels of land that are privately leased by individuals (plots), or a local community, and are typically used for horticultural purposes. Due to the variation in management of plots across a single allotment site, between 7 and 13 plots (mean±SD 7.1±4.2 plots) were sampled per allotment site. Consequently, the mean sampled area across all allotment plots was 170.2±242.4m², compared to 122.2± 63.1m² for whole garden surveys. Private gardens make up the largest proportion of green space across Glasgow (30%), whilst allotments make up one of the smallest proportions (<1%) (NatureScot., 2022). Sampling was conducted once a month, in each site from the 1st of April 2024 until the 31st of September 2024 resulting in six sampling events per site.

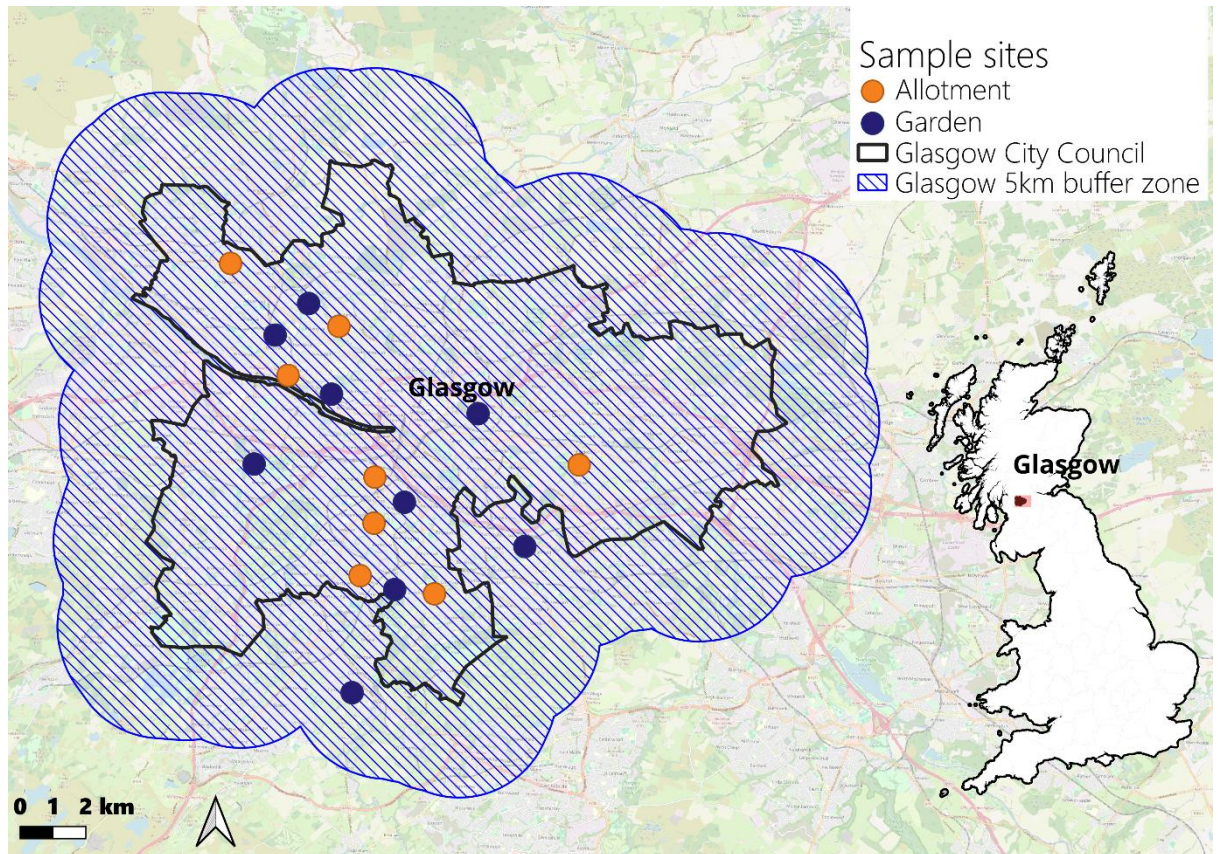


Figure 5.1: Sampling locations of nine gardens (orange) and eight allotments (blue) situated across Glasgow, Scotland and within a 5km buffer surrounding Glasgow. The location of Glasgow within the UK is shown on the right.

Pollinator sampling

Pollinators were sampled by recording visits to all flowers within a site. Meandering transects were conducted by walking in a zig-zag pattern over a 30-minute period, during which a single observer (E.P.) walked among all flowering plants and recorded the pollinators actively contacting the reproductive structures of a flower using instantaneous counts (Nicholls et al., 2023). Each 30 minute transect was carried out for whole garden surveys or for individual plots. Timed transects have commonly been used to record flower visitors in urban habitats, where green spaces are too small to allow transects to be standardised by size (Nicholls et al., 2023; Sirohi et al., 2022). Only individuals belonging to the target taxa, Syrphidae and Anthophila, were included in this recording. These target taxa were chosen as they are known pollinators and because taxonomic expertise was limited to these groups. Day flying Lepidoptera were also recorded, however they were removed from the analysis due to the lack of flower visiting

behaviour observed in this group, thus are sampling was unable to determine the presence of butterflies in these sites.

Environmental variables

Alongside pollinator sampling each month, floral species were recorded and abundance was estimated. Floral abundance was estimated following the protocol in Nicholls et al. (2023) by two trained recorders (E.P. and W.M.). Specifically, two plants of each species were randomly selected to calculate the floral units per plant species. Average floral units were then multiplied by an approximation of the total number of plants (0-10, 11-20, 21-30, 31-40, 41-60, 61-80, 81-100, 100+) per species at each site. Floral units were defined using protocol of Nicholls et al., 2023. Plants were classified as native or non-native to Great Britain using BSBI's database (<https://bsbi.org/taxon-lists>). From this, the total percentage abundance and richness of native plants were calculated to use in analysis. Green space size was measured using QGIS version 3.40.8 (QGIS Development Team, 2026), using garden boundaries and individual plot boundaries within allotments to define green space area (m²). Finally, the total area of green space surrounding a site was measured within a 500m buffer. Green space data was collected from Copernicus urban atlas (European Union, 2020) and included, sports and leisure facilities, pastures, arable land, wetlands and forests land use classes.

Regional and urban pollinators

To gain a regional pollinator pool, we followed the co-occurrence method used in (Fournier et al 2020), which gathers a list of species that could potentially colonise our study area. Our regional area was a 30km buffer zone that was defined outside of the 5km buffer around Glasgow City Council Boundary (Appendix E, Figure E.1). We used a 30km boundary as it encompassed a range of habitats outside of the core urban area sampled in our study, simultaneously excluding species that occur at southern latitudes in the UK, and as such are unlikely to colonise our study area. Data on species occurrence of our focal taxa (Syrphidae and Anthophila) within our regional boundary, were downloaded from the NBN atlas (accessed 25th of January 2026) (NBN Trust, 2026) (Appendix E, Figure E.1). We further filtered species records for those recorded after 2015, resulting in 7792 bee and 5591 hoverfly records. We then collated species lists for 1x1km grid cells across our

entire regional buffer. 175 grid cells were randomly selected, as it equates to the total area of Glasgow City Council (175km²), in which we identified any species that occurred alongside the species recorded in our urban pollinator sampling. The urban pool for bee and hoverfly species was obtained by pooling our species list from each sample site and across all sampling months from pollinator sampling in gardens and allotments. We recognise that our sampling may be an under representation of the species in Glasgow, however time constraints limited the number of sites we could visit. We downloaded all species records from the NBN Atlas (accessed 25th of January 2026) within the Glasgow City Council boundary and the surrounding 5km buffer in order to compare with the species list gathered from sampling across the gardens and allotments. The full species list and the corresponding species traits for Glasgow species gathered from the NBN Atlas can be seen in Appendix E, Table E. 2.

Pollinator traits

Trait information was gathered for each species from the open database on traits and phylogenetic data of European pollinators (Michez et al., 2023) (Table 5.1). For bee species, the traits selected for analysis were body size, lecty, phenology start and nesting position. For hoverflies, the traits body size and phenology start were gathered.

Table 5.1: Bee and hoverfly traits used in this study, gathered from the open database on traits and phylogenetic data of European pollinators (Miličić et al., 2023). Trait definitions are outlined in the database and were re-categorised for analysis in our study.

Trait	Definition	Study categorisation
Bees		
Body size	Mean inter-tegular distance in mm	Mean ITD for females used except for <i>Apis mellifera</i> and <i>Bombus</i> species.
Lecty	Oligolectic: bees that forage for pollen on a narrow range of plants.	yes/no =1/0
	Polylectic: bees that forage for pollen on a wide range of plants.	yes/no =1/0
	Cleptoparasite: brood parasite	Yes/no=1/0

Nesting position	Above ground: nest position above ground	Yes/no=1/0
	Below ground: nest position below ground	Yes/no=1/0
Phenology start	First month in which species is active	Months January to December given numeric values 1-12
Hoverflies		
Body size	Species were categorized in 3 groups based on its size: small (less than 7 mm), medium (7-12 mm) and robust (larger than 12 mm). 5 trait states are present, if the species covered the range of more than one category: small, small or medium, medium, medium or robust, robust	Species categorised as small to medium were redefined as small and species categorised as medium to robust were redefined as robust. Numerical values were then given to each category: Small=-1, Medium=0, Robust=1
Phenology start	Flight period of adults. 5 trait states, each in a separate column, as not all are mutually exclusive: early spring (February, March), spring (April, May), early summer (June), summer (July, August, September), autumn (October, November). Phenology start was therefore defined as the first season in which the adult flight period was present.	Early spring=1, Spring= 2, Early summer= 3, Summer=4 Autumn=5

Data analysis

HMSC model

Models for bee and hoverfly community assembly were fitted separately using the HMSC framework with Bayesian inference using the HMSC package (Tikhonov et al., 2025) in R (“R version 4.5.2,” 2025). Abundance data was transformed to presence absence data for each bee and hoverfly community recorded per plot, within each site, per month, and modelled using a probit distribution. For both models, monthly environmental variables collected at each plot within each site were included as fixed effects. Specifically, these variables were, floral abundance per m², floral richness, the percentage abundance of native flowers, the percentage richness of native flowers, green space size, the area of green space within a 500m radius, site type (garden or allotment), and month as a

continuous variable (1 to 6). All continuous variables were scaled and log transformed before implementation in the model. Site and plot were included as random effects.

The HMSC modelling framework estimates species specific coefficients for each environmental predictor. Variation in species specific coefficients are then modelled as a function of species traits. Trait data was implemented in the model as per the methodology section, except for body size in bees which was log transformed. Phylogenetic data was gathered from the tree of life database using the *rotl* package (Michonneau et al., 2016). The tree of life dataset uses certain species synonyms, which were verified against the GBIF species records. The complete list of synonyms is provided in Appendix E, Table E.1. Phylogenetic trees were then constructed and branch length computed using the *ape* package (Paradis and Schliep, 2019). A phylogenetic covariance matrix was incorporated into the model, which accounts for non-independence among species due to shared evolutionary history. *Eupeodes bucculatus* was removed from the hoverfly model due to a lack of available trait data and *Andrena denticulata* was removed due to lack of phylogenetic data. Weakly informative built-in HMSC priors were used in the model.

For both models, we ran four MCMC chains each with 5000 iterations, of which the first 3000 were discarded as burn-in. Every 10th iteration was retained to reduce autocorrelation. Trace plots, effective sampling sizes and PSRF values were assessed to check model convergence. We compared the best models for both bees and hoverflies by removing environmental variables one at a time and comparing WAIC values (Watanabe, 2010) (Appendix E, Table E.3).

Null models

We created null models for expected urban pollinator traits following the methods in Fournier et al (2025). Here, we randomly reshuffled the traits present in the regional pool to our urban pollinator samples, whilst retaining species abundances. This was repeated 10000 times, and community weighted mean was then calculated for each pollinator trait. Standardised effect sizes compared the observed with the expected community weighted means for the urban pollinator species pool.

Results

HMSC model convergence

All effective sampling sizes were high and PSRF values close to 1. WAIC scores for both bee and hoverfly models did not differ when environmental variables were removed (Appendix E, Table E.3). As the inclusion of additional variables did not worsen model fit, and because we were interested in their effects, we retained all environmental variables in the final model.

Urban pollinators

Across our sample sites, and the six sampling months we recorded 53 hoverfly species and 29 bee species. A full list of pollinator species from our sample sites can be seen in Appendix E, Table E.1. The sampled urban bee pool and the NBN Atlas urban bee pool had a Jaccard similarity of 0.46, while the corresponding species lists for hoverflies had a Jaccard similarity of 0.65. Nevertheless, there was incomplete overlap between the datasets, with some species recorded in our surveys absent in the NBN dataset, and vice versa (Appendix E, Table E.2).

Community assembly in urban green spaces

Species environmental relationships

At the 95% posterior probability threshold, associations between bee occurrence and environmental variables were unevenly distributed across species (Fig. 5.2a). Floral richness showed a positive regression coefficient with 24 out of 28 bee species. Floral abundance was also positively associated with species occurrence, with 46% of species showing positive effects. Temporal effects varied among species. Eight species were negatively associated with month whilst one species, *Bombus pascuorum*, was positively associated with month. Other environmental variables exhibited more species-specific relationships. For example, the percentage abundance of native plants was negatively related to occurrences of *Bombus lapidarius*, while five species were positively related to the percentage richness of native plants. Site type also influenced species occurrence. Around 21% of species were negatively associated with garden sites, and some species,

such as *Sphecodes geoffereilus*, were only observed in allotment sites. In contrast, *Bombus lapidarius* was positively associated with garden sites. Site size showed a positive association with six bee species, and surrounding green space a positive association with *Anthophora furcata*.

Similarly, hoverfly species associations with environmental variables were unevenly distributed across the hoverfly community when assessed at the 95% posterior probability threshold (Fig. 5.2b). Month was the most consistent, showing positive associations with 24 out of 58 species, whilst *Epistrophe eligans* showed a negative association. Nine hoverflies were positively associated with floral richness, six with floral abundance and four with green space size. *Epistrophe glossulariae* was the only species that was positively associated with surrounding green space and the percentage abundance of native flowers. Two species (*Platycheirus albimanus* and *Melanostoma scalare*), were positively associated with garden sites. *Eristalis pertinax* was negatively associated with the percentage richness of native flowers.

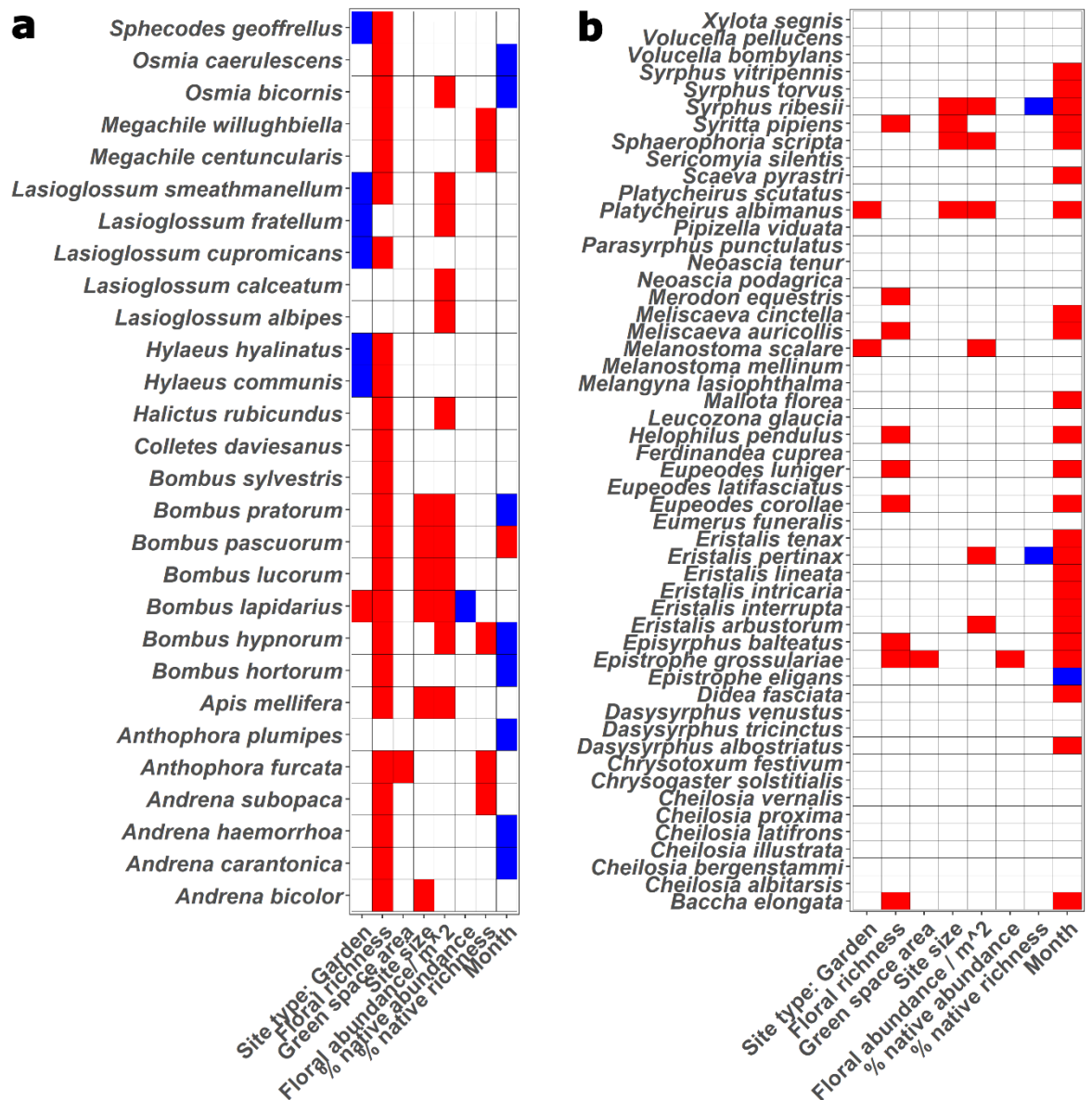


Figure 5.2: a) bee and b) hoverfly species responses to β coefficients in the HMSC models. Blue indicates a negative response and red a positive response of species occurrence to coefficients at a 95% posterior support threshold. White indicates no posterior support.

Variance partitioning was applied to assess the contributions of each environmental variable and the random effects to species occurrence. Within bee communities, floral richness explained the largest proportion of variance in 18 species (Fig. 5.3a). Across all bee species floral richness explained the largest mean proportion of variance (32.4%), followed by month (16.5%), floral abundance (11.6%), percentage richness of native flowers (8.6%), percentage abundance of native flowers (6.9%), green space size (6.3%), site type (3.5%) and surrounding green space (3.3%). Mean proportion of variation explained by the random effect of site and plot was 5.1% and 6.0%, respectively.

Similarly, the strength of environmental influences varied across hoverfly species (Fig. 5.3b). Month explained the largest proportion of variance in 28 hoverfly species. Across all hoverfly species month explained the largest mean proportion of variance (28.5%), followed by floral richness (16.4%), floral abundance (8.3%), percentage abundance of native flowers (8.0%), green space size (7.2%), percentage richness of native flowers (7.1%), surrounding green space (5.3%) and site type (3.5%). Mean proportion of variation explained by random effect of site and plot was 7.4% and 8.3%, respectively.

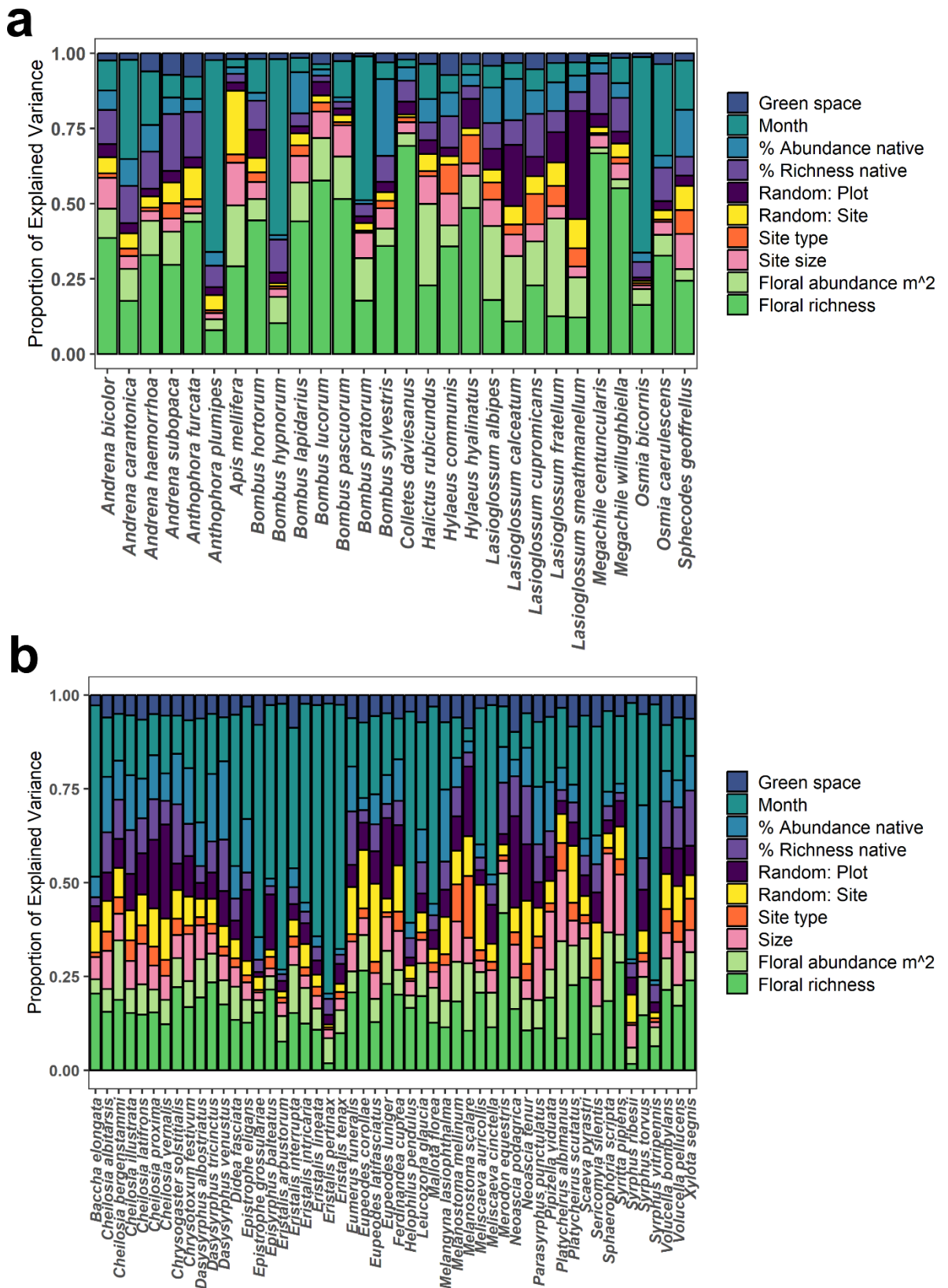


Figure 5.3: Variance partitioning of environmental and random effects influence on a) bee and b) hoverfly occurrence within urban green spaces in Glasgow.

Trait environmental relationships

At the 95% posterior probability threshold, body size in bees was positively associated with garden sites. No other trait-environmental associations were found in bees. No trait-environmental associations were found in hoverflies.

Species associations

Residual bee species associations lacked strong posterior support except for one species pair, *Anthophora furcata* and *Apis mellifera* ($r=-0.9$, $p>0.04$) (Fig.5.4). Of the 378 unique species pairs, 11 showed large estimated residual correlations ($r>0.7$) with both *Anthophora furcata* and *Apis mellifera* occurring in 6 of these 11 pairs. For the hoverflies, no strong residual species correlations received strong posterior support. There were proportionally fewer large estimated residual correlations among hoverfly species with 10 of 1326 unique species pairs showing correlations of $r>0.7$.

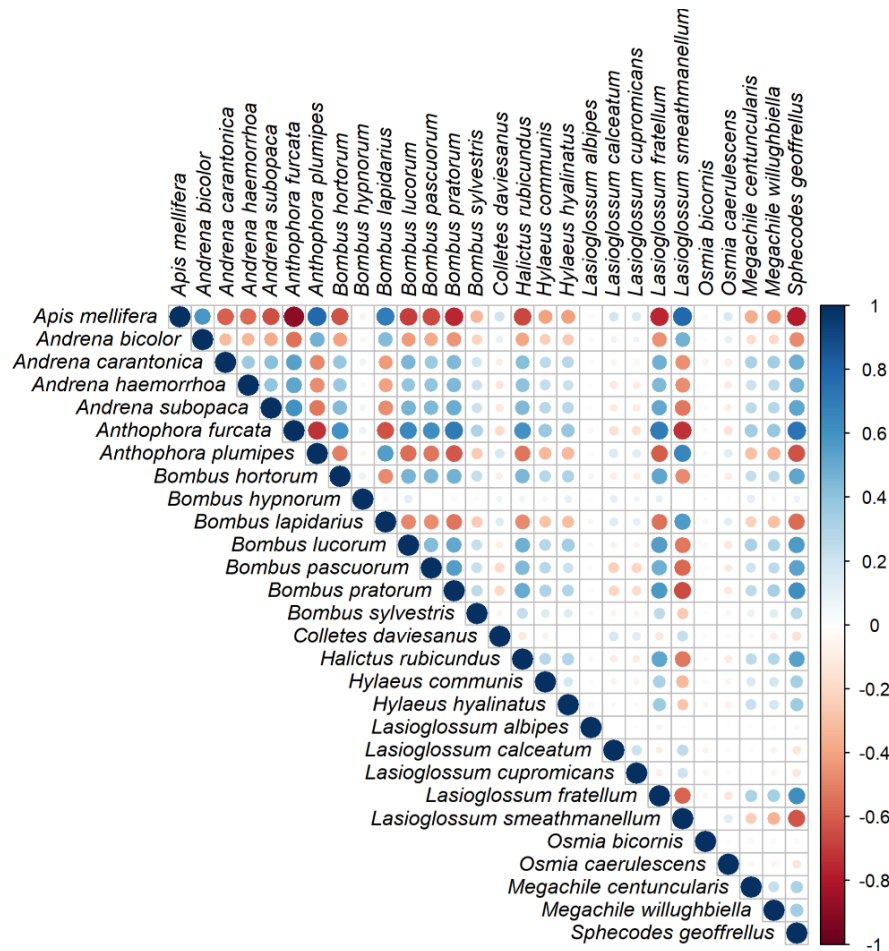
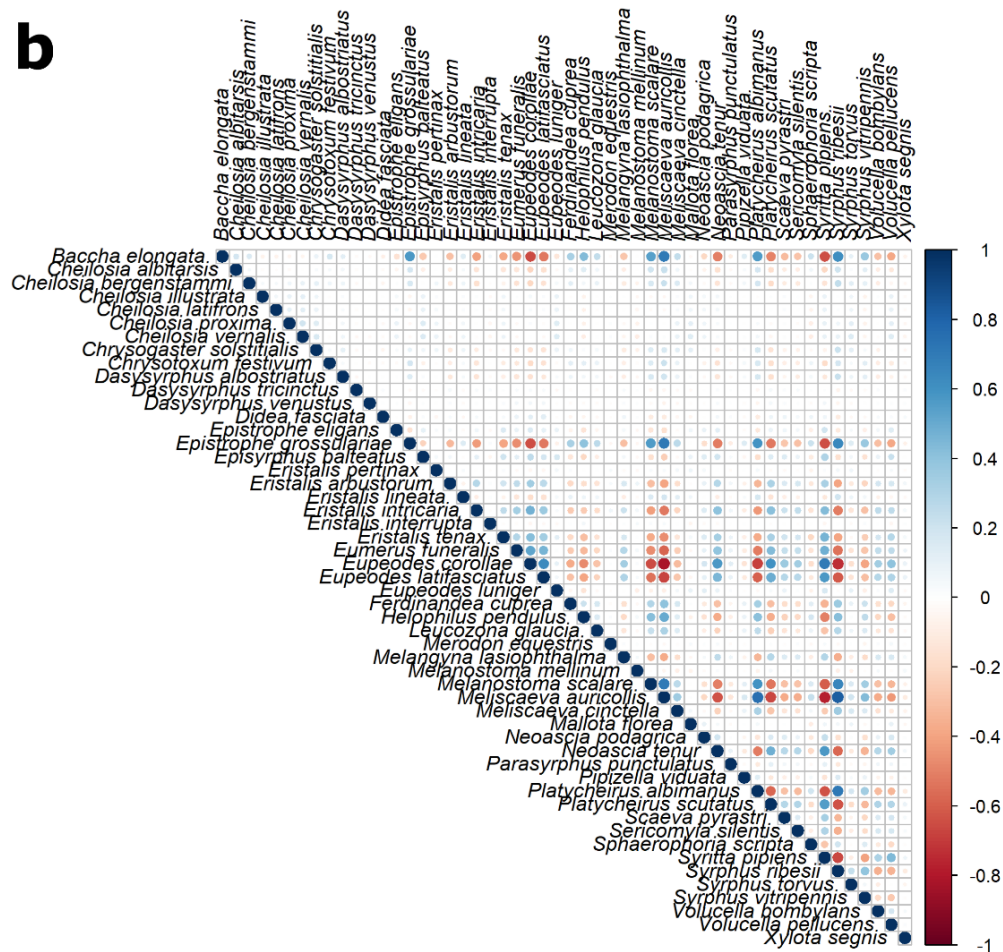
a**b**

Figure 5.4: Residual associations between a) bee species and b) hoverfly species. The size and colour (Red negative and blue positive) of points relate to the posterior support threshold. Only a strong association between *Apis mellifera* and *Anthophora furcata* had posterior support above a 0.95 threshold.

Regional pollinators and trait filtering at the city scale

Regional species lists constituted 98 hoverfly species and 49 bee species (Appendix E, Table E.4). As a result, the urban species pool contained 59% of bee species and 54% of hoverfly species from the regional pool.

The observed community weighted mean for the trait '*phenology start*' in the urban bee community was significantly lower than expected when compared to null models (Table 5.2). Moreover, the community weighted mean for the above ground nesting trait was significantly higher than expected when compared to null models (Table 5.2). This suggests that the urban bee community in Glasgow was filtered towards earlier emerging species that nest above ground. Similarly, the urban hoverfly community in Glasgow was filtered towards earlier emerging species as the community weighted mean for phenology start was lower than expected when compared to null models (Table 5.2).

Table 5.2: Results from the null model analysis comparing community weighted means of urban pollinators traits to those in the regional pool. The table shows the observed community weighted mean for each trait in urban bee and hoverfly communities, as well as the standardised effect sizes (SES) and p values.

Traits	Observed Community weighted mean	SES	P value
Bees			
Body size	3.76	1.66	NS
Oligolecty	0.02	-0.74	NS
Polylecty	0.98	1.55	NS
Cleptoparasite	0.002	-1.21	NS
Above ground nesting	0.70	3.33	0.003
Below ground nesting	0.30	-1.49	NS
Phenology start	1.20	-2.04	0.03
Hoverflies			
Body size	0.16	0.31	NS
Phenology start	1.48	-3.79	0.004

Discussion

Urban green spaces within cities are often targeted for conservation actions to support pollinator diversity, due to their comparatively lower diversity in contrast to natural areas (Baldock et al., 2015), and potential positive outcomes for human health through increased exposure to nature (Jimenez et al., 2021). Initiatives like planting pollinator friendly plants seek to boost urban pollinator diversity, but are often carried out within a handful of urban green spaces such as parks (Glasgow City Council, n.d.). While heterogeneous urban landscapes can contribute to high pollinator diversity within cities, it is unclear how environmental variables within these green spaces influence pollinator community assembly, including the trait pool. Our results suggest that community assembly arises from species-specific responses to urban environmental variables as opposed to trait-environment relationships. The lack of trait effects is likely a consequence of trait filtering at a broader spatial scale, as suggested by our null model, which hints that trait filtering has already occurred in our urban pollinator community. Results from this study could have implications for conservation actions in urban green spaces, wherein increasing habitat quality through small scale management interventions may only have positive implications on an already filtered pollinator community. Instead, interventions may need to be applied across larger spatial scales to promote the permeability of urban areas and facilitating the movement of pollinators into green spaces from surrounding regional populations. Additionally, habitat requirements for species traits filtered at the regional-city interface, for example, bare soil availability for ground nesting bees, need to be prioritised in urban conservation strategies.

Community assembly in urban green spaces

Many studies have consistently shown increasing floral richness within urban green spaces is positively associated with pollinator diversity (McCune et al., 2020; Theodorou et al., 2020c; Zaninotto et al., 2020), supporting our findings of generally positive species responses to floral richness. Some studies found landscape variables, such as the proportion of impervious surface, were more important drivers of pollinator diversity than local characteristics (Herrmann et al., 2023). However, these studies often focused on a single green space

type, such as urban grasslands, where floral richness may be relatively high and homogeneous across sites. In comparison, gardens and allotments are highly managed and heterogeneous systems, where variation in floral richness is likely more pronounced and may therefore explain more variation pollinator diversity.

Our findings show that green space type explained a relatively small proportion of variance in species occurrence (3.5%). The detectable effect of green space type indicates that broader habitat context plays a minor role in structuring pollinator communities in urban environments. Other studies have found differences in pollinator diversity across green space types; however, this relationship was mediated by differences in floral diversity within these sites (Baldock et al., 2019). Similarly, in our study environmental drivers such as floral richness were found to be a stronger determinant of pollinator occurrence than green space type, suggesting that gardens and allotments may have similar pollinator diversity if they contain comparable floral richness.

Additionally, our findings revealed little evidence of trait-based filtering between urban green spaces, except for a positive association between body size and garden sites in bees. Consistent with this, previous work found that taxonomic, rather than trait-based variation is a key component of bee community dissimilarity between urban green spaces (Fournier et al., 2020). Overall, our findings support the idea that variation in urban communities between green spaces is primarily driven by species responses to local environmental variables, with relatively limited filtering based on functional traits.

Contrary to this, other studies have reported trait-environmental relationships within urban green spaces (Brasil et al., 2024; Theodorou et al., 2020b). For example, Theodorou et al., (2020), found positive associations between ground nesting bees and the percentage of bare soil, and between body size and flower depth. In our study, the association between body size and gardens may reflect the relatively small size of gardens and consequently fewer resources, requiring bees to forage across larger areas and selecting for greater mobility (Wenzel et al., 2020). However, no such relationship was found between green space area and body size. The lack of other trait-environmental relationships in our study may reflect unmeasured variables, particularly plant functional traits. Moreover, previous studies assessing trait-environmental relationships used fourth-corner analysis, which test pair wise associations between trait and environmental

variables without accounting for species co-occurrence and phylogenetic structure. This contrasts with our HMSC modelling framework, which explicitly models species co-occurrence and phylogenetic structure, potentially providing a more comprehensive assessment of trait-environmental relationships.

Although few trait-environmental relationships were identified, the residual correlation structure indicated some species associations that remained after accounting for trait-environmental and species-environmental relationships in the models. Whilst many residual species correlations were large, only one had posterior support. The significant correlation between *Apis mellifera* and *Anthophora furcata* suggests that their occurrences were negatively associated beyond what could be explained by the environmental and trait relationships included in the model. The mechanism behind this result remains unclear as the species cooccurrence results could suggest some level of competition between these two species, alternatively it may also represent unmeasured trait and environmental variables.

Urban trait filtering

Our findings indicate trait filtering of urban bee communities when compared to the regional trait pool, whereby the city favours above-ground nesting species. Similarly, studies have reported positive associations between urbanisation and the abundance of above-ground nesting bees (Geslin et al., 2013; Wilson and Jamieson, 2019). High proportions of impervious surface in urban environments likely increase the availability of artificial nesting cavities for above-ground nesting bees, whilst reducing suitable substrates for ground nesters (Wenzel et al., 2020).

We also detected filtering for early emerging species in both bee and hoverfly urban communities. The mechanisms underlying this pattern are unclear. Although elevated urban temperatures can advance flowering times, no such evidence has been found for the pollinator emergence (Fisogni et al., 2020). Furthermore, it has been suggested that the prevalence of non-native plants in urban areas, which have later blooming phenologies, favour late emerging pollinators (Harrison et al., 2018).

Using the same analytical approach to assess whether urban communities were filtered in comparison to a regional trait pool, Fournier et al. (2020) also found filtering for early emerging, above ground nesting species in the urban bee community. However, they also reported selection for larger-bodied, pollen generalists, for which we found no evidence in our study. These discrepancies may reflect differences in the spatial scale of the regional area used to define the regional bee species pool. Our study defined the regional pool within a 30km buffer around our study city, whereas Fournier et al. (2020), compiled records at a national scale across Switzerland. Consequently, our regional pool may already represent partially filtered subset of traits, reducing our ability to detect additional trait filtering.

Limitations and future work

Our findings can only be interpreted in the context of the urban green spaces examined in our study, which were limited to gardens and allotments. These green spaces can represent intensely managed habitats for pollinators, and patterns of community assembly may differ from those in other green spaces. This was shown in Fournier et al. (2020) where gardens and allotments were similar in their community composition but differed compared to parks, cemeteries and brownfields. Including a broader range of green spaces may better reflect the landscape heterogeneity, and thus community assembly within the urban environment. However, broader sampling was not possible in this study due to time constraints.

Although we detected limited evidence of trait-environmental relationships, our study did not incorporate plant traits. Given that we recorded plant-pollinator interactions, incorporating plant traits (colour, morphology, phenology) into the HMSC modelling framework could reveal whether fine-scale biotic filtering occurs through pollinator-plant trait matching. This may be particularly relevant in gardens and allotments where the floral community is highly managed.

Finally, our regional pollinator pool was defined using biological records from citizen science data. While we applied temporal filtering (records after 2015) to reduce temporal bias, such records may not reliably capture the true regional trait distribution. Independent sampling of pollinator communities across the surrounding landscape would provide a more robust estimate of the regional trait

pool and could be used in HMSC modelling to identify trait-environmental relationships outside of the city. Nevertheless, biological records were also used in Fournier et al. (2020), providing comparability between the two studies, as well as being a practical approach to defining regional species pools.

Conclusion

We show evidence of trait filtering in bee and hoverfly communities at the regional scale, but little evidence of trait-filtering structuring community assembly processes at the urban green space scale when assessed in gardens and allotments. Instead, community assembly between green spaces was primarily driven by species responses to environmental variables. Our study is the first to assess the environmental drivers of trait assembly in pollinator communities across urban green spaces, using a joint species distribution modelling framework. Moreover, we contribute to the comparatively sparse literature assessing hoverfly trait-environmental relationships.

These results could have implications for urban pollinator conservation. Management actions to increase pollinator diversity in gardens and allotments, such as increasing floral richness, may enhance local pollinator diversity, without increasing heterogeneity of the urban trait pool. Such conservation actions should prioritise habitat management for species traits filtered at the regional-city interface to promote the movement of pollinators into the city from surrounding regional populations. Additionally, positive management strategies may need to be applied across larger spatial scales. Given the large contribution of land cover by gardens within cities, management of gardens for pollinator diversity could be of great conservation value.

Chapter 6 Discussion

Summary of research findings

In this thesis I assess three main themes in urban pollinator ecology by exploring the environmental drivers associated with diversity, plant interaction network structure and traits within bee, butterfly and hoverfly taxa. Moreover, I address a key knowledge gap by investigating these themes in two contrasting green spaces, gardens and allotments, to account for the variation in pollinator habitat within the urban landscape.

Chapter 1 comprehensively reviewed the recent research in urban pollinator ecology and identified the contribution of different green spaces as potential pollinator habitat through a comparison of land use types in Scotland's main cities. In Chapter 2, the utility of cameras to visual observations was compared when assessing flower visitor diversity and plant-flower visitor network structure. Here, visual observations were found to be a superior method to recording flower visits, yet both methods were equitable in recording plant-flower visitor network structure.

Environmental influences on flower visits were then investigated using visual methods. This focused on gardens in Chapter 3 followed by a comparison between gardens and allotments in Chapter 4. The main drivers of flower visits were similar in both studies: floral richness was a key variable associated with both flower visits and flower visitor richness. Moreover, visits to native and non-native plants followed seasonal patterns, in which visits to non-native plants increased across the season whilst visits to native plants remained relatively stable. Importantly, native plants always received more flower visitors. Despite this, increasing non-native plants resulted in a greater increase in flower visits than when native plants increased. Finally, results suggested there was little influence of green space area surrounding sites on flower visits.

Additionally, within these chapters the association between environmental variables and plant-flower visitor network structure was assessed. Here, some discrepancies in results between Chapter 3 and 4 were found. In Chapter 3, there was no significant effect of any environmental variables on network structure.

However, the interactions of a dominant, generalist species (*Bombus pascuorum*), seemed to influence network structure across the season, as it increased in abundance. In contrast, in Chapter 4, floral richness was a key factor associated with network specialisation.

Chapter 5, aimed to determine whether trait filtering associated with urban environmental drivers occurred at the urban green space scale in gardens and allotments. Here, no trait-environmental relationships within pollinator communities in gardens and allotments were found. However, results indicated trait filtering when comparing community weighted means of traits observed within the city to those in the wider regional pool. Moreover, a selection towards early emerging, above ground nesting species, such as *Anthophora plumipes*, within the city was observed.

Importantly, across Chapters 4 and 5, no difference between gardens and allotments were found in terms of pollinator diversity, flower visitor network structure, nor traits was found. Results showed considerable variation in flower visits between sites, suggesting differing management regimes, independent of site type or function, are important predictors of pollinator diversity.

In this final chapter, I discuss the research findings of this thesis in the context of pollinator conservation within cities. Moreover, I examine limitations of this research as well as providing suggestions for future research.

Biodiversity in cities

Globally, urbanisation has been increasing at rapid rates and is expected to expand in both spatial extent and human population size (United Nations, 2020). Urbanisation is particularly concerning in the context of global biodiversity loss, as numerous studies have reported negative impacts of urbanisation on biodiversity across a range of taxa (McKinney, 2008). However, cities can also support considerable biodiversity, including some rare or declining species (Gentili et al., 2024).

Beyond their ecological value, biodiversity is increasingly recognised for its benefits to human health. Exposure to nature in cities has been linked to improvements in physical and mental health (Pinto et al., 2022), and the integration of green infrastructure is now considered an important component in

urban planning and sustainable city initiatives (e.g. Berlin Nature Pact (CitiesWithNature, 2024) and National Planning Framework 4 (Scottish Government, 2023)). Consequently, many cities have begun implementing conservation initiatives aimed at increasing biodiversity within urban landscapes.

Pollinators represent one group that may benefit from such initiatives. Urban areas are thought to provide important habitat for certain pollinators, including endangered species, particularly where diverse floral resources are available (Grossmann et al., 2023). Pollinators provide valuable ecosystem services as they facilitate the reproduction of wild and cultivated plants and improve yield in 75% of crop plant species (Klein et al., 2007). As a result, the global economic value of pollinators is estimated at \$235bn- \$577bn (Gallai et al., 2016). At the local scale, pollinators also contribute to food production in urban agricultural settings such as allotments, thereby supporting the provision of fresh fruit and vegetables to local communities (Nicholls et al., 2023).

Recognition of the importance of pollinators, alongside the potential for cities to support their populations, led to the development of conservation policies including pollinators in urban areas (e.g. Pollinator Strategy for Scotland (NatureScot, 2017)). At the local level, Glasgow City Council has developed Glasgow's Pollinator Plan, which provides a targeted approach to pollinator conservation within the city (Glasgow City Council, n.d.). These conservation actions primarily focus on increasing floral resources through wildflower meadows and supplementary planting within publicly managed green spaces such as parks. While these initiatives are important steps towards enhancing pollinator diversity, public green spaces constitute a relatively small proportion of the urban landscape in comparison to private green spaces such as gardens. Within Glasgow, private residential gardens contribute to approximately 31km² of land in contrast to 12km² of parks, with a similar proportion of green spaces across other Scottish cities.

Environmental drivers of pollinator diversity

Findings from this research suggests that increasing floral richness within gardens and allotments can support greater diversity of bee and hoverfly pollinators. This relationship has been found across multiple studies (Neumann et al., 2024; Philpott et al., 2025; Theodorou et al., 2020c) and represents a simple

management intervention that can be applied in green spaces across the city. Sites with greater surrounding green space showed a stronger increase in flower visits when floral richness increased compared to sites with lower surrounding green space (Chapter 4). Previously, studies have reported a positive association of surrounding green space on pollinator diversity, likely due to species spillover from nearby areas into sites (Liao et al., 2025; Martini et al., 2025). Results from this thesis indicate that greater amounts of green space around sites may provide additional resources for pollinators, in turn supporting greater pollinator diversity within gardens and allotments. However, interpretation is limited as land use maps were used to categorise surrounding green space, which do not capture variation in habitat quality within these sites. Future work that directly assesses habitat quality within surrounding green spaces could provide better insight into how landscape context influences pollinator diversity.

The association between floral resources and pollinator diversity became more nuanced once plant origin was accounted for. Visits to native and non-native plants followed seasonal patterns, with an increase in visits to non-native plants increasing across the season. Importantly, native plants received more visits across all seasons. While this suggests that native plants are important resources for pollinators in the urban environment, pollinator visits tracked changes in the seasonal availability of non-native plants. As such, non-native plants could be used in the context of providing supplemental floral resources later in the year. This was further supported by the finding that increasing floral abundance of non-native plants resulted in a greater increase in flower visits than when native plant abundance increased. These results are supported by other studies which have found preferences for native plants in pollinators (Pardee and Philpott, 2014; Salisbury et al., 2015), but that non-native plants increase in their utility as pollinator forage, particularly towards the end of the season (Staab et al., 2020; Zaninotto et al., 2023b). Additionally, mismatches between plant and pollinator phenologies have been recorded in urban areas, due to warmer urban temperatures advancing flowering times (Fisogni et al., 2022). Given the urban heat island effect will be exacerbated by global warming (Colom et al., 2026) potentially increasing the mismatch between plants and pollinators, non-native

plants could mitigate these effects by providing alternative floral resources over longer periods.

Our findings were likely influenced by the fact that a large proportion of flower visitors in this study were generalist species. For example, *Bombus pascuorum* accounted for 25% of the total interactions. This species is a known generalist, and as a eusocial bumblebee with high colony densities, can be a dominant species in urban environments (Plowright and Lavery, 1984; Silva et al., 2023). Generalist species are thought to be more capable of foraging on non-native plants, whereas specialists have closer evolutionary associations with native plant species (Seitz et al., 2020). As such, increasing abundance of non-native plants may be associated with greater abundances of generalists in these environments. Previous work using experimental plant plots found native plants hosted more specialised pollinator interactions; however, species involved in these interactions were polylectic (Seitz et al., 2020). This suggests that results in Seitz et al. (2020), were describing a change in pollinator foraging behaviour rather than increased numbers of specialists. Evidence that non-native plants drive declines in specialist pollinators are sparse, with many studies carried out in the field lacking appropriate controls to study the mechanisms behind losses of specialist species (Harrison and Winfree, 2015). As specialists are sensitive to disturbance, numerous environmental drivers including non-native plant abundance may contribute to declines in specialists (Aizen et al., 2012).

Another dominant generalist in our study was *Apis mellifera*, the European Honeybee. Honeybees may be introduced into cities to supplement bee diversity or regarded as enhancing pollinator diversity (Ropars et al., 2019b; Smith and Saunders, 2016). However, as a managed species, increasing the number of apiaries within a city can result in unnaturally high densities of honeybees (Ropars et al., 2019b). Moreover, the addition of a single species does not substantially increase bee species richness, and high densities of honeybees could increase competition with wild bees for floral richness. In this thesis, honeybees were the third most recorded flower visitor (2023 n=82; 2024 n=660) after *Bombus pascuorum* and *Bombus lucorum/ terrestris* agg. The lower abundance of Honeybees suggests that they are not the dominant flower visiting species within Glasgow. It was not possible to determine locations of apiaries within Glasgow, thus it was unknown whether the honeybees recorded in this study were wild or

managed and as such their density was not considered as an environmental variable. Consequently, this study cannot assess whether managed honeybees influenced wild pollinator communities, despite the potential effects of honeybee densities highlighted in previous literature.

Finally, no association of green space type with pollinator diversity was found, suggesting gardens and allotments provide equitable habitat for pollinators. However, substantial variation in floral resources were recorded in both green spaces, indicating the ability of sites to support pollinators may depend more on their floral availability which is independent of their primary function. Previous studies have reported differences between green spaces, although allotments and gardens often hosted similar pollinator diversity compared to habitats such as cemeteries and brownfields (Baldock et al., 2019; Fournier et al., 2020). These findings highlight the need for closer examination of environmental variables that shape pollinator diversity within a wider range of green spaces.

Plant-pollinator networks

Network structure followed seasonal patterns, with network specialisation peaking in the middle of the season and lowest at the beginning and end of the season (Chapter 3). We suggested that these results were mainly driven by the foraging patterns of *B. pascuorum*, which showed more specialist foraging patterns at the end of the season. In contrast, Chapter 4 did reveal urban environmental drivers associated with variation in network structure. Specifically, a positive association was found between floral richness and network specialisation. Similar results were found in Philpott et al. (2025).

While *B. pascuorum* accounted for the highest number of interactions in both Chapter 3 and Chapter 4, methodological and temporal differences may have led to variations in results. For instance, differences in weather conditions between years may have significantly affected the foraging behaviour and abundance of species. Networks are highly dynamic from year to year (Prendergast and Ollerton, 2022), and more long-term monitoring may be necessary to identify emerging trends. Similarly, total sampling time per sit per month was shorter in Chapter 4 than in Chapter 3. Sampling effort has been shown to influence network structure (Chacoff et al., 2012); however, time constraints necessitated a reduction in sampling duration.

Previous work by Proesmans et al. (2024) and Baldock et al. (2015) suggests that higher floral richness in urban areas increases the number of plant-pollinator interactions while a smaller proportion of the potential interactions are realised. Proesmans et al. (2024), further demonstrated that urban plant-pollinator networks can appear more resistant to perturbation, yet once an extinction cascade begins, they may result in greater overall species loss. A similar pattern may be present in this study. Floral richness was associated with greater pollinator richness and higher network specialisation, but the prevalence of generalist pollinators may represent a reduction in specialist species. In this context, network structure may represent already degraded ecosystems, where interactions are maintained by generalist species. Consequently, further species loss could disproportionately affect the remaining species.

Pollinator traits

No evidence of trait-environmental relationships in gardens and allotments was found in this study (Chapter 5). Models predicted species to respond to environmental variables in similar directions but at different magnitudes. Moreover, results show that trait filtering of pollinator communities likely already occurred across broader spatial scales at the regional-city interface; pollinators in gardens and allotments were selected towards early-emerging and above ground nesting species compared to the regional trait pool. This was supported by Fournier et al. (2020), who found gardens and allotments selected for similar traits and broader trait filtering at the regional-city interface within bee communities. However, Fournier et al. (2020) found green spaces such as parks, cemeteries and brownfields selected for contrasting traits when compared to gardens and allotments. Again, this highlights the need for future research to assess trait filtering across a wider range of green space types.

The results from Chapter 5 suggest that while greater pollinator diversity may be supported in gardens and allotments through interventions such as a higher floral richness, these interventions may only increase taxonomic, not functional diversity. As such, it is important to determine which species traits are filtered at the regional-city interface and implement specific conservation actions to facilitate these species within the city. Due to the filtering towards above ground nesting species, providing more bare soil in gardens and allotments could supply

nesting resources for more below ground nesting species. Moreover, these interventions should be applied across greater spatial scales to increase the permeability of the urban matrix and promote the movement of pollinators from regional areas into the city. However, associations between the proportion of bare soil and pollinator diversity or trait occurrence within sites was not directly examined in this study. As such future research should include this as a potential important variable alongside floral richness.

Implications for pollinator conservation and policies

Given the large spatial extent of gardens within cities, these green spaces offer the opportunity to scale up conservation efforts. Alongside providing floral resources in gardens, conservation actions should actively increase the amount of bare soil availability to facilitate more ground nesting bee diversity within cities. However, local strategies such as the Glasgow Pollinator Plan (Glasgow City Council, n.d.) primarily focus on increasing floral availability and lack strategies to increase nesting resources.

While gardens could provide conservation opportunities, the private management of these spaces means that their value as pollinator habitat depends on the floral resources provided by individual household owners. Improving communication around pollinators and the ecosystem services they provide can help encourage positive management in gardens (Braman and Griffin, 2022). Citizen science programs offer a useful mechanism for this engagement, fostering environmental education and nature stewardship within local communities (Church et al., 2025; Dickinson et al., 2012), alongside generating long term data across broad spatial scales (Plummer et al., 2024). Garden based citizen science could therefore be a useful tool for supporting pollinator conservation within cities whilst improving the representation of pollinator data across these widespread habitats. Although the Glasgow Pollinator Plan aims to raise awareness and promote citizen science initiatives such as the Bee Walk (Glasgow City Council, n.d.), a more targeted approach to encouraging pollinator recording within gardens would likely increase the impact of these efforts.

Allotments were shown to provide pollinator habitat of comparable suitability to residential gardens. However, in contrast to gardens, allotments represent a small proportion of urban land, covering just 1% of green space within cities, which

limits their potential to support pollinator diversity at the city scale. Within Scotland, the broader benefits of allotments for human health have been recognised and are included in urban planning policies such the National Planning Framework 4 (Scottish Government, 2023). However, the ecological role of allotments is rarely made explicit within planning policies. At the same time, the Pollinator Strategy for Scotland provides limited guidance on how urban planning can be used to benefit pollinator conservation within cities (NatureScot, 2017). As such there remains a disconnect between pollinator conservation policies and urban planning, particularly regarding the role of allotments in supporting pollinators in cities.

Limitations and future work

Several limitations of this research highlight directions for future research on urban pollinators. First, the findings presented here are restricted to gardens and allotments. As discussed, urban environments contain a diverse range of green spaces that contribute to pollinator habitat. While gardens are increasingly represented in urban ecology research, allotments remain comparatively understudied (Silva et al., 2023), meaning our results still provide a valuable contribution. However, other green spaces, such as sport fields and amenity land, receive less attention and thus represent areas for future research. Additionally, this study focused on Glasgow City as a case study. Although findings may be broadly applicable to other cities, their generalisability is likely limited to cities of similar size and structure in the global north. Replicating similar studies across a wider range of cities throughout the world would help determine the extent to which geographical or climate differences influence urban pollinator diversity.

Second, this research examined only bee, butterfly and hoverfly taxa. Many other insect groups also act as pollinators, but these taxa were selected due to resource constraints. Previously, urban pollinator research primarily focused on bees, although studies on butterflies and hoverflies have become increasingly common. Future research should therefore aim to expand the taxonomic range of pollinator species studied. Specifically, moths have been identified as important pollinators (Hahn and Brühl, 2016), and urbanisation may disrupt nocturnal pollinator networks through increases in artificial light at night (Knop et al., 2017), yet these taxa are often understudied due to difficulties in data collection.

Finally, several environmental variables identified as potentially important were not directly examined in this study. For example, bare soil availability may be a key factor influencing trait environmental relationships in bees. Additionally, habitat connectivity could also play an important role in shaping urban pollinator diversity. While this thesis quantified surrounding landscape context through the proportion of urban green space and land use diversity, the spatial configuration of the urban mosaic may be more important for pollinator diversity. Given our finding that trait filtering occurred at the urban-regional interface, habitat connectivity both within cities and between urban and surrounding landscapes could help facilitate the movement of pollinators into urban areas (Bracken et al., 2026).

Conclusion

Urbanisation can have negative consequences for biodiversity, yet urban green spaces present important conservation opportunities. Cities are at the forefront of novel solutions to support biodiversity while also providing benefits for human health and wellbeing. Specifically, gardens and allotments can host diverse pollinator communities, as demonstrated in this thesis, where 93 pollinator species were recorded across two field seasons. By examining environmental drivers of pollinator diversity, plant-pollinator interactions and patterns of trait filtering, this research contributes to a better understanding of how urban environments shape pollinator communities. Such insights can inform management strategies aimed at mitigating the negative impacts of urbanisation and help to identify key pollinator species that need more support in cities. In a time of widespread biodiversity loss and global warming across both natural and anthropogenic landscapes, supporting diverse urban habitats may be increasingly important for future pollinator conservation.

Appendices

Appendix A: Supplementary material for chapter 1

S.1- Green space type definitions

Table A.1: Definitions of 18 green space categories from OS MasterMap.

Green space type	Definition
Allotment	Areas of land for growing fruit, vegetables, and other plants, either in individual allotments or as a community activity. Produce is for the growers' own consumption and not primarily for commercial activity.
Amenity- residential or business	Landscaped areas providing visual amenity or separating different buildings or land uses for environmental, visual or safety reasons. Where the area is better described by another category this will be used in preference (for example, playing field, public park, play space).
Amenity - Transport	Landscaped areas providing visual amenity or separating different buildings or land uses for environmental, visual or safety reasons when related to a transport function, such as a road, or within a transport hub.
Land Use Changing	Areas of land that are currently under development or awaiting redevelopment.
Bowling green	A specially prepared area intended for playing bowls.
Cemetery	Areas of land associated with burial areas or crematoriums.
Camping or caravan park	An organised area of ground designated for tents or caravans, intended for temporary occupation by holidaymakers.
Golf course	A specially prepared area intended for playing golf
Institutional grounds	Areas of land normally enclosed and associated with institutions. Grounds may be reserved for private use or have restricted access. Includes: Universities, Hospitals, Nursing homes, Emergency Services, Prisons, Military Sites, Government and Community Buildings providing public services, Libraries, Museums, Zoos and Theatres.
Natural	Land use areas with no other greenspace function but with Form attribute of woodland, open semi-natural, open water, beach or foreshore.

Other sports facility	Land used for other sports not specifically described by other categories. Includes facilities for sports spectating (for example, stadiums) as well as participation.
Religious grounds	Areas of land associated with churches and other places of worship.
Play space	A specially prepared area intended for children's play, usually linked to housing areas or parks and containing purpose-built equipment. Not captured if within schools or paid-for tourist attractions.
Playing field	Large, flat areas of grass or specially designed surfaces, generally with marked pitches, used primarily for outdoor sports (i.e. football, rugby, cricket).
Private garden	Areas of land normally enclosed and associated with private residences and reserved for private use.
Public Park or garden	Areas of land designed, constructed, managed and maintained as a public park or garden. These normally have a defined perimeter and free public access and generally sit within or close to urban areas. Access is granted for a wide range of uses and not usually restricted to paths or tracks within the area. May include areas with managed facilities such as benches and flowerbeds, and more natural areas.
School grounds	Areas of land normally enclosed that is associated with a school and primarily reserved for their use.
Tennis court	A specially prepared area intended for playing tennis.

Appendix B: Supplementary material for chapter 2

S.1- Urban land use definitions

Table B.1 Urban land use definitions from Copernicus Urban Atlas, used to categories sample sites into high or low urbanisation.

Urban Land Use Category	Description
Continuous urban fabric	Predominant residential use: areas with a high degree of soil sealing, independent of their housing scheme.

Discontinuous dense urban fabric	Average degree of soil sealing: > 50 - 80% Residential buildings, roads and other artificially surfaced areas.
Industrial, commercial, public, military and private units	a. Industrial uses and related areas Sites of industrial activities, including their related areas such as storage areas, production sites, energy plants: nuclear, solar, hydroelectric, thermal, electric and wind farms sewage treatment plants, farming industries (farms with large buildings and / or greenhouses), antennas, even with predominant vegetated areas. The vegetated areas may be predominant, but the land is not dedicated to forestry or agriculture, water treatment plants, sewage plants. b. Commercial uses, retail parks and related areas Surfaces purely occupied by commercial activities, including their related areas, high-rise office buildings, petrol and service stations within built-up areas. c. Public, military and private services not related to the transport system Schools and universities, hospitals and other health services or buildings, places of worship (churches / cathedrals / religious buildings), archaeological sites and museums, administration buildings, ministries, penitentiaries, military areas including bases and ports, military exercise areas fenced and under current use, castles, private storage areas without a residential component, such as compounds of garages. d. Civil protection and supply infrastructure Dams, dikes, irrigation and drainage canals and ponds and other technical public infrastructure, to be mapped with the roads, embankments and associated land included, breakwaters, piers and jetties, sea walls and flood defences, (Ancient) city walls, other protecting walls, bunkers, avalanche barriers.

Construction sites	Spaces under construction or development, soil or bedrock excavations for construction purposes or other earthworks visible in the image.

S.2- Flower visitors recorded from visual observations

Table B.2 : Species list from visual observations of flower visits, alongside the abundance of each species, collected across 18 gardens and 4 months.

Flower visitor	Abundance
<i>Bombus pascuorum</i>	256
<i>Bombus lucorum</i> .agg.	174
<i>Episyrphus balteatus</i>	82
<i>Apis mellifera</i>	73
<i>Bombus hypnorum</i>	47
<i>Platycheirus albimanus</i>	46
<i>Bombus pratorum</i>	37
<i>Bombus lapidarius</i>	35
<i>Eristalis tenax</i>	23
<i>Syrphus ribesii</i>	23
<i>Syrpitta pipiens</i>	22
<i>Eupeodes corollae</i>	19
<i>Melanostoma scalare</i>	18
<i>Bombus hortorum</i>	16
<i>Megachilidae centuncularis</i>	11
<i>Colletes daviesanus</i>	9
<i>Eristalis pertinax</i>	8
<i>Helophilus pendulus</i>	8
<i>Syrphus torvus</i>	8
<i>Syrphus vitripennis</i>	8
<i>Lasioglossum smeathmanellum</i>	7
<i>Osmia bicornis</i>	7

<i>Meliscaeva cinctella</i>	7
<i>Eupeodes luniger</i>	6
<i>Lasioglossum fratellum</i>	5
<i>Syrphus rectus</i>	5
<i>Meredon equestris</i>	4
<i>Myathropa florea</i>	4
<i>Lasioglossum albipes</i>	3
<i>Lasioglossum leucopus</i>	3
<i>Sphegina verecunda</i>	3
<i>Syrphus rectus/vitripennis</i>	3
<i>Pieris rapae</i>	3
<i>Lasioglossum calceatum</i>	2
<i>Baccha elongata</i>	2
<i>Chrysogaster solstitialis</i>	2
<i>Dasysyrphus albostratus</i>	2
<i>Dasysyrphus tricinctus</i>	2
<i>Platycyrtus scutatus</i>	2
<i>Sphaerophoria scripta</i>	2
<i>Pieris brassicae</i>	2
<i>Vanessa atalanta</i>	2
<i>Andrena subopaca</i>	1
<i>Anthophora furcata</i>	1
<i>Hylaeus hyalinatus</i>	1
<i>Megachilidae willughbiella</i>	1
<i>Sphecodes geoffrellus</i>	1
<i>Cheilosia bergenstammi</i>	1
<i>Epistrophe grossulariae</i>	1
<i>Eristalis horticola</i>	1
<i>Meligramma guttatum</i>	1
<i>Meliscaeva auricollis</i>	1
<i>Melanostoma mellinum</i>	1
<i>Xylota segnis</i>	1
<i>Aglais urticae</i>	1

S.3- Flower visitors from camera recordings

Table B.3 : Species list from camera recordings of flower visits, alongside the abundance of each species, collected across 18 gardens and 4 months.

Flower visitor	Abundance
<i>Bombus pratorum</i>	35
<i>Bombus hypnorum</i>	22
<i>Bombus lucorum</i> agg.	129
<i>Syrphus</i> sp.	137
<i>Bombus pascuorum</i>	146
<i>Apis mellifera</i>	61
<i>Bombus lapidarius</i>	20
<i>Bombus hortorum</i>	4
<i>Megachilidae</i>	4
<i>Colletes</i>	10

S.4- Plant species list

Table B.4: Species list of plants that were observed/ recorded for their flower visitors, across 18 gardens and four months. Total plant abundance for each species is shown.

Plants	Floral Abundance
<i>Bellis perennis</i>	1202
<i>Geranium</i> sp.	407
<i>Lavandula</i> sp.	386
<i>Brassica rapa</i>	280
<i>Lobelia</i> sp.	184
<i>Salvia</i> sp.	164
<i>Epilobium</i> sp.	161
<i>Hydrangea</i> sp.	130
<i>Aster</i> sp.	129
<i>Ranunculus</i> sp.	125
<i>Rhinanthus</i> sp.	118
<i>Trifolium repens</i>	116
<i>Cymbalaria muralis</i>	112
<i>Jacobaea vulgaris</i>	101
<i>Fallopia baldschuanica</i>	97
<i>Jasminum</i> sp.	96
<i>Buddleja</i> sp.	95
<i>Alchemilla mollis</i>	92
<i>Mentha</i> sp.	92
<i>Pelargonium</i> sp.	89
<i>Phlox</i> sp.	82
<i>Crocasmia</i> sp.	77
<i>Origanum vulgare</i>	75
<i>Eupatorium</i> sp.	72
<i>Lysimachia vulgaris</i>	72
<i>Eruca vesicaria</i>	71
<i>Ligustrum ovalifolium</i>	71
<i>Papaver</i> sp.	71
<i>Digitalis purpurea</i>	69
<i>Cotoneaster</i> sp.	65

<i>Campanula</i> sp.	64
<i>Hieracium</i> sp.	63
<i>Petunia</i> sp.	61
<i>Rosa</i> sp.	59
<i>Philadelphus</i> sp.	55
<i>Begonia</i> sp.	51
<i>Hypericum</i> sp.	49
<i>Spiraea</i> sp.	48
<i>Myosotis arvensis</i>	43
<i>Prunella vulgaris</i>	42
<i>Ocimum basilicum</i>	39
<i>Borago officinalis</i>	38
<i>Pilosella aurantiaca</i>	38
<i>Erica</i> sp.	36
<i>Veronica</i> sp.	35
<i>Fragaria</i> sp.	32
<i>Geum urbanum</i>	32
<i>Lupinus</i> sp.	32
<i>Leucanthemum vulgare</i>	31
<i>Clematis</i> sp.	30
<i>Linaria vulgaris</i>	30
<i>Eryngium</i> sp.	27
<i>Impatiens walleriana</i>	27
<i>Lobularia</i> sp.	27
<i>Primula</i> sp.	27
<i>Raphanus</i> sp.	26
<i>Silene dioica</i>	25
<i>Malva</i> sp.	24
<i>Auberita</i> sp.	23
<i>Erysimum</i> sp.	23
<i>Fuschia</i> sp.	23
<i>Centaurea cyanus</i>	22
<i>Matthiola</i> sp.	22
<i>Sambucus</i> sp.	22

<i>Sedum</i> sp.	22
<i>Lotus corniculatus</i>	21
<i>Petrosedum</i> sp.	21
<i>Solanum lycopersicum</i>	21
<i>Allium</i> sp.	20
<i>Astilbe</i> sp.	20
<i>Rhododendron</i> sp.	19
<i>Bistorta</i> sp.	18
<i>Foeniculum vulgare</i>	18
<i>Symphotrichum</i> sp.	18
<i>Tropaeolum majus</i>	17
<i>Oenothera biennis</i>	16
<i>Oxalis acetosella</i>	16
<i>Rubus</i> sp.	16
<i>Silene coronaria</i>	16
<i>Centaurea nigra</i>	15
<i>Prunella</i> sp.	15
<i>Achillea millefolium</i>	14
<i>Antirrhinum majus</i>	14
<i>Scabiosa</i> sp.	13
<i>Delphinium</i> sp.	12
<i>Echinops</i> sp.	12
<i>Alcea rosea</i>	11
<i>Calendula officinalis</i>	11
<i>Phedimus</i> sp.	11
<i>Libertia grandiflora</i>	10
<i>Thymus vulgaris</i>	10
<i>Aquilegia</i> sp.	9
<i>Chamaenerion</i> sp.	9
<i>Daucus carota</i>	9
<i>Sonchus</i> sp.	9
<i>Viola tricolor</i>	9
<i>Chamaemelum</i> sp.	8
<i>Hedera</i> sp.	8

<i>Iberis</i> sp.	8
<i>Anemone</i> sp.	7
<i>Arabis</i> sp.	7
<i>Taraxacum</i> agg.	7
<i>Celosia argentea</i>	6
<i>Helianthus annuus</i>	6
<i>Solidago</i> sp.	6
<i>Tagetes patula</i>	6
<i>Hylotelephium</i> sp.	5
<i>Lythrum salicaria</i>	5
<i>Phacelia tanacetifolia</i>	5
<i>Stellaria</i> sp.	5
<i>Cyclamen</i> sp.	4
<i>Leycesteria formosa</i>	4
<i>Cephalaria gigantea</i>	3
<i>Fagopyrum</i> sp.	3
<i>Lonicera</i> sp.	3
<i>Orchis</i> sp.	3
<i>Trifolium pratense</i>	3
<i>Viburnum</i> sp.	3
<i>Alstroemeria</i> sp.	2
<i>Armeria maritima</i>	2
<i>Lapsana communis</i>	2
<i>Nepeta</i> sp.	2
<i>Betonica officinalis</i>	1
<i>Calystegia sepium</i>	1
<i>Cucurbita pepo</i>	1
<i>Delosperma</i> sp.	1
<i>Geum rivale</i>	1

Appendix C: Supplementary material for chapter 3

S.1- Sample site locations

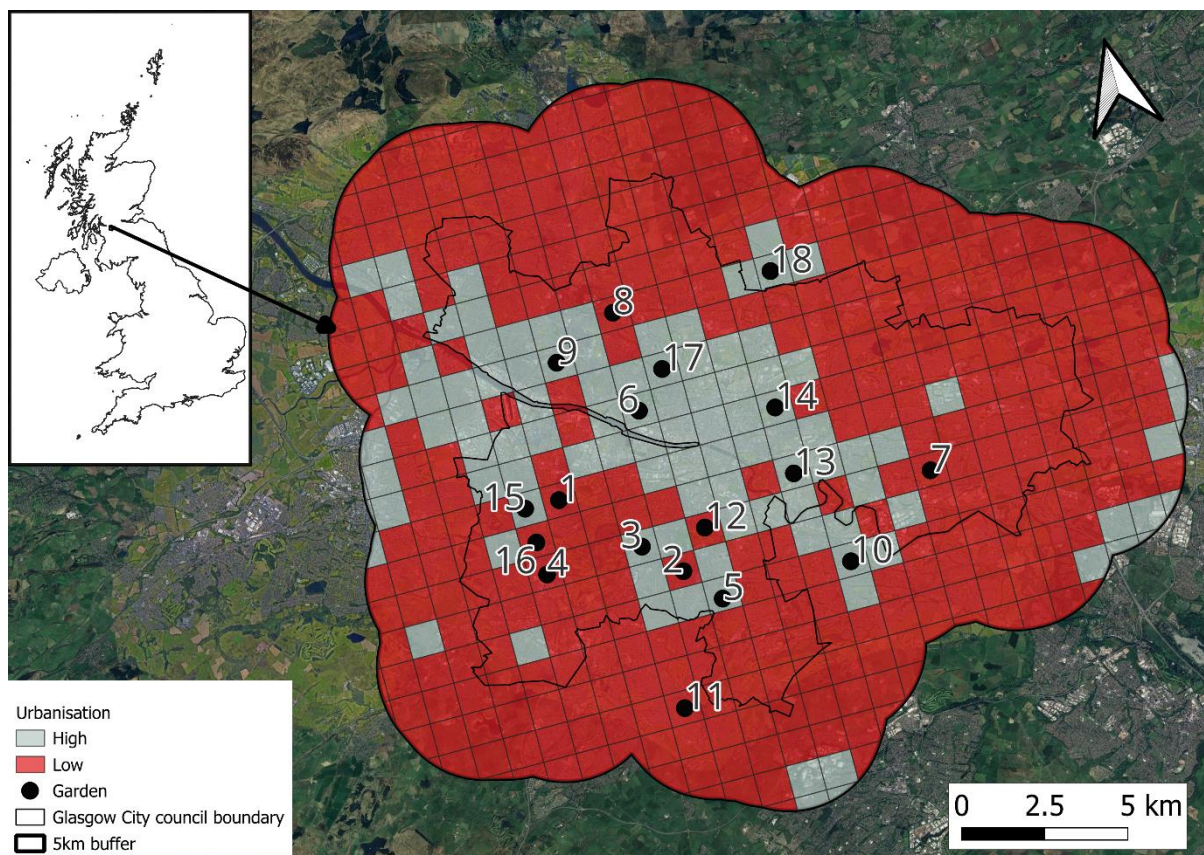


Figure C.1 A map showing the locations of private gardens sampled in the study. Gardens were located across Glasgow City Council including a 5km buffer of the council boundary. Gardens were at least 1km apart from each other and stratified across high(grey) and low (red) urbanisation categories.

S.2- Flower visitor species

Table C.1 : A list of flower visitor species recorded in private gardens from June until September. The table shows the total abundance of each flower visitor across the study.

Flower visitor	Abundance
<i>Bombus pascuorum</i>	256
<i>Bombus lucorum</i> .agg.	174
<i>Episyrphus balteatus</i>	82
<i>Apis mellifera</i>	73
<i>Bombus hypnorum</i>	47
<i>Platycheirus albimanus</i>	46
<i>Bombus pratorum</i>	37
<i>Bombus lapidarius</i>	35
<i>Eristalis tenax</i>	23
<i>Syrphus ribesii</i>	23
<i>Syritta pipiens</i>	22
<i>Eupeodes corollae</i>	19
<i>Melanostoma scalare</i>	18
<i>Bombus hortorum</i>	16
<i>Megachilidae centuncularis</i>	11
<i>Colletes daviesanus</i>	9
<i>Eristalis pertinax</i>	8
<i>Helophilus pendulus</i>	8
<i>Syrphus torvus</i>	8
<i>Syrphus vitripennis</i>	8
<i>Lasioglossum smeathmanellum</i>	7
<i>Osmia bicornis</i>	7
<i>Meliscaeva cinctella</i>	7
<i>Eupeodes luniger</i>	6
<i>Lasioglossum fratellum</i>	5
<i>Syrphus</i> sp.	5
<i>Meredon equestris</i>	4
<i>Myathropa florea</i>	4
<i>Lasioglossum albipes</i>	3
<i>Lasioglossum leucopus</i>	3

<i>Sphegina verecunda</i>	3
<i>Syrphus rectus/vitripennis</i>	3
<i>Pieris rapae</i>	3
<i>Lasioglossum calceatum</i>	2
<i>Baccha elongata</i>	2
<i>Chrysogaster solstitialis</i>	2
<i>Dasysyrphus albostratus</i>	2
<i>Dasysyrphus tricinctus</i>	2
<i>Platycheirus scutatus</i>	2
<i>Sphaerophoria scripta</i>	2
<i>Pieris brassicae</i>	2
<i>Vanessa atalanta</i>	2
<i>Andrena subopaca</i>	1
<i>Anthophora furcata</i>	1
<i>Hylaeus hyalinatus</i>	1
<i>Megachilidae willughbiella</i>	1
<i>Sphecodes geoffrellus</i>	1
<i>Cheilosia bergenstammi</i>	1
<i>Epistrophe grossulariae</i>	1
<i>Eristalis horticola</i>	1
<i>Meligramma guttatum</i>	1
<i>Meliscaeva auricollis</i>	1
<i>Melanostoma mellinum</i>	1
<i>Xylota segnis</i>	1
<i>Aglais urticae</i>	1

S.3- Plant species

Table C.2 : A list of plants observed within gardens from June until September. The table shows the total floral abundance recorded for each plant as well as its origin status for Great Britain (Native or Non-native). Plants were identified to the lowest taxonomic level (genus or species).

Plants	Plant origin	Floral Abundance
<i>Bellis perennis</i>	Native	1202
<i>Geranium</i> sp.	Native	407
<i>Lavandula</i> sp.	Non native	386
<i>Brassica rapa</i>	Native	280
<i>Lobelia</i> sp.	Native	184
<i>Salvia</i> sp.	Native	164
<i>Epilobium</i> sp.	Native	161
<i>Hydrangea</i> sp.	Non native	130
<i>Aster</i> sp.	Non native	129
<i>Ranunculus</i> sp.	Native	125
<i>Rhinanthus</i> sp.	Native	118
<i>Trifolium repens</i>	Native	116
<i>Cymbalaria muralis</i>	Non native	112
<i>Jacobaea vulgaris</i>	Native	101
<i>Fallopia baldschuanica</i>	Non native	97
<i>Jasminum</i> sp.	Non native	96
<i>Buddleja</i> sp.	Non native	95
<i>Alchemilla mollis</i>	Native	92
<i>Mentha</i> sp.	Native	92
<i>Pelargonium</i> sp.	Non native	89
<i>Phlox</i> sp.	Non native	82
<i>Crocasmia</i> sp.	Non native	77
<i>Origanum vulgare</i>	Native	75
<i>Eupatorium</i> sp.	Native	72
<i>Lysimachia vulgaris</i>	Native	72
<i>Eruca vesicaria</i>	Non native	71
<i>Ligustrum ovalifolium</i>	Native	71
<i>Papaver</i> sp.	Native	71
<i>Digitalis purpurea</i>	Native	69

<i>Cotoneaster</i> sp.	Native	65
<i>Campanula</i> sp.	Native	64
<i>Hieracium</i> sp.	Native	63
<i>Petunia</i> sp.	Non native	61
<i>Rosa</i> sp.	Native	59
<i>Philadelphus</i> sp.	Non native	55
<i>Begonia</i> sp.	Non native	51
<i>Hypericum</i> sp.	Native	49
<i>Spiraea</i> sp.	Non native	48
<i>Myosotis arvensis</i>	Native	43
<i>Prunella vulgaris</i>	Native	42
<i>Ocimum basilicum</i>	Non native	39
<i>Borago officinalis</i>	Non native	38
<i>Pilosella aurantiaca</i>	Native	38
<i>Erica</i> sp.	Native	36
<i>Veronica</i> sp.	Native	35
<i>Fragaria</i> sp.	Native	32
<i>Geum urbanum</i>	Native	32
<i>Lupinus</i> sp.	Non native	32
<i>Leucanthemum vulgare</i>	Native	31
<i>Clematis</i> sp.	Native	30
<i>Linaria vulgaris</i>	Native	30
<i>Eryngium</i> sp.	Native	27
<i>Impatiens walleriana</i>	Native	27
<i>Lobularia</i> sp.	Non native	27
<i>Primula</i> sp.	Native	27
<i>Raphanus</i> sp.	Native	26
<i>Silene dioica</i>	Native	25
<i>Malva</i> sp.	Native	24
<i>Auberita</i> sp.	Non native	23
<i>Erysimum</i> sp.	Non native	23
<i>Fuschia</i> sp.	Non native	23
<i>Centaurea cyanus</i>	Native	22
<i>Matthiola</i> sp.	Native	22

<i>Sambucus</i> sp.	Native	22
<i>Sedum</i> sp.	Native	22
<i>Lotus corniculatus</i>	Native	21
<i>Petrosedum</i> sp.	Native	21
<i>Solanum lycopersicum</i>	Native	21
<i>Allium</i> sp.	Native	20
<i>Astilbe</i> sp.	Non native	20
<i>Rhododendron</i> sp.	Non native	19
<i>Bistorta</i> sp.	Non native	18
<i>Foeniculum vulgare</i>	Non native	18
<i>Symphyotrichum</i> sp.	Non native	18
<i>Tropaeolum majus</i>	Non native	17
<i>Oenothera biennis</i>	Non native	16
<i>Oxalis acetosella</i>	Native	16
<i>Rubus</i> sp.	Native	16
<i>Silene coronaria</i>	Native	16
<i>Centaurea nigra</i>	Native	15
<i>Prunella</i> sp.	Native	15
<i>Achillea millefolium</i>	Native	14
<i>Antirrhinum majus</i>	Non native	14
<i>Scabiosa</i> sp.	Native	13
<i>Delphinium</i> sp.	Non native	12
<i>Echinops</i> sp.	Non native	12
<i>Alcea rosea</i>	Non native	11
<i>Calendula officinalis</i>	Non native	11
<i>Phedimus</i> sp.	Non native	11
<i>Libertia grandiflora</i>	Non native	10
<i>Thymus vulgaris</i>	Native	10
<i>Aquilegia</i> sp.	Native	9
<i>Chamaenerion</i> sp.	Native	9
<i>Daucus carota</i>	Native	9
<i>Sonchus</i> sp.	Native	9
<i>Viola tricolor</i>	Native	9
<i>Chamaemelum</i> sp.	Native	8

<i>Hedera</i> sp.	Native	8
<i>Iberis</i> sp.	Native	8
<i>Anemone</i> sp.	Native	7
<i>Arabis</i> sp.	Non native	7
<i>Taraxacum</i> agg.	Native	7
<i>Celosia argente</i>	Non native	6
<i>Helianthus annuus</i>	Non native	6
<i>Solidago</i> sp.	Native	6
<i>Tagets patula</i>	Non native	6
<i>Hylotelephium</i> sp.	Unknown	5
<i>Lythrum salicaria</i>	Native	5
<i>Phacelia tanacetifolia</i>	Non native	5
<i>Stellaria</i> sp.	Native	5
<i>Cyclamen</i> sp.	Non native	4
<i>Leycesteria formosa</i>	Non native	4
<i>Cephalaria gigantea</i>	Non native	3
<i>Fagopyrum</i> sp.	Non native	3
<i>Lonicera</i> sp.	Native	3
<i>Orchis</i> sp.	Native	3
<i>Trifolium pratense</i>	Native	3
<i>Viburnum</i> sp.	Native	3
<i>Alstroemeria</i> sp.	Non native	2
<i>Armeria maritima</i>	Native	2
<i>Lapsana communis</i>	Native	2
<i>Nepeta</i> sp.	Native	2
<i>Betonica officinalis</i>	Unknown	1
<i>Calystegia sepium</i>	Native	1
<i>Cucurbita pepo</i>	Non native	1
<i>Delosperma</i> sp.	Non native	1
<i>Geum rivale</i> sp.	Native	1

S.4- Flower visitor plant preferences

Table C.3: Results from the null model analysis in the econullnetr package, showing the plants species that certain flower visitor species interacted with more than expected based on chance whilst accounting for the floral abundance of each plant. Here networks from each garden were grouped together but separated by month. The observed value shows the number of flower visitors observed visiting the plant, and the expected value is the number of flower visits expected to visit the plant based on its floral abundance. SES is the standard error values with the plant origin (Native or Non-native) and month of the observation shown in the table.

Plants	Flower visitor	Observed	Null	SES	Plant origin	Month
<i>Allium</i> sp.	<i>Bombus pascuorum</i>	2	0.29	3.431	Native	September
<i>Anemone</i> sp.	<i>Syrphus ribesii</i>	3	0.1	8.700	Native	September
<i>Bistorta</i> sp.	<i>Bombus pascuorum</i>	7	1.38	4.427	Non native	September
<i>Chamaenerion</i> sp.	<i>Bombus pascuorum</i>	4	0.11	11.272	Native	September
<i>Fragaria</i> sp.	<i>Bombus pascuorum</i>	2	0.03	11.490	Native	September
<i>Geranium</i> sp.	<i>Episyrphus balteatus</i>	4	0.84	3.669	Native	September
<i>Lavandula</i> sp.	<i>Bombus pascuorum</i>	24	3.92	10.231	Non native	September
<i>Papaver</i> sp.	<i>Bombus lucorum</i> .agg.	2	0.05	8.902	Native	September
<i>Papaver</i> sp.	<i>Episyrphus balteatus</i>	2	0.14	4.357	Native	September
<i>Pelargonium</i> sp.	<i>Chrysogaster solstitialis</i>	2	0.14	4.939	Non native	September
<i>Fallopia baldschuanica</i>	<i>Eristalis pertinax</i>	2	0.25	3.500	Non native	September
<i>Fallopia baldschuanica</i>	<i>Syrphus</i> sp.	2	0.09	6.641	Non native	September
<i>Fallopia baldschuanica</i>	<i>Apis mellifera</i>	5	0.3	8.141	Non native	September
<i>Scabiosa</i> sp.	<i>Bombus pascuorum</i>	3	0.1	8.700	Native	September
<i>Sonchus</i> sp.	<i>Syrphus ribesii</i>	3	0.07	11.426	Native	September
<i>Symphyotrichum</i> sp.	<i>Eristalis tenax</i>	4	0.5	5.080	Non native	September
<i>Symphyotrichum</i> sp.	<i>Bombus pascuorum</i>	6	1.98	3.224	Non native	September
<i>Allium</i> sp.	<i>Bombus pascuorum</i>	3	0.56	3.634	Native	August
<i>Bistorta</i> sp.	<i>Bombus pascuorum</i>	2	0.28	3.482	Non native	August

<i>Bistorta</i> sp.	<i>Apis mellifera</i>	2	0.09	5.953	Non native	August
<i>Buddleja</i> sp.	<i>Apis mellifera</i>	2	0.12	5.756	Non native	August
<i>Chamaenerion</i> sp.	<i>Apis mellifera</i>	6	0.11	18.730	Native	August
<i>Chamaenerion</i> sp.	<i>Bombus lucorum</i> .agg	3	0.17	7.015	Native	August
<i>Echinops</i> sp.	<i>Syrphus vitripennis</i>	2	0	NA	Non native	August
<i>Echinops</i> sp.	<i>Bombus pascuorum</i>	2	0.08	6.244	Non native	August
<i>Echinops</i> sp.	<i>Apis mellifera</i>	2	0.04	9.952	Non native	August
<i>Fuschia</i> sp.	<i>Bombus pascuorum</i>	3	0.54	3.247	Non native	August
<i>Geranium</i> sp.	<i>Melanostoma scalare</i>	3	0.4	4.197	Native	August
<i>Lavandula</i> sp.	<i>Bombus lapidarius</i>	5	0.88	4.356	Non native	August
<i>Lavandula</i> sp.	<i>Bombus pascuorum</i>	15	7.43	2.900	Non native	August
<i>Lavandula</i> sp.	<i>Bombus lucorum</i> .agg	17	2.67	8.841	Non native	August
<i>Matthiola</i> sp.	<i>Bombus pascuorum</i>	2	0.15	5.155	Native	August
<i>Mentha</i> sp.	<i>Syrpita pipiens</i>	3	0.36	4.715	Native	August
<i>Mentha</i> sp.	<i>Platycheirus albimanus</i>	9	0.46	14.000	Native	August
<i>Reynoutria</i> sp.	<i>Meliscaeva cinctella</i>	2	0.26	3.591	Non native	August
<i>Reynoutria</i> sp.	<i>Sphegina verecunda</i>	2	0.08	7.042	Non native	August
<i>Scabiosa</i> sp.	<i>Bombus pascuorum</i>	2	0.03	11.490	Native	August
<i>Solidago</i> sp.	<i>Colletes daviesanus</i>	4	0	NA	Native	August
<i>Solidago</i> sp.	<i>Syrpita pipiens</i>	2	0.05	8.902	Native	August
<i>Aqueligia</i> sp.	<i>Bombus lucorum</i> .agg	2	0.31	3.477	Native	July
<i>Aqueligia</i> sp.	<i>Bombus hypnorum</i>	2	0.22	4.046	Native	July
<i>Campanula</i> sp.	<i>Bombus lapidarius</i>	2	0.08	7.042	Native	July
<i>Cotoneaster</i> sp.	<i>Bombus hypnorum</i>	4	1.33	2.444	Native	July
<i>Delphinium</i> sp.	<i>Bombus lucorum</i> .agg	2	0.31	3.213	Non native	July
<i>Epilobium</i> sp.	<i>Platycheirus albimanus</i>	2	0.12	5.278	Native	July

<i>Epilobium</i> sp.	<i>Eupeodes corollae</i>	2	0.2	4.221	Native	July
<i>Geranium</i> sp.	<i>Bombus pascuorum</i>	8	3.09	2.641	Native	July
<i>Geranium</i> sp.	<i>Meredon equestris</i>	3	0.31	5.312	Native	July
<i>Hieracium</i> sp.	<i>Bombus lapidarius</i>	2	0.04	9.952	Native	July
<i>Hypericum</i> sp.	<i>Bombus hypnorum</i>	6	0.24	11.641	Native	July
<i>Papaver</i> sp.	<i>Bombus lucorum.agg</i>	9	1.53	5.859	Native	July
<i>Papaver</i> sp.	<i>Bombus hypnorum</i>	4	0.69	4.425	Native	July
<i>Ranunculus</i> sp.	<i>Bombus pratorum</i>	9	0.81	8.174	Native	July
<i>Rhododendron</i> sp.	<i>Bombus pratorum</i>	3	0.31	4.377	Non native	July
<i>Rhododendron</i> sp.	<i>Osmia bicornis</i>	2	0.07	7.526	Non native	July
<i>Rhododendron</i> sp.	<i>Bombus hypnorum</i>	4	0.34	6.829	Non native	July
<i>Rubus</i> sp.	<i>Bombus hypnorum</i>	4	0.2	9.452	Native	July
<i>Rubus</i> sp.	<i>Bombus pratorum</i>	4	0.16	9.724	Native	July
<i>Salvia</i> sp.	<i>Bombus pascuorum</i>	4	0.24	7.933	Native	July
<i>Sambucus</i> sp.	<i>Bombus hypnorum</i>	3	0.43	3.287	Native	July
<i>Taraxacum</i> sp.	<i>Bombus lucorum.agg</i>	2	0.19	4.319	Native	July
<i>Aquilegia</i> sp.	<i>Bombus hypnorum</i>	2	0.11	5.477	Native	June
<i>Campanula</i> sp.	<i>Bombus lapidarius</i>	2	0.02	14.072	Native	June
<i>Epilobium</i> sp.	<i>Platycheirus albimanus</i>	2	0.17	4.279	Native	June
<i>Epilobium</i> sp.	<i>Eupeodes corollae</i>	2	0.22	3.850	Native	June
<i>Geranium</i> sp.	<i>Bombus pascuorum</i>	8	2.81	3.270	Native	June
<i>Geranium</i> sp.	<i>Meredon equestris</i>	3	0.26	4.878	Native	June
<i>Hieracium</i> sp.	<i>Bombus lapidarius</i>	2	0.03	11.490	Native	June
<i>Hypericum</i> sp.	<i>Bombus hypnorum</i>	6	0.27	12.236	Native	June

<i>Lupinus</i> sp.	<i>Bombus lucorum</i> .agg	4	0.96	2.810	Non native	June
<i>Papaver</i> sp.	<i>Bombus lucorum</i> .agg	9	1.12	7.201	Native	June
<i>Papaver</i> sp.	<i>Bombus hypnorum</i>	4	0.7	4.011	Native	June
<i>Ranunculus</i> sp.	<i>Bombus pratorum</i>	9	1.3	7.144	Native	June
<i>Rhododendron</i> sp.	<i>Bombus pratorum</i>	3	0.35	4.033	Non native	June
<i>Rhododendron</i> sp.	<i>Osmia bicornis</i>	2	0.04	9.952	Non native	June
<i>Rhododendron</i> sp.	<i>Bombus hypnorum</i>	4	0.4	5.811	Non native	June
<i>Rubus</i> sp.	<i>Bombus hypnorum</i>	4	0.23	8.914	Native	June
<i>Rubus</i> sp.	<i>Bombus pratorum</i>	4	0.17	9.494	Native	June
<i>Salvia</i> sp.	<i>Bombus lucorum</i> .agg	2	0.37	2.996	Native	June
<i>Salvia</i> sp.	<i>Bombus pascuorum</i>	4	0.34	6.600	Native	June
<i>Sambucus</i> sp.	<i>Bombus hypnorum</i>	3	0.5	3.354	Native	June
<i>Taraxacum</i> agg.	<i>Bombus lucorum</i> .agg	2	0.19	4.319	Native	June

S.5- Optimal models

Table C.4 : The table shows the explanatory variables selected to explain floral visitation (the number and richness of flower visitors at the community level, the number and richness of flower visitors at the plant species level and the percentage of plants that were interacted with in the community), floral abundance and floral richness in gardens and network structure (H_2 , NODF, Interaction evenness and d' for pollinators). Variables were selected by a backwards step wise selection process. The degrees of freedom (df), chi squared (χ^2) values and p values for which the variables were selected on are displayed in the table. P values shown in the table were adjusted using the FDR method.

Response	Predictors	DF	χ^2	P value
Floral visits				
Flower visits at the community	Floral richness	1	14.32	<0.001
	Origin	1	5.00	0.035
	Month	1	8.47	0.004
	Floral abundance/ m ²	1	3.94	0.047
	Floral abundance*Origin	1	4.80	0.041
Flower visitor richness at the community	Floral richness	1	33.97	<0.001
	Floral abundance * Origin	1	4.16	0.041
Flower visits at the plant level	Month	1	10.84	0.002
	Floral abundance	1	11.32	0.001
Flower visitor richness at the plant level	Month	1	10.03	0.002
	Origin	1	3.91	0.048
	Floral abundance	1	11.20	0.001
Percentage of plants to receive visits	Origin	1	4.51	0.034
<i>B. pascuorum</i> flower visits	Floral richness	1	9.44	0.002
	Floral abundance	1	46.62	<0.001
	Origin	1	6.00	0.027
	Month*Origin	1	52.28	<0.001
	Floral richness * Origin	1	16.56	<0.001
Flower visits excluding <i>B.pascuorum</i>	Floral abundance	1	10.98	0.001
	Floral richness	1	29.42	<0.001
	Month	1	13.52	<0.001
Flower visitor richness excluding <i>B.pascuorum</i>	Floral abundance	1	8.96	0.003
	Floral richness	1	60.89	<0.001
	Month	1	6.23	0.013

	Origin	1	4.66	0.036
Floral resource				
Floral abundance	Month	1	14.46	<0.001
	Month ²	1	5.82	0.024
	Origin	1	6.97	0.027
	Month*Origin	1	13.85	<0.001
Floral richness	Origin	1	44.44	<0.001
	Month*Origin	1	10.09	0.001
Network indices				
H2'	Month ²	1	14.46	<0.001
Interaction evenness	Month ²	1	6.72	0.019
WNODF	Month ²	1	4.31	0.038
D' pollinators	Month ²	1	4.98	0.031
D' for <i>B.pascuorum</i>	Month ²	1	16.74	<0.001
Network indices without <i>B.pascuorum</i>				
H2'	NULL			
Interaction evenness	NULL			
WNODF	NULL			
D' pollinators	NULL			

Appendix D: Supplementary material for chapter 4

S.1 Sample sites

Table D.1: The table details sampling units (individual plots within allotments and garden sites) for the flower visitor surveys. Area of each sampling unit is given in m²

Site Acronym	Plot	Site type	Size (m ²)
QP	1	Allotment	179.244
QP	2	Allotment	156.607
QP	3	Allotment	72.259
QP	4	Allotment	162.233
QP	5	Allotment	46.265
QP	6	Allotment	182.607
QP	7	Allotment	89.188
QP	8	Allotment	154.681
CROFT	1	Allotment	51.219
CROFT	2	Allotment	209.487
CROFT	3	Allotment	107.691
CROFT	4	Allotment	115.187
CROFT	5	Allotment	97.014
CROFT	6	Allotment	98.14
CROFT	7	Allotment	204.43
CROFT	8	Allotment	201.775
CROFT	9	Allotment	226.914
MERRY	1	Allotment	229.284
MERRY	2	Allotment	238.421
MERRY	3	Allotment	217.888
MERRY	4	Allotment	189.685
MERRY	5	Allotment	102.33
MERRY	6	Allotment	352.328
MERRY	7	Allotment	112.062
MERRY	8	Allotment	153.359
MERRY	9	Allotment	78.56
NVG	1	Allotment	168.558
NVG	2	Allotment	175.308
NVG	3	Allotment	179.842
NVG	4	Allotment	142.83
NVG	5	Allotment	177.007
NVG	6	Allotment	162.611
NVG	7	Allotment	160.913
NVG	8	Allotment	132.933
NVG	9	Allotment	170.628
KIRKL	1	Allotment	104.321
KIRKL	2	Allotment	111.182
KIRKL	3	Allotment	90.711
KIRKL	4	Allotment	138.445
KIRKL	5	Allotment	94.932
KIRKL	6	Allotment	106.549

KIRKL	7	Allotment	126.166
KIRKL	8	Allotment	75.471
KIRKL	9	Allotment	73.059
KIRKL	10	Allotment	60.189
KIRKL	11	Allotment	49.491
KIRKL	12	Allotment	74.028
KIRKL	13	Allotment	115.072
TRINL	1	Allotment	123.931
TRINL	2	Allotment	120.068
TRINL	3	Allotment	122.06
TRINL	4	Allotment	83.115
TRINL	5	Allotment	79.264
TRINL	6	Allotment	83.468
TRINL	7	Allotment	189.526
BELLA	NA	Garden	158.728
KEVL	NA	Garden	176.723
BROOM	NA	Garden	137.763
MUIR	NA	Garden	66.671
DENNI	NA	Garden	89.245
RUTH	NA	Garden	74.415
CLARK	NA	Garden	247.928
YORK	NA	Garden	57.918
GOVAN	NA	Garden	91.373
SCGP	NA	Community allotment	1909.879
SRGP	NA	Community allotment	302.558

S.2. Plant species list

Table D.2: A list of plant species recorded across all the sample sites. Plant origin is listed as either native or non-native based on the BSBI's categorisation according to their status within Great Britain. The plants use was also categorised as with spontaneous (weed like plants, not purposely cultivated), ornamental (deliberately cultivated) or crop plants (grown to harvest).

Species	Origin	Purpose
<i>Acca sellowiana</i>	Non-native	Ornamental
<i>Achillea</i>	Native	Ornamental
<i>Achillea millefolium</i>	Native	Ornamental
<i>Aconitum</i>	Native	Ornamental
<i>Actaea racemosa</i>	Non-native	Ornamental
<i>Aegopodium podagraria</i>	Native	Spontaneous
<i>Agapanthus praecox</i>	Non-native	Ornamental
<i>Agastache</i>	Non-native	Ornamental

<i>Agastache rugosa</i>	Non-native	Ornamental
<i>Agrostemma githago</i>	Non-native	Ornamental
<i>Ajuga reptans</i>	Native	Ornamental
<i>Alcea</i>	Non-native	Ornamental
<i>Alchemilla mollis</i>	Non-native	Ornamental
<i>Alliaria petiolata</i>	Native	Spontaneous
<i>Allium</i>	Native	Ornamental
<i>Allium moly</i>	Non-native	Ornamental
<i>Allium schoenoprasum</i>	Native	Crop
<i>Allium triquetrum</i>	Non-native	Ornamental
<i>Allium tuberosum</i>	Non-native	Ornamental
<i>Allium ursinum</i>	Native	Ornamental
<i>Amaranthus caudatus</i>	Non-native	Ornamental
<i>Anemone blanda</i>	Non-native	Ornamental
<i>Anemone coronaria</i>	Non-native	Ornamental
<i>Anemone hupehensis</i>	Non-native	Ornamental
<i>Anemonoides nemorosa</i>	Native	Ornamental
<i>Anethum graveolens</i>	Non-native	Crop
<i>Angelica</i>	Native	Ornamental
<i>Anthericum</i>	Non-native	Ornamental
<i>Anthriscus sylvestris</i>	Native	Spontaneous
<i>Antirrhinum majus</i>	Non-native	Ornamental
<i>Apium graveolens</i>	Native	Ornamental
<i>Aquilegia</i>	Native	Ornamental
<i>Arabis caucasica</i>	Non-native	Ornamental
<i>Argyranthemum</i>	Non-native	Ornamental
<i>Armeria</i>	Native	Ornamental
<i>Armoracia rusticana</i>	Native	Crop
<i>Asparagus officinalis</i>	Native	Crop
<i>Aster</i>	Non-native	Ornamental
<i>Astilbe</i>	Non-native	Ornamental
<i>Astilbe japonica</i>	Non-native	Ornamental
<i>Astrantia</i>	Non-native	Ornamental
<i>Aubrieta</i>	Non-native	Ornamental

<i>Begonia</i>	Non-native	Ornamental
<i>Begonia boliviensis</i>	Non-native	Ornamental
<i>Bellis perennis</i>	Native	Spontaneous
<i>Berberis</i>	Native	Ornamental
<i>Bergenia</i>	Non-native	Ornamental
<i>Beta vulgaris</i>	Native	Crop
<i>Betonica officinalis</i>	Native	Ornamental
<i>Bidens aurea</i>	Non-native	Ornamental
<i>Bistorta officinalis</i>	Native	Ornamental
<i>Borago officinalis</i>	Non-native	Ornamental
<i>Brachyglottis</i>	Non-native	Ornamental
<i>Brachyscome</i>	Non-native	Ornamental
<i>Brassica</i>	Native	Crop
<i>Brassica oleracea</i>	Native	Crop
<i>Brassica rapa</i>	Native	Crop
<i>Brunnera</i>	Non-native	Ornamental
<i>Buddleja</i>	Non-native	Ornamental
<i>Buddleja globosa</i>	Non-native	Ornamental
<i>Bupthalmum salicifolium</i>	Non-native	Ornamental
<i>Calendula officinalis</i>	Non-native	Ornamental
<i>Calibrachoa</i>	Non-native	Ornamental
<i>Callistephus chinensis</i>	Non-native	Ornamental
<i>Caltha palustris</i>	Native	Ornamental
<i>Calystegia sepium</i>	Native	Spontaneous
<i>Camellia</i>	Non-native	Ornamental
<i>Campanula</i>	Native	Ornamental
<i>Campanula lactiflora</i>	Non-native	Ornamental
<i>Cardamine pratensis</i>	Native	Spontaneous
<i>Ceanothus thyrsiflorus</i>	Non-native	Ornamental
<i>Centaurea cyanus</i>	Native	Ornamental
<i>Centaurea macrocephala</i>	Non-native	Ornamental
<i>Centaurea montana</i>	Non-native	Ornamental
<i>Centaurea nigra</i>	Native	Ornamental
<i>Centaurea triumfettii</i>	Non-native	Ornamental

<i>Centranthus ruber</i>	Non-native	Ornamental
<i>Cephalaria gigantea</i>	Non-native	Ornamental
<i>Cerastium</i>	Native	Ornamental
<i>Cerastium tomentosum</i>	Non-native	Ornamental
<i>Cerinthe major</i>	Non-native	Ornamental
<i>Chaenomeles</i>	Non-native	Ornamental
<i>Chaenostoma</i>	Non-native	Ornamental
<i>Chamaemelum</i>	Native	Ornamental
<i>Chamaenerion angustifolium</i>	Native	Spontaneous
<i>Chrysanthemum</i>	Non-native	Ornamental
<i>Cichorium intybus</i>	Native	Ornamental
<i>Circaea lutetiana</i>	Native	Spontaneous
<i>Cirsium</i>	Native	Ornamental
<i>Cirsium arvense</i>	Native	Ornamental
<i>Clematis</i>	Native	Ornamental
<i>Coreopsis</i>	Non-native	Ornamental
<i>Coriandrum sativum</i>	Non-native	Crop
<i>Cosmos bipinnatus</i>	Non-native	Ornamental
<i>Cotoneaster</i>	Native	Ornamental
<i>Crocsmia</i>	Non-native	Ornamental
<i>Cucurbita</i>	Non-native	Crop
<i>Cyclamen</i>	Non-native	Ornamental
<i>Cymbalaria muralis</i>	Non-native	Spontaneous
<i>Cynara cardunculus</i>	Non-native	Ornamental
<i>Cytisus scoparius</i>	Native	Ornamental
<i>Dahlia</i>	Non-native	Ornamental
<i>Dasiphora</i>	Native	Ornamental
<i>Dasiphora fruticosa</i>	Native	Ornamental
<i>Daucus carota</i>	Native	Ornamental
<i>Delosperma</i>	Non-native	Ornamental
<i>Delphinium</i>	Non-native	Ornamental
<i>Dendranthema grandiflorum</i>	Non-native	Ornamental
<i>Deutzia</i>	Non-native	Ornamental
<i>Dianthus</i>	Native	Ornamental
<i>Diascia rigescens</i>	Non-native	Ornamental

<i>Digitalis purpureum</i>	Native	Ornamental
<i>Dimorphotheca</i>	Non-native	Ornamental
<i>Dipsacus fullonum</i>	Native	Ornamental
<i>Drymocalis</i>	Native	Ornamental
<i>Echinacea</i>	Non-native	Ornamental
<i>Echinops</i>	Non-native	Ornamental
<i>Echium</i>	Native	Ornamental
<i>Epilobium</i>	Native	Spontaneous
<i>Erica</i>	Native	Ornamental
<i>Erigeron karvinskianus</i>	Non-native	Ornamental
<i>Eruca</i>	Non-native	Crop
<i>Eryngium bourgatii</i>	Non-native	Ornamental
<i>Erysimum</i>	Non-native	Ornamental
<i>Erysimum cheiri</i>	Native	Ornamental
<i>Erysimum linifolium</i>	Non-native	Ornamental
<i>Erythranthe guttata</i>	Non-native	Ornamental
<i>Escalonia</i>	Non-native	Ornamental
<i>Eschscholzia californica</i>	Non-native	Ornamental
<i>Eupatorium cannabinum</i>	Native	Ornamental
<i>Euphorbia griffithii</i>	Non-native	Ornamental
<i>Eurybia divaricata</i>	Non-native	Ornamental
<i>Fagopyrum esculentum</i>	Non-native	Crop
<i>Ficaria verna</i>	Native	Spontaneous
<i>Filipendula ulmaria</i>	Native	Ornamental
<i>Filipendula vulgaris</i>	Native	Ornamental
<i>Foeniculum vulgare</i>	Non-native	Crop
<i>Fragaria</i>	Native	Crop
<i>Fritilaria</i>	Native	Ornamental
<i>Fuchsia</i>	Non-native	Ornamental
<i>Galega officinalis</i>	Non-native	Ornamental
<i>Galeopsis</i>	Native	Ornamental
<i>Galium aparine</i>	Native	Spontaneous
<i>Galium verum</i>	Native	Ornamental
<i>Geranium</i>	Native	Ornamental
<i>Geranium purpureum</i>	Native	Spontaneous
<i>Geranium robertianum</i>	Native	Spontaneous
<i>Geum</i>	Native	Ornamental

<i>Geum coccineum</i>	Non-native	Ornamental
<i>Geum rivale</i>	Native	Ornamental
<i>Geum urbanum</i>	Native	Spontaneous
<i>Gladiolus</i>	Native	Ornamental
<i>Glebionis segetum</i>	Native	Ornamental
<i>Helenium</i>	Non-native	Ornamental
<i>Helenium autumnale</i>	Non-native	Ornamental
<i>Helianthemum nummularium</i>	Native	Ornamental
<i>Helianthus</i>	Non-native	Ornamental
<i>Helianthus annuus</i>	Non-native	Ornamental
<i>Helleborus</i>	Native	Ornamental
<i>Hemerocallis</i>	Non-native	Ornamental
<i>Heracleum sphondylium</i>	Native	Spontaneous
<i>Hesperantha coccinea</i>	Non-native	Ornamental
<i>Hesperis matronalis</i>	Non-native	Ornamental
<i>Heuchera</i>	Non-native	Ornamental
<i>Hieracium</i>	Native	Spontaneous
<i>Hosta</i>	Non-native	Ornamental
<i>Hyacinthoides</i>	Native	Ornamental
<i>Hyacinthus</i>	Non-native	Ornamental
<i>Hydrangea</i>	Non-native	Ornamental
<i>Hylotelephium</i>	Non-native	Ornamental
<i>Hypericum</i>	Native	Ornamental
<i>Iberis</i>	Native	Ornamental
<i>Ilex</i>	Native	Ornamental
<i>Impatiens glandulifera</i>	Non-native	Spontaneous
<i>Impatiens walleriana</i>	Non-native	Ornamental
<i>Inula</i>	Native	Ornamental
<i>Iris</i>	Native	Ornamental
<i>Jacobaea vulgaris</i>	Native	Ornamental
<i>Jasminum</i>	Non-native	Ornamental
<i>Kniphofia</i>	Non-native	Ornamental
<i>Koenigia campanulata</i>	Non-native	Ornamental
<i>Laburnum</i>	Non-native	Ornamental
<i>Lactuca sativa</i>	Non-native	Crop
<i>Lamium album</i>	Native	Ornamental
<i>Lamium galeobdolon</i>	Native	Ornamental

<i>Lamium hybridum</i>	Native	Ornamental
<i>Lamium purpureum</i>	Native	Ornamental
<i>Lamprocapnos spectabilis</i>	Non-native	Ornamental
<i>Lapsana communis</i>	Native	Spontaneous
<i>Lathyrus odoratus</i>	Non-native	Ornamental
<i>Lathyrus oleraceus</i>	Non-native	Ornamental
<i>Lavandula</i>	Non-native	Ornamental
<i>Leonurus cardiaca</i>	Non-native	Ornamental
<i>Leucanthemum</i>	Native	Ornamental
<i>Levisticum officinale</i>	Non-native	Ornamental
<i>Lewisia</i>	Non-native	Ornamental
<i>Leycesteria formosa</i>	Non-native	Ornamental
<i>Liatris spicata</i>	Non-native	Ornamental
<i>Libertia</i>	Non-native	Ornamental
<i>Ligularia</i>	Non-native	Ornamental
<i>Ligusticopsis</i>		Ornamental
<i>Ligustrum</i>	Native	Ornamental
<i>Lilium</i>	Non-native	Ornamental
<i>Lilium bulbiferum</i>	Non-native	Ornamental
<i>Limnathes douglasii</i>	Non-native	Ornamental
<i>Linaria</i>	Native	Ornamental
<i>Linaria purpurea</i>	Non-native	Ornamental
<i>Linaria vulgaris</i>	Native	Ornamental
<i>Linum</i>	Native	Ornamental
<i>Linum grandiflorum</i>	Non-native	Ornamental
<i>Linum usitatissimum</i>		Ornamental
<i>Lobelia</i>	Native	Ornamental
<i>Lobularia maritima</i>	Non-native	Ornamental
<i>Lonicera</i>	Native	Ornamental
<i>Lotus corniculatus</i>	Native	Ornamental
<i>Lunaria annua</i>	Non-native	Ornamental
<i>Lupinus</i>	Non-native	Ornamental
<i>Lysimachia ciliata</i>	Native	Ornamental
<i>Lysimachia nemorum</i>	Native	Ornamental
<i>Lysimachia nummularia</i>	Native	Ornamental
<i>Lysimachia vulgaris</i>	Native	Ornamental
<i>Lythrum salicaria</i>	Native	Ornamental

<i>Malcolmia maritima</i>	Non-native	Ornamental
<i>Malus</i>	Native	Crop
<i>Malva</i>	Native	Ornamental
<i>Matricaria discoidea</i>	Non-native	Spontaneous
<i>Matthiola longipetala</i>	Non-native	Ornamental
<i>Meconopsis</i>	Native	Ornamental
<i>Melissa officinalis</i>	Non-native	Ornamental
<i>Mentha</i>	Native	Crop
<i>Mentha aquatica</i>	Native	Ornamental
<i>Mimulus guttatus</i>	Non-native	Ornamental
<i>Monarda didyma</i>	Non-native	Ornamental
<i>Muscari armeniacum</i>	Non-native	Ornamental
<i>Myosotis arvensis</i>	Native	Ornamental
<i>Myrrhis odorata</i>	Non-native	Ornamental
<i>Narcissus</i>	Native	Ornamental
<i>Nemesia</i>	Non-native	Ornamental
<i>Nepeta</i>	Native	Ornamental
<i>Nicandra physalodes</i>	Non-native	Ornamental
<i>Nicotiana glauca</i>	Non-native	Ornamental
<i>Nigella damascena</i>	Non-native	Ornamental
<i>Oenanthe</i>	Native	Ornamental
<i>Oenothera biennis</i>	Non-native	Ornamental
<i>Onopordum acanthium</i>	Native	Ornamental
<i>Orchis</i>	Native	Ornamental
<i>Origanum vulgare</i>	Native	Ornamental
<i>Osteospermum</i>	Non-native	Ornamental
<i>Oxalis</i>	Native	Ornamental
<i>Paeonia</i>	Non-native	Ornamental
<i>Papaver</i>	Native	Ornamental
<i>Papaver cambricum</i>	Native	Spontaneous
<i>Pastinaca sativa</i>	Native	Crop
<i>Pelargonium</i>	Non-native	Ornamental
<i>Pentaglottis sempervirens</i>	Non-native	Ornamental
<i>Persicaria maculosa</i>	Native	Ornamental
<i>Petroselinum crispum</i>	Native	Crop
<i>Petunia</i>	Non-native	Ornamental
<i>Phacelia tanacetifolia</i>	Non-native	Ornamental

<i>Phaseolus</i>	Non-native	Crop
<i>Phaseolus coccineus</i>	Non-native	Crop
<i>Philadelphius</i>	Non-native	Ornamental
<i>Phlomis</i>	Non-native	Ornamental
<i>Phlox</i>	Non-native	Ornamental
<i>Pilosella aurantiaca</i>	Non-native	Spontaneous
<i>Pisum sativum</i>	Non-native	Crop
<i>Plantago lanceolata</i>	Native	Spontaneous
<i>Polemonium caeruleum</i>	Native	Ornamental
<i>Potentilla</i>	Native	Ornamental
<i>Primula</i>	Native	Ornamental
<i>Primula veris</i>	Native	Ornamental
<i>Prunella vulgaris</i>	Native	Ornamental
<i>Prunus</i>	Native	Crop
<i>Prunus laurocerasus</i>	Non-native	Ornamental
<i>Pulmonaria officinalis</i>	Non-native	Ornamental
<i>Pulsatilla</i>	Native	Ornamental
<i>Pyrus</i>	Native	Crop
<i>Ranunculus</i>	Native	Spontaneous
<i>Raphanus sativus</i>	Native	Ornamental
<i>Reseda odorata</i>	Non-native	Ornamental
<i>Rheum</i>	Non-native	Ornamental
<i>Rhinanthus minor</i>	Native	Ornamental
<i>Rhodanthemum hosmariense</i>	Non-native	Ornamental
<i>Rhododendron</i>	Non-native	Ornamental
<i>Ribes</i>	Native	Ornamental
<i>Rodgersia</i>	Non-native	Ornamental
<i>Rosa</i>	Native	Ornamental
<i>Rosa canina</i>	Native	Ornamental
<i>Rosa multiflora</i>	Non-native	Ornamental
<i>Rosa pimpinellifolia</i>	Native	Ornamental
<i>Rosa rugosa</i>	Non-native	Spontaneous
<i>Rosa setigera</i>	Non-native	Ornamental
<i>Rosmarinus officinalis</i>	Non-native	Crop
<i>Rubus</i>	Native	Crop
<i>Rudbeckia</i>	Non-native	Ornamental
<i>Salsify</i>		Ornamental

<i>Salvia</i>	Native	Ornamental
<i>Salvia officinalis</i>	Non-native	Ornamental
<i>Sambucus</i>	Native	Ornamental
<i>Sanguisorba</i>	Native	Ornamental
<i>Sanguisorba hakusanensis</i>	Non-native	Ornamental
<i>Sanvitalia</i>	Non-native	Ornamental
<i>Satureja hortensis</i>	Non-native	Ornamental
<i>Saxifraga</i>	Native	Ornamental
<i>Scabiosa</i>	Native	Ornamental
<i>Scilla</i>		Ornamental
<i>Scorzonera hispanicum</i>	Non-native	Ornamental
<i>Scrophularia umbrosa</i>	Native	Spontaneous
<i>Scutellaria altissima</i>	Non-native	Ornamental
<i>Sedum</i>	Native	Ornamental
<i>Sempervivum</i>	Non-native	Ornamental
<i>Senecio</i>	Native	Spontaneous
<i>Sidalcea</i>	Non-native	Ornamental
<i>Silene chalcedonica</i>	Non-native	Ornamental
<i>Silene coronaria</i>	Non-native	Ornamental
<i>Silene diocia</i>	Native	Ornamental
<i>Silene latifolia</i>	Native	Ornamental
<i>Silene vulgaris</i>	Native	Ornamental
<i>Sinapis arvensis</i>	Native	Ornamental
<i>Skimmia japonica</i>	Non-native	Ornamental
<i>Solanum dulcamara</i>	Native	Spontaneous
<i>Solanum lycopersicum</i>	Non-native	Crop
<i>Solanum tuberosum</i>	Non-native	Crop
<i>Solidago canadensis</i>	Non-native	Ornamental
<i>Sonchus oleraceus</i>	Native	Spontaneous
<i>Spiraea</i>	Non-native	Ornamental
<i>Spiraea douglasii</i>	Non-native	Ornamental
<i>Spiraea japonica</i>	Non-native	Ornamental
<i>Stachys byzantina</i>	Non-native	Ornamental
<i>Stachys officinalis</i>	Native	Ornamental
<i>Stachys palustris</i>	Native	Ornamental
<i>Stachys sylvatica</i>	Native	Ornamental
<i>Stellaria holostea</i>	Native	Spontaneous

<i>Stellaria media</i>	Native	Spontaneous
<i>Stokesia</i>	Non-native	Ornamental
<i>Succisa pratensis</i>	Native	Ornamental
<i>Symphytum officinale</i>	Native	Ornamental
<i>Syringa</i>	Non-native	Ornamental
<i>Tagetes patula</i>	Non-native	Ornamental
<i>Tanacetum parthenium</i>	Native	Ornamental
<i>Tanacetum vulgare</i>	Native	Ornamental
<i>Taraxacum</i>	Native	Spontaneous
<i>Telekia speciosa</i>	Non-native	Ornamental
<i>Tellima grandiflora</i>	Non-native	Ornamental
<i>Thalictrum aquilegifolium</i>	Non-native	Ornamental
<i>Thymus</i>	Native	Crop
<i>Trifolium incarnatum</i>	Native	Spontaneous
<i>Trifolium pratense</i>	Native	Spontaneous
<i>Trifolium repens</i>	Native	Spontaneous
<i>Trollius</i>	Native	Ornamental
<i>Tropaeolum majus</i>	Non-native	Ornamental
<i>Tulipa</i>	Non-native	Ornamental
<i>Tussilago farfara</i>	Native	Spontaneous
<i>Urtica dioica</i>	Native	Spontaneous
<i>Vaccinium corymbosum</i>	Non-native	Ornamental
<i>Verbascum</i>	Native	Ornamental
<i>Verbena bonariensis</i>	Non-native	Ornamental
<i>Verbena officinalis</i>	Native	Ornamental
<i>Veronica</i>	Native	Ornamental
<i>Veronica filiformis</i>	Non-native	Ornamental
<i>Veronica longifolia</i>	Non-native	Ornamental
<i>Veronica repens</i>	Non-native	Ornamental
<i>Veronica spicata</i>	Native	Ornamental
<i>Veronicastrum virginicum</i>	Non-native	Ornamental
<i>Viburnum</i>	Native	Ornamental
<i>Vicia faba</i>	Non-native	Crop
<i>Vicia sativa</i>	Native	Spontaneous
<i>Vinca major</i>	Non-native	Ornamental
<i>Viola tricolor</i>	Native	Ornamental
<i>Visnaga daucoides</i>	Non-native	Ornamental

<i>Weigela</i>	Non-native	Ornamental
<i>Wisteria</i>	Non-native	Ornamental
<i>Xerochrysum bracteatum</i>	Non-native	Ornamental
<i>Zinnia</i>	Non-native	Ornamental

S.3. Flower visitor species list

Table D.3: A list of the 87 flower visitor species recorded across all sites, including the group they belong to (bee, hoverflies or butterflies) and their total abundance.

Species	Group	No. flower visits
<i>Apis mellifera</i>	bees	660
<i>Andrena bicolor</i>	bees	25
<i>Andrena denticulata</i>	bees	6
<i>Andrena haemorrhoa</i>	bees	6
<i>Andrena scotica</i>	bees	9
<i>Andrena subopaca</i>	bees	3
<i>Anthophora furcata</i>	bees	12
<i>Anthophora plumipes</i>	bees	18
<i>Bombus hortorum</i>	bees	95
<i>Bombus hypnorum</i>	bees	356
<i>Bombus lapidarius</i>	bees	101
<i>Bombus lucorum terrestris</i>	bees	920
<i>Bombus pascuorum</i>	bees	1681
<i>Bombus pratorum</i>	bees	415
<i>Bombus sylvestris</i>	bees	7
<i>Colletes daviesanus</i>	bees	63
<i>Halictus rubicundus</i>	bees	5
<i>Hylaeus communis</i>	bees	2
<i>Hylaeus hyalinatus</i>	bees	26
<i>Lasioglossum albipes</i>	bees	3
<i>Lasioglossum calceatum</i>	bees	9
<i>Lasioglossum cupromicans</i>	bees	2
<i>Lasioglossum fratellum</i>	bees	7
<i>Lasioglossum smeathmanellum</i>	bees	81
<i>Osmia bicornis</i>	bees	47
<i>Osmia caerulea</i>	bees	3
<i>Megachile centuncularis</i>	bees	41

<i>Megachile willughbiella</i>	bees	7
<i>Sphecodes geoffrellus</i>	bees	2
<i>Baccha elongata</i>	hoverflies	13
<i>Cheilsoia albitarsis</i>	hoverflies	1
<i>Cheilosia bergenstammi</i>	hoverflies	8
<i>Cheilosia illustrata</i>	hoverflies	1
<i>Cheilosia latifrons</i>	hoverflies	1
<i>Cheilosia proxima</i>	hoverflies	2
<i>Cheilosia vernalis</i>	hoverflies	3
<i>Chrysogaster solstitialis</i>	hoverflies	3
<i>Chrysotoxum festivum</i>	hoverflies	1
<i>Dasysyrphus albostratus</i>	hoverflies	8
<i>Dasysyrphus tricinctus</i>	hoverflies	2
<i>Dasysyrphus venustus</i>	hoverflies	2
<i>Didea fasciata</i>	hoverflies	2
<i>Epistrophe eligans</i>	hoverflies	16
<i>Epistrophe grossulariae</i>	hoverflies	39
<i>Episyrphus balteatus</i>	hoverflies	214
<i>Eristalis pertinax</i>	hoverflies	339
<i>Eristalis arbustorum</i>	hoverflies	25
<i>Eristalis horticola</i>	hoverflies	4
<i>Eristalis intricaria</i>	hoverflies	12
<i>Eristalis nemorum</i>	hoverflies	5
<i>Eristalis tenax</i>	hoverflies	61
<i>Eumerus funeralis</i>	hoverflies	2
<i>Eupeodes bucculatus</i>	hoverflies	1
<i>Eupeodes corollae</i>	hoverflies	38
<i>Eupeodes latifasciatus</i>	hoverflies	9
<i>Eupeodes luniger</i>	hoverflies	26
<i>Ferdinandea cuprea</i>	hoverflies	2
<i>Helophilus pendulus</i>	hoverflies	78
<i>Leucozona glaucia</i>	hoverflies	3
<i>Merodon equestris</i>	hoverflies	32
<i>Melangyna lasiophthalma</i>	hoverflies	1

<i>Melanostoma mellinum</i>	hoverflies	9
<i>Melanostoma scalare</i>	hoverflies	231
<i>Meliscaeva auricollis</i>	hoverflies	61
<i>Meliscaeva cinctella</i>	hoverflies	18
<i>Myathropa florea</i>	hoverflies	51
<i>Neoascia podagrica</i>	hoverflies	61
<i>Neoascia tenur</i>	hoverflies	4
<i>Parasyrphus punctulatus</i>	hoverflies	1
<i>Pipizella viduata</i>	hoverflies	1
<i>Platycheirus albimanus</i>	hoverflies	335
<i>Platycheirus scutatus</i>	hoverflies	8
<i>Scaeva pyrastris</i>	hoverflies	17
<i>Sericomyia silentis</i>	hoverflies	1
<i>Sphaerophoria</i>	hoverflies	37
<i>Syritta pipiens</i>	hoverflies	232
<i>Syrphus ribesii</i>	hoverflies	190
<i>Stryphus torvus</i>	hoverflies	7
<i>Syrphus vitripennis</i>	hoverflies	51
<i>Volucella bombylans</i>	hoverflies	1
<i>Volucella pellucens</i>	hoverflies	5
<i>Xylota.segnis</i>	hoverflies	3
<i>Aglais io</i>	butterflies	20
<i>Anthocharis cardamines</i>	butterflies	4
<i>Maniola jurtina</i>	butterflies	1
<i>Pieris brassica</i>	butterflies	6
<i>Pieris rapa</i>	butterflies	22

S.4. Final model results table

Table D.4: Final GLMMs for the environmental drivers (predictors) of the response variables floral abundance, floral richness, the number of flower visits, the richness of flower visitors, network specialisation (H2'), network interaction evenness, network nestedness (WNODF), flower visitor specialisation (d'), the number of flower visits to crop plants and the richness of flower visits to crop plants. The table shows the degrees of freedom (DF), chi-square and P value from the model selection process and Z values from the final model summary.

Response	Explanatory	Estimate	SE	Z	Conf. low	Conf. high	Adj. P value
Floral resources							

Floral abundance	Size	0.29	0.08	3.83	0.14	0.45	<0.001
	Month	0.22	0.16	1.32	-0.11	0.54	0.02
	Origin	-0.55	0.07	-8.22	-0.68	-0.42	<0.001
	I(Month)^2	-0.53	0.16	-3.23	-0.85	-0.21	0.004
	Month*Origin	0.65	0.07	9.84	0.52	0.78	<0.001
Floral richness	Size	0.19	0.48	3.91	0.09	0.28	<0.001
	Month	1.11	0.09	11.85	0.93	1.29	<0.001
	Origin	-0.44	0.03	-13.40	-0.51	-0.38	<0.001
	Site type*Origin	-0.20	0.08	-2.49	-0.36	-0.04	0.044
	Month*Origin	0.07	0.16	0.41	-0.25	0.39	<0.001
	I(Month)^2	-1.09	0.09	-11.67	-1.27	-0.90	<0.001
	I(Month)^2 *Origin	0.38	0.15	2.45	0.08	0.68	0.014
Flower visit observations							
Flower visits	Floral abundance m ²	0.14	0.03	4.17	0.08	0.21	<0.001
	Floral richness	0.46	0.04	10.70	0.37	0.54	<0.001
	Month	0.13	0.04	3.69	0.06	0.20	<0.001
	Origin	-0.28	0.06	-4.87	-0.40	-0.17	0.002
	Month*Origin	0.23	0.06	3.78	0.11	0.35	<0.001
	Abundance*Origin	0.23	0.06	3.57	0.10	0.35	<0.001
	Richness*Origin	0.12	0.06	2.06	0.01	0.24	0.003
	Richness * green space	0.008	0.03	2.79	0.02	0.14	0.001
Flower visitor richness	Floral abundance m ²	0.11	0.02	4.65	0.06	0.16	<0.001
	Floral richness	0.29	0.03	10.17	0.23	0.34	<0.001
	Month	0.09	0.03	3.23	0.03	0.14	<0.001
	Origin	-0.30	0.05	-6.42	-0.40	-0.21	0.03
	Month*Origin	0.21	0.05	4.35	0.12	0.31	<0.001
	Abundance*Origin	0.15	0.04	3.48	0.07	0.24	<0.001
	Richness*Origin	0.09	0.04	2.20	0.01	0.16	0.018

	Richness* green space	0.008	0.02	2.76	0.02	0.10	0.002
Pan traps							
Insect abundance	Average richness	0.09	0.09	1.00	-0.09	0.28	0.04
	I(Month)^2	-1.04	0.27	-3.82	-1.58	-0.50	0.002
	Average abundance m ²	0.12	0.06	2.07	0.01	0.24	0.037
Insect richness	Average abundance m ²	0.12	0.04	3.03	0.04	0.19	0.002
	Average richness	0.03	0.06	0.54	-0.09	0.15	0.02
	I(Month)^2	-0.73	0.18	-4.05	-1.08	-0.37	<0.001
	Size	0.18	0.07	2.45	0.03	0.33	0.02
Network indices							
H ₂ z-score	Floral abundance m ²	0.21	0.10	2.04	0.07	0.40	<0.001
	Floral richness	1.05	0.10	10.23	0.84	1.25	<0.001
	Percentage abundance native	0.26	0.10	2.64	0.07	0.45	0.01
Interaction evenness z-score	Floral abundance m ²	-0.21	0.10	-2.05	-0.40	-0.01	<0.001
	Floral richness	-1.05	0.10	-10.27	-1.25	-0.85	<0.001
	Percentage abundance native	-0.26	0.10	-2.65	-0.45	-0.07	0.01
NODF z-score	Floral abundance m ²	-0.21	0.10	-2.05	-0.40	-0.01	<0.001
	Floral richness	-1.05	0.10	-10.27	-1.25	-0.85	<0.001
	Percentage abundance native	-0.26	0.10	-2.65	-0.45	-0.07	0.01
D'	Floral richness*LUD	0.30	0.09	3.17	-0.48	0.49	0.003
	Month*percentage native richness	-0.25	0.12	-2.20	0.12	-0.02	0.015
Crop visits							

Flower	Crop richness	1.25	0.07	17.16	1.11	1.40	<0.001
visits to	Crop abundance m ²	0.23	0.05	4.11	0.12	0.34	<0.001
crop plants	Spontaneous richness	-0.15	0.06	-2.60	-0.26	-0.04	<0.001
	Origin	-1.79	0.14	-12.57	-2.07	-1.51	<0.001
	Origin*Month	0.64	0.13	5.04	0.39	0.89	<0.001
	Ornamental abundance m ² * origin	0.42	0.10	4.13	0.22	0.61	<0.001
Flower	Crop richness	0.95	0.06	16.92	0.84	1.06	<0.001
visitor	Crop abundance m ²	0.15	0.03	4.59	0.09	0.21	<0.001
richness to	Spontaneous richness	-0.10	0.05	-2.21	-0.19	-0.01	<0.001
	Origin	-1.41	0.13	-11.27	-1.66	1.17	<0.001
crop plants	Origin*Month	0.58	0.11	5.41	0.37	0.80	<0.001
	Ornamental abundance*Origin	0.37	0.08	4.55	0.21	0.53	<0.001

S.5. Model AIC values

Table D.5: A comparison of model AIC values, which were used to select the spatial scale of data analysis for the landscape scale variables. For each response variable, three spatial scales were compared that included both land use diversity and area of green space in either a 250m, 500m or 1000m buffer. Model AIC values were also used to select the appropriate random effects. For each response variable the random effects were either, plot, site or plot nested within site (Site/plot).

Model	AIC
Landscape variables	
Floral abundance scale 250	11094.15
Floral abundance scale 500	11090.87
Floral abundance scale 1000	11092.11
Floral richness scale 250	3565.90
Floral richness scale 500	3565.91
Floral richness scale 1000	3560.07
Flower visits scale 250	4200.14
Flower visits scale 500	4198.27
Flower visits scale 1000	4193.35
Flower visitor richness scale 250	3113.73
Flower visitor richness scale 500	3107.98
Flower visitor richness scale 1000	3101.73
H2 scale 250	1362.36

H2 scale 500	1361.22
H2 scale 1000	1354.66
Interaction evenness scale 250	1356.24
Interaction evenness scale 500	1354.90
Interaction evenness scale 1000	1352.63
NODF scale 250	1356.23
NODF scale 500	1354.90
NODF scale 1000	1349.48
d' scale 250	-3888.37
d' scale 500	-3888.16
d' scale 1000	-3894.76
Crop plant flower visits- 250	3107.07
Crop plant flower visits- 500	3105.25
Crop plant flower visits- 1000	3108.27
Crop plant flower visitor richness- 250	2544.64
Crop plant flower visitor richness- 500	2542.29
Crop plant flower visitor richness- 1000	2542.56
Random effects	
Floral abundance- Site	11212.86
Floral abundance- Plot	11088.87
Floral abundance- Site/Plot	11089.16
Floral richness - Site	378.27
Floral richness - Plot	3567.13
Floral richness- Site/Plot	3565.91
Flower visits - Site	4212.82
Flower visits - Plot	4198.27
Flower visits- Site/Plot	NA
Flower visitor richness - Site	3125.79
Flower visitor richness - Plot	3107.98
Flower visitor richness - Site/Plot	3125.79
H2 - Site	1361.22
H2 - Plot	1356.57
H2 - Site/Plot	1362.59
Interaction evenness - Site	1360.59

Interaction evenness - Plot	1354.90
Interaction evenness- Site/Plot	1356.56
NODF - Site	1356.46
NODF - Plot	1354.90
NODF - Site/Plot	1356.46
d' - Site	-3774.74
d' - Plot	-3884.27
d' - Site/Plot	-3882.27
Crop plant flower visits- Site	3155.86
Crop plant flower visits- Plot	3103.25
Crop plant flower visits- Site/plot	3105.25
Crop plant flower visitor richness- Site	2588.50
Crop plant flower visitor richness- Plot	2540.29
Crop plant flower visitor richness- Site/plot	2542.29

S.6. Preferred plants by pollinators

We generated a list of preferred plant species using the *econullnet* package in R (Vaughan et al., 2018). Here, plant preference by flower visitors was calculated based on whether flower visitors interact with plants, more or less than expected by chance based on the floral abundance of each plant species. 1000 random null models based on floral abundance were generated for each plant-flower visitor network per site, per month, to calculate the expected plant-flower visitor networks given the availability of individual floral resources. We then filtered the resulting plant list to those that were preferred by more than 5 pollinator species, giving a list of attractive plants to a high number of flower visitor species.

Table D.6: Results from the plant preference analysis using *econullnet* package. Plant species that received more interactions based on plant abundance than expected from null models are shown in the table alongside the month these plants were preferred and whether they were native or non-native to Great Britain.

Plant	Month	Plant origin	No. Pollinators
<i>Acca sellowiana</i>	August	Non native	3
<i>Acca sellowiana</i>	September	Non native	1
<i>Achillea</i> sp.	July	Native	1
<i>Achillea</i> sp.	June	Native	1
<i>Achillea millefolium</i>	June	Native	2
<i>Aconitum</i> sp.	June	Native	1
<i>Aegopodium podagraria</i>	July	Native	2
<i>Aegopodium podagraria</i>	June	Native	4
<i>Aegopodium podagraria</i>	May	Native	1
<i>Agrostemma githago</i>	August	Non native	3
<i>Agrostemma githago</i>	July	Non native	3
<i>Agrostemma githago</i>	September	Non native	2

<i>Ajuga reptans</i>	April	Native	1
<i>Alcea</i> sp.	September	Non native	1
<i>Allium</i> sp.	August	Native	3
<i>Allium</i> sp.	June	Native	4
<i>Allium</i> sp.	May	Native	5
<i>Allium</i> sp.	September	Native	2
<i>Allium schoenoprasum</i>	August	Native	3
<i>Allium schoenoprasum</i>	June	Native	2
<i>Allium schoenoprasum</i>	May	Native	9
<i>Allium schoenoprasum</i>	September	Native	3
<i>Allium triquetrum</i>	May	Non native	1
<i>Allium tuberosum</i>	August	Non native	2
<i>Allium tuberosum</i>	September	Non native	1
<i>Allium ursinum</i>	April	Native	1
<i>Anemone hupehensis</i>	August	Non native	4
<i>Anemone hupehensis</i>	September	Non native	1
<i>Anethum graveolens</i>	July	Non native	1
<i>Angelica</i> sp.	June	Native	2
<i>Angelica</i> sp.	May	Native	2
<i>Angelica</i> sp.	September	Native	1
<i>Antirrhinum majus</i>	July	Non native	1
<i>Antirrhinum majus</i>	September	Non native	1
<i>Apium graveolens</i>	August	Native	1
<i>Apium graveolens</i>	September	Native	1
<i>Aquilegia</i> sp.	May	Native	1
<i>Argyranthemum</i> sp.	August	Non native	2
<i>Armeria</i> sp.	August	Native	1
<i>Armeria</i> sp.	June	Native	2
<i>Armeria</i> sp.	May	Native	2
<i>Aster</i> sp.	August	Non native	2
<i>Aster</i> sp.	September	Non native	1
<i>Astilbe</i> sp.	August	Non native	1
<i>Astilbe japonica</i>	August	Non native	1
<i>Astilbe japonica</i>	July	Non native	1
<i>Astrantia</i> sp.	July	Non native	3
<i>Astrantia</i> sp.	June	Non native	2
<i>Begonia</i> sp.	July	Non native	1
<i>Begonia</i> sp.	September	Non native	1
<i>Bellis perennis</i>	April	Native	1
<i>Bellis perennis</i>	July	Native	1
<i>Bellis perennis</i>	June	Native	1
<i>Beta vulgaris</i>	July	Native	1
<i>Beta vulgaris</i>	September	Native	1
<i>Betonica officinalis</i>	July	Native	1
<i>Bidens aurea</i>	August	Non native	1
<i>Bistorta officinalis</i>	August	Native	2
<i>Bistorta officinalis</i>	July	Native	3
<i>Bistorta officinalis</i>	May	Native	3
<i>Bistorta officinalis</i>	August	Non native	4

<i>Bistorta officinalis</i>	July	Non native	3
<i>Bistorta officinalis</i>	June	Non native	1
<i>Bistorta officinalis</i>	September	Non native	3
<i>Brachyglottis</i> sp.	June	Non native	1
<i>Brassica</i> sp.	April	Native	1
<i>Brassica</i> sp.	June	Native	1
<i>Brassica</i> sp.	May	Native	1
<i>Brassica oleracea</i>	April	Native	1
<i>Brassica oleracea</i>	August	Native	2
<i>Brassica oleracea</i>	May	Native	1
<i>Brassica oleracea</i>	September	Native	2
<i>Brassica rapa</i>	August	Native	7
<i>Brassica rapa</i>	July	Native	5
<i>Brassica rapa</i>	June	Native	5
<i>Brassica rapa</i>	September	Native	6
<i>Buddleja</i> sp.	August	Non native	4
<i>Buddleja</i> sp.	September	Non native	4
<i>Buddleja globosa</i>	June	Non native	4
<i>Buphthalmum salicifolium</i>	July	Non native	2
<i>Buphthalmum salicifolium</i>	June	Non native	1
<i>Calendula officinalis</i>	August	Non native	9
<i>Calendula officinalis</i>	July	Non native	2
<i>Calendula officinalis</i>	June	Non native	1
<i>Calendula officinalis</i>	September	Non native	7
<i>Callistephus chinensis</i>	May	Non native	1
<i>Caltha palustris</i>	April	Native	3
<i>Caltha palustris</i>	May	Native	1
<i>Calystegia sepium</i>	July	Native	1
<i>Calystegia sepium</i>	September	Native	2
<i>Campanula</i> sp.	July	Native	3
<i>Campanula</i> sp.	June	Native	1
<i>Campanula lactiflora</i>	July	Non native	3
<i>Cardamine pratensis</i>	May	Native	1
<i>Cardamine pratensis</i>	August	Native	1
<i>Centaurea cyanus</i>	July	Native	4
<i>Centaurea cyanus</i>	June	Native	1
<i>Centaurea cyanus</i>	September	Native	3
<i>Centaurea montana</i>	August	Non native	1
<i>Centaurea montana</i>	June	Non native	4
<i>Centaurea montana</i>	May	Non native	1
<i>Centaurea nigra</i>	August	Native	2
<i>Centaurea nigra</i>	July	Native	3
<i>Centaurea nigra</i>	September	Native	1
<i>Centaurea triumphetti</i>	May	Non native	2
<i>Centranthus ruber</i>	August	Non native	1
<i>Cephalaria gigantea</i>	June	Non native	1
<i>Cephalaria gigantea</i>	September	Non native	1
<i>Cerastium tomentosum</i>	June	Non native	3
<i>Chaenostoma</i> sp.	September	Non native	1

<i>Chamaemelum</i> sp.	August	Native	2
<i>Chamaemelum</i> sp.	July	Native	1
<i>Chamaemelum</i> sp.	September	Native	2
<i>Cichorium intybus</i>	August	Native	1
<i>Circaea lutetiana</i>	August	Native	1
<i>Circaea lutetiana</i>	July	Native	1
<i>Cirsium</i> sp.	July	Native	1
<i>Cirsium</i> sp.	June	Native	3
<i>Cirsium</i> sp.	May	Native	7
<i>Cirsium arvense</i>	August	Native	5
<i>Clematis</i> sp.	June	Native	1
<i>Coreopsis</i> sp.	August	Non native	1
<i>Coriandrum sativum</i>	August	Non native	1
<i>Coriandrum sativum</i>	July	Non native	1
<i>Coriandrum sativum</i>	September	Non native	2
<i>Cosmos bipinnatus</i>	August	Non native	6
<i>Cosmos bipinnatus</i>	July	Non native	2
<i>Cosmos bipinnatus</i>	September	Non native	11
<i>Cotoneaster</i> sp.	July	Native	1
<i>Cotoneaster</i> sp.	June	Native	1
<i>Cotoneaster</i> sp.	May	Native	1
<i>Crocasmia</i> sp.	August	Non native	2
<i>Crocasmia</i> sp.	July	Non native	1
<i>Cucurbita</i> sp.	August	Non native	3
<i>Cucurbita</i> sp.	September	Non native	3
<i>Cyclamen</i> sp.	August	Non native	1
<i>Cynara cardunculus</i>	August	Non native	3
<i>Cynara cardunculus</i>	September	Non native	3
<i>Dahlia</i> sp.	August	Non native	4
<i>Dahlia</i> sp.	September	Non native	3
<i>Dasiphora</i> sp.	May	Native	1
<i>Daucus carota</i>	August	Native	1
<i>Daucus carota</i>	September	Native	2
<i>Dianthus</i> sp.	July	Native	1
<i>Digitalis purpureum</i>	July	Native	2
<i>Digitalis purpureum</i>	June	Native	4
<i>Digitalis purpureum</i>	May	Native	2
<i>Dipsacus fullonum</i>	August	Native	2
<i>Dipsacus fullonum</i>	July	Native	2
<i>Echinops</i> sp.	August	Non native	2
<i>Echinops</i> sp.	July	Non native	2
<i>Echinops</i> sp.	September	Non native	2
<i>Echium</i> sp.	July	Native	2
<i>Echium</i> sp.	September	Native	1
<i>Epilobium</i> sp.	August	Native	1
<i>Epilobium</i> sp.	June	Native	2
<i>Epilobium</i> sp.	September	Native	1
<i>Erica</i> sp.	September	Native	1
<i>Erigeron karvinskianus</i>	June	Non native	1

<i>Erigeron karvinskianus</i>	September	Non native	1
<i>Eruca</i> sp.	August	Non native	3
<i>Eruca</i> sp.	September	Non native	7
<i>Eryngium bourgatii</i>	July	Non native	1
<i>Erysimum</i> sp.	August	Non native	2
<i>Erysimum</i> sp.	July	Non native	1
<i>Erysimum</i> sp.	June	Non native	1
<i>Erysimum</i> sp.	September	Non native	1
<i>Erysimum linifolium</i>	April	Non native	1
<i>Escalonia</i> sp.	June	Non native	2
<i>Eschscholzia californica</i>	August	Non native	2
<i>Eschscholzia californica</i>	July	Non native	4
<i>Eschscholzia californica</i>	September	Non native	3
<i>Eupatorium cannabinum</i>	August	Native	4
<i>Eupatorium cannabinum</i>	July	Native	1
<i>Fagopyrum esculentum</i>	July	Non native	1
<i>Filipendula ulmaria</i>	July	Native	5
<i>Filipendula ulmaria</i>	June	Native	1
<i>Foeniculum vulgare</i>	August	Non native	7
<i>Foeniculum vulgare</i>	September	Non native	4
<i>Galega officinalis</i>	July	Non native	1
<i>Galeopsis</i> sp.	July	Native	1
<i>Galium aparine</i>	June	Native	1
<i>Geranium</i> sp.	August	Native	2
<i>Geranium</i> sp.	July	Native	1
<i>Geranium</i> sp.	June	Native	12
<i>Geranium</i> sp.	May	Native	2
<i>Geranium</i> sp.	September	Native	2
<i>Geranium purpureum</i>	September	Native	1
<i>Geranium robertianum</i>	April	Native	1
<i>Geranium robertianum</i>	August	Native	1
<i>Geranium robertianum</i>	July	Native	2
<i>Geranium robertianum</i>	May	Native	4
<i>Geranium robertianum</i>	September	Native	1
<i>Geum</i> sp.	June	Native	1
<i>Geum</i> sp.	May	Native	2
<i>Geum coccineum</i>	September	Non native	2
<i>Geum rivale</i>	August	Native	1
<i>Geum urbanum</i>	August	Native	2
<i>Geum urbanum</i>	July	Native	1
<i>Geum urbanum</i>	May	Native	4
<i>Geum urbanum</i>	September	Native	1
<i>Gladiolus</i> sp.	August	Native	2
<i>Gladiolus</i> sp.	May	Native	1
<i>Glebionis segetum</i>	August	Native	5
<i>Glebionis segetum</i>	July	Native	1
<i>Glebionis segetum</i>	September	Native	4
<i>Helenium autumnale</i>	September	Non native	2
<i>Helianthemum nummularium</i>	July	Native	2

<i>Helianthemum nummularium</i>	June	Native	1
<i>Helianthus</i> sp.	August	Non native	2
<i>Helianthus</i> sp.	September	Non native	4
<i>Helianthus annuus</i>	July	Non native	3
<i>Helianthus annuus</i>	September	Non native	4
<i>Hemerocallis</i>	July	Non native	1
<i>Heracleum sphondylium</i>	July	Native	1
<i>Hesperis matronalis</i>	May	Non native	2
<i>Hieracium</i> sp.	August	Native	2
<i>Hieracium</i> sp.	July	Native	7
<i>Hieracium</i> sp.	June	Native	3
<i>Hieracium</i> sp.	September	Native	6
<i>Hyacinthoides</i> sp.	April	Native	1
<i>Hydrangea</i> sp.	July	Non native	2
<i>Hylotelephium</i> sp.	August	Non native	1
<i>Hylotelephium</i> sp.	September	Non native	2
<i>Hypericum</i> sp.	August	Native	3
<i>Hypericum</i> sp.	July	Native	3
<i>Hypericum</i> sp.	June	Native	1
<i>Hypericum</i> sp.	September	Native	1
<i>Iberis</i> sp.	May	Native	1
<i>Ilex</i> sp.	April	Native	1
<i>Impatiens glandulifera</i>	August	Non native	2
<i>Inula</i> sp.	August	Native	4
<i>Inula</i> sp.	July	Native	2
<i>Iris</i> sp.	June	Native	3
<i>Iris</i> sp.	May	Native	2
<i>Jacobaea vulgaris</i>	July	Native	3
<i>Jacobaea vulgaris</i>	September	Native	2
<i>Jasminum</i> sp.	July	Non native	1
<i>Jasminum</i> sp.	September	Non native	1
<i>Lamium album</i>	August	Native	1
<i>Lamium album</i>	May	Native	1
<i>Lamium galeobdolon</i>	April	Native	1
<i>Lamium purpureum</i>	April	Native	1
<i>Lapsana communis</i>	August	Native	5
<i>Lapsana communis</i>	July	Native	2
<i>Lapsana communis</i>	September	Native	5
<i>Lathyrus odoratus</i>	August	Non native	2
<i>Lavandula</i> sp.	August	Non native	1
<i>Lavandula</i> sp.	September	Non native	1
<i>Leucanthemum</i> sp.	August	Native	6
<i>Leucanthemum</i> sp.	July	Native	3
<i>Leucanthemum</i> sp.	June	Native	5
<i>Leucanthemum</i> sp.	May	Native	1
<i>Leucanthemum</i> sp.	September	Native	5
<i>Libertia</i> sp.	May	Non native	1
<i>Ligularia</i> sp.	July	Non native	1
<i>Lilium</i> sp.	August	Non native	2

<i>Linaria purpurea</i>	August	Non native	1
<i>Linum grandiflorum</i>	August	Non native	2
<i>Lobelia</i> sp.	August	Native	1
<i>Lobularia maritima</i>	August	Non native	3
<i>Lobularia maritima</i>	July	Non native	3
<i>Lobularia maritima</i>	September	Non native	2
<i>Lonicera</i> sp.	August	Native	1
<i>Lonicera</i> sp.	July	Native	1
<i>Lonicera</i> sp.	September	Native	2
<i>Lotus corniculatus</i>	July	Native	2
<i>Lythrum salicaria</i>	July	Native	1
<i>Malcolmia maritima</i>	August	Non native	1
<i>Malcolmia maritima</i>	July	Non native	1
<i>Malva</i> sp.	August	Native	3
<i>Malva</i> sp.	July	Native	1
<i>Malva</i> sp.	September	Native	1
<i>Mentha</i> sp.	August	Native	1
<i>Mentha</i> sp.	September	Native	1
<i>Mimulus guttatus</i>	July	Non native	1
<i>Monarda didyma</i>	September	Non native	1
<i>Myosotis arvensis</i>	April	Native	1
<i>Myosotis arvensis</i>	June	Native	1
<i>Myosotis arvensis</i>	May	Native	1
<i>Myrrhis odorata</i>	June	Non native	1
<i>Narcissus</i> sp.	April	Native	1
<i>Nicandra physalodes</i>	July	Non native	1
<i>Nigella damascena</i>	August	Non native	1
<i>Oenothera biennis</i>	August	Non native	1
<i>Oenothera biennis</i>	June	Non native	1
<i>Oenothera biennis</i>	September	Non native	2
<i>Origanum vulgare</i>	July	Native	2
<i>Osteospermum</i> sp.	September	Non native	1
<i>Oxalis</i> sp.	August	Native	1
<i>Papaver</i> sp.	August	Native	2
<i>Papaver</i> sp.	June	Native	2
<i>Papaver</i> sp.	May	Native	3
<i>Papaver</i> sp.	September	Native	4
<i>Papaver cambricum</i>	April	Native	1
<i>Papaver cambricum</i>	August	Native	2
<i>Papaver cambricum</i>	July	Native	5
<i>Papaver cambricum</i>	June	Native	1
<i>Papaver cambricum</i>	May	Native	3
<i>Papaver cambricum</i>	September	Native	2
<i>Pentaglottis sempervirens</i>	April	Non native	2
<i>Pentaglottis sempervirens</i>	August	Non native	2
<i>Persicaria maculosa</i>	August	Native	1
<i>Petroselinum crispum</i>	August	Native	1
<i>Petroselinum crispum</i>	July	Native	1
<i>Phacelia tanacetifolia</i>	August	Non native	3

<i>Phacelia tanacetifolia</i>	July	Non native	2
<i>Phacelia tanacetifolia</i>	June	Non native	1
<i>Phacelia tanacetifolia</i>	May	Non native	2
<i>Phacelia tanacetifolia</i>	September	Non native	2
<i>Phaseolus coccineus</i>	August	Non native	1
<i>Philadelphius</i> sp.	July	Non native	1
<i>Pilosella aurantiaca</i>	August	Non native	2
<i>Pilosella aurantiaca</i>	May	Non native	2
<i>Pilosella aurantiaca</i>	September	Non native	5
<i>Plantago lanceolata</i>	September	Native	2
<i>Polemonium caeruleum</i>	June	Native	1
<i>Potentilla</i> sp.	September	Native	3
<i>Primula</i> sp.	April	Native	1
<i>Pulmonaria officinalis</i>	April	Non native	3
<i>Pulmonaria officinalis</i>	May	Non native	3
<i>Pyrus</i> sp.	June	Native	1
<i>Ranunculus</i> sp.	August	Native	3
<i>Ranunculus</i> sp.	July	Native	8
<i>Ranunculus</i> sp.	June	Native	6
<i>Ranunculus</i> sp.	May	Native	9
<i>Ranunculus</i> sp.	September	Native	3
<i>Raphanus sativus</i>	April	Native	1
<i>Raphanus sativus</i>	August	Native	7
<i>Raphanus sativus</i>	July	Native	2
<i>Raphanus sativus</i>	June	Native	1
<i>Rhinanthus minor</i>	June	Native	1
<i>Rhinanthus minor</i>	May	Native	1
<i>Ribes</i> sp.	April	Native	3
<i>Rodgersia</i> sp.	June	Non native	1
<i>Rosa</i> sp.	June	Native	1
<i>Rosa</i> sp.	May	Native	1
<i>Rosa</i> sp.	September	Native	1
<i>Rosa canina</i>	June	Native	1
<i>Rosa canina</i>	May	Native	1
<i>Rosa multiflora</i>	June	Non native	3
<i>Rosa pimpinellifolia</i>	August	Native	1
<i>Rosa pimpinellifolia</i>	September	Native	1
<i>Rosa rugosa</i>	July	Non native	1
<i>Rubus</i> sp.	August	Native	3
<i>Rubus</i> sp.	July	Native	2
<i>Rubus</i> sp.	June	Native	2
<i>Rubus</i> sp.	May	Native	2
<i>Rubus</i> sp.	September	Native	2
<i>Rudbeckia</i> sp.	August	Non native	2
<i>Rudbeckia</i> sp.	September	Non native	1
<i>Salvia</i> sp.	June	Native	2
<i>Salvia</i> sp.	September	Native	2
<i>Sanguisorba</i> sp.	June	Native	2
<i>Sanguisorba</i> sp.	May	Native	1

<i>Sanguisorba hakusanensis</i>	August	Non native	1
<i>Sanguisorba hakusanensis</i>	September	Non native	1
<i>Scabiosa</i> sp.	August	Native	3
<i>Scabiosa</i> sp.	July	Native	2
<i>Scabiosa</i> sp.	June	Native	3
<i>Scabiosa</i> sp.	May	Native	1
<i>Scabiosa</i> sp.	September	Native	4
<i>Scorzonera hispanicum</i>	June	Non native	2
<i>Scorzonera hispanicum</i>	May	Non native	2
<i>Scrophularia umbrosa</i>	August	Native	1
<i>Scrophularia umbrosa</i>	July	Native	1
<i>Scrophularia umbrosa</i>	September	Native	1
<i>Sedum</i> sp.	July	Native	5
<i>Sedum</i> sp.	June	Native	1
<i>Sempervivum</i> sp.	July	Non native	1
<i>Senecio</i> sp.	August	Native	1
<i>Silene coronaria</i>	August	Non native	2
<i>Silene coronaria</i>	July	Non native	3
<i>Silene coronaria</i>	September	Non native	3
<i>Silene diocia</i>	May	Native	1
<i>Silene latifolia</i>	July	Native	3
<i>Silene latifolia</i>	September	Native	2
<i>Solanum dulcamara</i>	July	Native	1
<i>Solanum dulcamara</i>	June	Native	1
<i>Solidago canadensis</i>	August	Non native	3
<i>Solidago canadensis</i>	September	Non native	1
<i>Sonchus oleraceus</i>	August	Native	3
<i>Sonchus oleraceus</i>	July	Native	1
<i>Sonchus oleraceus</i>	June	Native	3
<i>Sonchus oleraceus</i>	September	Native	2
<i>Spiraea</i> sp.	August	Non native	1
<i>Spiraea</i> sp.	July	Non native	1
<i>Spiraea douglasii</i>	September	Non native	1
<i>Stachys byzantina</i>	July	Non native	1
<i>Stellaria holostea</i>	May	Native	1
<i>Stellaria media</i>	August	Native	1
<i>Succisa pratensis</i>	August	Native	6
<i>Symphytum officinale</i>	April	Native	1
<i>Symphytum officinale</i>	August	Native	1
<i>Symphytum officinale</i>	July	Native	1
<i>Symphytum officinale</i>	June	Native	3
<i>Symphytum officinale</i>	May	Native	3
<i>Symphytum officinale</i>	September	Native	1
<i>Syringa</i> sp.	May	Non native	1
<i>Tagetes patula</i>	August	Non native	1
<i>Tagetes patula</i>	July	Non native	2
<i>Tagetes patula</i>	June	Non native	1
<i>Tanacetum parthenium</i>	August	Native	3
<i>Tanacetum parthenium</i>	June	Native	1

<i>Tanacetum vulgare</i>	August	Native	2
<i>Tanacetum vulgare</i>	July	Native	1
<i>Taraxacum</i> sp.	April	Native	9
<i>Taraxacum</i> sp.	August	Native	3
<i>Taraxacum</i> sp.	July	Native	1
<i>Taraxacum</i> sp.	June	Native	1
<i>Taraxacum</i> sp.	May	Native	11
<i>Taraxacum</i> sp.	September	Native	3
<i>Telekia speciosa</i>	July	Non native	2
<i>Trifolium pratense</i>	August	Native	1
<i>Trifolium pratense</i>	July	Native	1
<i>Trifolium repens</i>	July	Native	1
<i>Trifolium repens</i>	June	Native	1
<i>Tropaeolum majus</i>	August	Non native	3
<i>Tropaeolum majus</i>	July	Non native	2
<i>Tropaeolum majus</i>	May	Non native	1
<i>Tropaeolum majus</i>	September	Non native	4
<i>Tulipa</i> sp.	April	Non native	1
<i>Vaccinium corymbosum</i>	April	Non native	1
<i>Verbascum</i> sp.	August	Native	2
<i>Verbascum</i> sp.	June	Native	1
<i>Verbena bonariensis</i>	July	Non native	1
<i>Verbena bonariensis</i>	September	Non native	2
<i>Veronica</i> sp.	August	Native	1
<i>Veronica</i> sp.	July	Native	1
<i>Veronica</i> sp.	May	Native	1
<i>Veronica filiformis</i>	August	Non native	3
<i>Veronica spicata</i>	August	Native	1
<i>Veronicastrum virginicum</i>	August	Non native	1
<i>Viburnum</i> sp.	April	Native	1
<i>Vicia faba</i>	May	Non native	1
<i>Visnaga daucoides</i>	August	Non native	5
<i>Visnaga daucoides</i>	September	Non native	4
<i>Xerochrysum bracteatum</i>	September	Non native	3
<i>Zinnia</i> sp.	August	Non native	4

Appendix E: Supplementary material for chapter 5

S.1- Regional species data

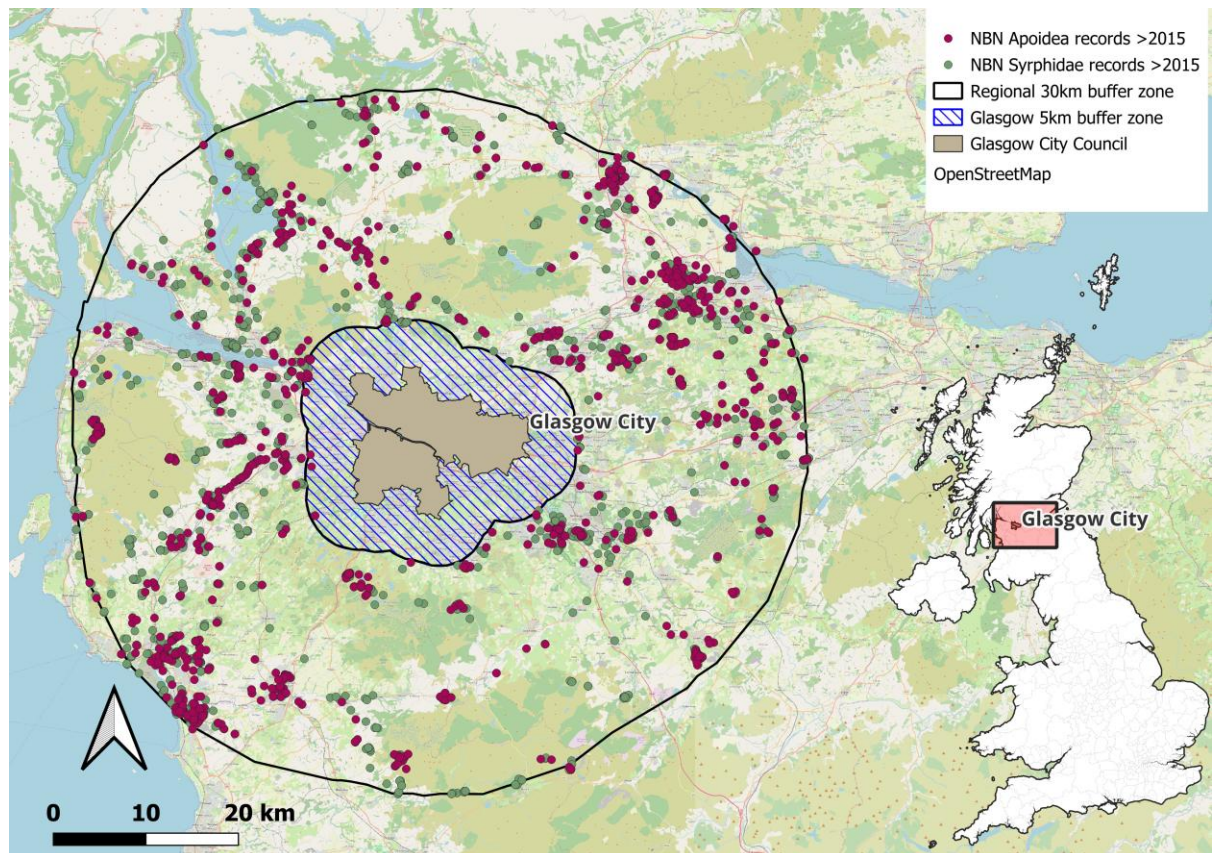


Figure E.1: Bee (purple) and hoverfly (green) records after 2015, downloaded from the NBN data base, within a 30km buffer around our core sampling area in Glasgow City Council boundary (brown), plus a 5km buffer (hatched blue lines). The 30km buffer allowed a range of habitats to be sampled whilst excluding other major urban areas. These records were used to define our regional species pool. Right map shows where the regional buffer is located within Great Britain.

Bee data contributed by the following providers:

- Records provided by Biological Records Centre, accessed through NBN Atlas website. (). For more information: email brc@ceh.ac.uk, or <https://registry.nbnatlas.org/public/show/dp77>
- Records provided by Bumblebee Conservation Trust, accessed through NBN Atlas website. (). For more information: email enquiries@bumblebeeconservation.org, or <https://registry.nbnatlas.org/public/show/dp99>
- Biological Records Centre. [Year downloaded: 2026]. Bee, wasp and ant (Hymenoptera: Aculeata) records verified via iRecord. (Creative Commons with Attribution 4.0 (CC-BY) CC BY Creative Commons Attribution). For more information: <https://registry.nbnatlas.org/public/show/dr2140>

- NatureScot (2020). Aculeate Hymenoptera records extracted from Invertebrate Site Register for Scotland (Open Government Licence (OGL)). For more information: <https://registry.nbnatlas.org/public/show/dr2288>
- West Lothian Council ([Year downloaded: 2026]). Local Biodiversity Site Surveys. Occurrence dataset on the NBN Atlas (Open Government Licence (OGL) It is acknowledged that this data has been supplied by West Lothian Council through the NBN Atlas). For more information: <https://registry.nbnatlas.org/public/show/dr2683>
- Records provided by Natural Resources Wales, accessed through NBN Atlas website. (). For more information: email opendata@cyfoethnaturiolcymru.gov.uk, or <https://registry.nbnatlas.org/public/show/dp122>
- Records provided by Natural History Museum, London, accessed through NBN Atlas website. (). For more information: <https://registry.nbnatlas.org/public/show/dp266>
- The Wildlife Information Centre ([Year downloaded: 2026]). A.T. Sumner's Records. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY)). For more information: <https://registry.nbnatlas.org/public/show/dr2785>
- Natural Resources Wales. ([Year downloaded: 2026]) Welsh Invertebrate Database (WID). Occurrence dataset accessed through the NBNAtlas (Open Government Licence (OGL) © CNC/NRW Data may be re-used under the terms of the Open Government Licence providing it is done so, acknowledging both the source and NRW's copyright. It is the recipient's responsibility to ensure the data is fit for the intended purpose. Attribution statement: Contains Natural Resources Wales information © Natural Resources Wales and Database Right. All rights Reserved.). For more information: <https://registry.nbnatlas.org/public/show/dr1212>
- Cumbria Biodiversity Data Centre ([Year downloaded: 2026]). Tullie House Museum Natural History Collections. Occurrence dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC). For more information: email nature@tulliehouse.co.uk, or <https://registry.nbnatlas.org/public/show/dr1311>
- UK Pollinator Monitoring Scheme. [Year downloaded: 2026]. Bee and hoverfly species data from the UK Pollinator Monitoring Scheme. (Open Government Licence (OGL) OGL Open Government Licence). For more information: <https://registry.nbnatlas.org/public/show/dr3654>
- Fife Nature Records Centre ([Year downloaded: 2026]). Fife Nature Records Centre Combined Dataset. Occurrence dataset on the NBN Atlas. (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC). For more information: <https://registry.nbnatlas.org/public/show/dr840>

- Records provided by iSpot, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: <https://registry.nbnatlas.org/public/show/dp267>
- Records provided by Cumbria Biodiversity Data Centre, accessed through NBN Atlas website. ([Year downloaded: 2026]) . For more information: email info@cbdc.org.uk, or <https://registry.nbnatlas.org/public/show/dp102>
- Natalie Harmsworth's Records (2010-2019), TWIC (2019) (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC). For more information: email admin@wildlifeinformation.co.uk, or <https://registry.nbnatlas.org/public/show/dr1510>
- Scottish Wildlife Trust ([Year downloaded: 2026]). Casual records for Scottish Wildlife Trust reserves - Unassessed data. Occurrence dataset on the NBN Atlas. (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr763>
- Royal Society for the Protection of Birds ([Year downloaded: 2026]). 2017 Onwards Muirkirk & North Lowther Uplands SPA species records. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) Co-operation Across Borders for Biodiversity project (CABB) is funded by the European Regional Development Fund as part of the INTERREG VA Programme which is managed by the Special European Union Programmes Body. RSPB Northern Ireland (RSPB NI) is the lead partner in the CABB project and is working with RSPB Scotland, BirdWatch Ireland, Northern Ireland Water, Butterfly Conservation and Moors for the Future to improve conditions for wading birds, blanket and lowland raised bogs and associated species.). For more information: <https://registry.nbnatlas.org/public/show/dr2643>
- East Ayrshire Countryside Ranger Service ([Year downloaded: 2026]). East Ayrshire Species Database. Occurrence dataset on the NBN Atlas (Open Government Licence (OGL) OGL). For more information: email James.macdonald@east-ayrshire.gov.uk, or <https://registry.nbnatlas.org/public/show/dr1339>
- Scottish Wildlife Trust ([Year downloaded: 2026]). Casual records for Scottish Wildlife Trust reserves - Verified data. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr780>
- Friends of the Earth ([Year downloaded: 2026]). Great British Bee Count 2015 - Stage 2 (records verified from photo). Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For

more information: email info@foe.co.uk, or
<https://registry.nbnatlas.org/public/show/dr1416>

- Records provided by Fife Nature Records Centre, accessed through NBN Atlas website. ([Year downloaded: 2026] . For more information: email nature.info@fife.gov.uk, or
<https://registry.nbnatlas.org/public/show/dp162>
- iSpot ([Year downloaded: 2026]). iSpot British Isles observations. Occurrence dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC)). For more information: <https://registry.nbnatlas.org/public/show/dr2701>
- Scottish Wildlife Trust ([Year downloaded: 2026] Survey and monitoring records for Scottish Wildlife Trust reserves from reserve convenors and Trust volunteers - Verified data. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or
<https://registry.nbnatlas.org/public/show/dr766>
- Scottish Wildlife Trust ([Year downloaded: 2026]). Commissioned surveys and staff surveys and reports for Scottish Wildlife Trust reserves - Verified data. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or
<https://registry.nbnatlas.org/public/show/dr765>
- The Wildlife Information Centre ([Year downloaded: 2026]). TWIC Biodiversity Field Trip Data (1995-present). Occurrence dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC). For more information: email admin@wildlifeinformation.co.uk, or
<https://registry.nbnatlas.org/public/show/dr922>
- Highland Biological Recording Group ([Year downloaded: 2026]). HBRG Insects Dataset Vol 1. Occurrence dataset accessed through the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email records@hbrg.org.uk, or
<https://registry.nbnatlas.org/public/show/dr965>
- Scottish Wildlife Trust ([Year downloaded: 2026]). Survey and monitoring records for Scottish Wildlife Trust reserves from reserve convenors and Trust volunteers - Unassessed data. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or
<https://registry.nbnatlas.org/public/show/dr767>

- Records provided by Friends of the Earth, accessed through NBN Atlas website. ([Year downloaded: 2026]) . For more information: <https://registry.nbnatlas.org/public/show/dp106>
- Records provided by Buglife, accessed through NBN Atlas website. (). For more information: email scotland@buglife.org.uk, or <https://registry.nbnatlas.org/public/show/dp1>
- Records provided by The Wildlife Information Centre, accessed through NBN Atlas website. ([Year downloaded: 2026]) . For more information: email info@wildlifeinformation.co.uk, or <https://registry.nbnatlas.org/public/show/dp43>
- Records provided by Royal Society for the Protection of Birds, accessed through NBN Atlas website. ([Year downloaded: 2026]) . For more information: email Dataunit@rspb.org.uk, or <https://registry.nbnatlas.org/public/show/dp0>
- Records provided by Scottish Wildlife Trust, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dp2>
- TWIC Site Surveys (2010 - present) (2020) (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC)). For more information: <https://registry.nbnatlas.org/public/show/dr2010>
- Records provided by Highland Biological Recording Group, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email chair@hbrg.org.uk, or <https://registry.nbnatlas.org/public/show/dp7>
- North Ayrshire Countryside Ranger Service ([Year downloaded: 2026]). Species within North Ayrshire from 1984 - Present. Occurrence dataset on the NBN Atlas (Open Government Licence (OGL) OGL). For more information: email rangerservice@north-ayrshire.gov.uk, or <https://registry.nbnatlas.org/public/show/dr1160>
- Records provided by NatureScot, accessed through NBN Atlas website. (). For more information: <https://registry.nbnatlas.org/public/show/dp9>
- Friends of the Earth ([Year downloaded: 2026] Great British Bee Count 2016 - Stage 2 (records verified from photo). Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email info@foe.co.uk, or <https://registry.nbnatlas.org/public/show/dr1244>
- Bumblebee Conservation Trust ([Year downloaded: 2026]). BeeWalk bumblebee distributions for Great Britain 2008-2022. Occurrence dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial

v4.0 (CC-BY-NC) CC-BY-NC). For more information:
<https://registry.nbnatlas.org/public/show/dr1263>

- Buglife ([Year downloaded: 2026]). Invertebrate records from sites that are mainly across Scotland. Occurrence record dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC). For more information:
<https://registry.nbnatlas.org/public/show/dr1363>
- Lothian Wildlife Information Centre surveys (Invertebrates - general), TWIC (2020) (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC)). For more information:
<https://registry.nbnatlas.org/public/show/dr2199>
- Natural History Museum (2023). Data Portal query on 1 resources <https://doi.org/10.5519/qd.i4tk4lrk> (Creative Commons Zero v1.0 (CC0) CC0-1.0). For more information: email data@nhm.ac.uk, or <https://registry.nbnatlas.org/public/show/dr2677>
- Highland Biological Recording Group ([Year downloaded: 2026]). HBRG Insects Dataset Vol 2. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY)). For more information:
<https://registry.nbnatlas.org/public/show/dr2730>
- Commissioned surveys and staff surveys and reports for Scottish Wildlife Trust reserves - Unassessed data, SWT (2020) (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr793>
- Records provided by UK Pollinator Monitoring Scheme, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information:
<https://registry.nbnatlas.org/public/show/dp296>
- Records provided by East Ayrshire Countryside Ranger Service, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: <https://registry.nbnatlas.org/public/show/dp175>
- Records provided by North Ayrshire Countryside Ranger Service, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: <https://registry.nbnatlas.org/public/show/dp153>

Hoverfly data contributed by the following providers:

- Records provided by Royal Horticultural Society, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email membership@rhs.org.uk, or <https://registry.nbnatlas.org/public/show/dp56>

- Records provided by Biological Records Centre, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email brc@ceh.ac.uk, or <https://registry.nbnatlas.org/public/show/dp77>
- Biological Records Centre. ([Year downloaded: 2026]) Hoverfly records verified via iRecord. (Creative Commons with Attribution 4.0 (CC-BY) CC BY Creative Commons Attribution). For more information: <https://registry.nbnatlas.org/public/show/dr3370>
- Glasgow Museums Biological Records Centre: Diptera: Syrphidae (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) Glasgow Life). For more information: <https://registry.nbnatlas.org/public/show/dr3352>
- The Conservation Volunteers Scotland ([Year downloaded: 2026]). BTCV wildlife counts recording workshops. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email j.mcfarlane@btcv.org.uk, or <https://registry.nbnatlas.org/public/show/dr1194>
- West Lothian Council ([Year downloaded: 2026]). Local Biodiversity Site Surveys. Occurrence dataset on the NBN Atlas (Open Government Licence (OGL) It is acknowledged that this data has been supplied by West Lothian Council through the NBN Atlas). For more information: <https://registry.nbnatlas.org/public/show/dr2683>
- Records provided by Natural Resources Wales, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email opendata@cyfoethnaturiolcymru.gov.uk, or <https://registry.nbnatlas.org/public/show/dp122>
- Records provided by Natural History Museum, London, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: <https://registry.nbnatlas.org/public/show/dp266>
- Dipterists Forum ([Year downloaded: 2026]). Dipterists Forum: Field Week 2019 (Stirling). Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY)). For more information: <https://registry.nbnatlas.org/public/show/dr2642>
- Natural Resources Wales. ([Year downloaded: 2026]) Welsh Invertebrate Database (WID). Occurrence dataset accessed through the NBNAtlas (Open Government Licence (OGL) © CNC/NRW Data may be re-used under the terms of the Open Government Licence providing it is done so, acknowledging both the source and NRW's copyright. It is the recipient's responsibility to ensure the data is fit for the intended purpose. Attribution statement: Contains Natural Resources Wales information © Natural Resources Wales and Database Right. All rights Reserved.). For more information: <https://registry.nbnatlas.org/public/show/dr1212>

- Records provided by The Conservation Volunteers Scotland, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email citizenscience-scotland@tcv.org.uk, or <https://registry.nbnatlas.org/public/show/dp145>
- The Wildlife Information Centre ([Year downloaded: 2026]). A.T. Sumner's Records. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY)). For more information: <https://registry.nbnatlas.org/public/show/dr2785>
- Cumbria Biodiversity Data Centre ([Year downloaded: 2026]). Tullie House Museum Natural History Collections. Occurrence dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC). For more information: email nature@tulliehouse.co.uk, or <https://registry.nbnatlas.org/public/show/dr1311>
- UK Pollinator Monitoring Scheme. ([Year downloaded: 2026]). Bee and hoverfly species data from the UK Pollinator Monitoring Scheme. (Open Government Licence (OGL) OGL Open Government Licence). For more information: <https://registry.nbnatlas.org/public/show/dr3654>
- Records provided by iSpot, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: <https://registry.nbnatlas.org/public/show/dp267>
- Scottish Wildlife Trust ([Year downloaded: 2026]). Casual records for Scottish Wildlife Trust reserves - Unassessed data. Occurrence dataset on the NBN Atlas. (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr763>
- Records provided by Cumbria Biodiversity Data Centre, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email info@cbdc.org.uk, or <https://registry.nbnatlas.org/public/show/dp102>
- Scottish Wildlife Trust ([Year downloaded: 2026]). Casual records for Scottish Wildlife Trust reserves - Verified data. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr780>
- iSpot ([Year downloaded: 2026]). iSpot British Isles observations. Occurrence dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC)). For more information: <https://registry.nbnatlas.org/public/show/dr2701>
- Royal Horticultural Society ([Year downloaded: 2026]). Records from the RHS insect reference collection. Dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC).

For more information: email andrewsalisbury@rhs.org.uk, or <https://registry.nbnatlas.org/public/show/dr309>

- Scottish Wildlife Trust ([Year downloaded: 2026]). Survey and monitoring records for Scottish Wildlife Trust reserves from reserve convenors and Trust volunteers - Verified data. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr766>
- Scottish Wildlife Trust ([Year downloaded: 2026]). Commissioned surveys and staff surveys and reports for Scottish Wildlife Trust reserves - Verified data. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr765>
- The Wildlife Information Centre ([Year downloaded: 2026]). TWIC Biodiversity Field Trip Data (1995-present). Occurrence dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC). For more information: email admin@wildlifeinformation.co.uk, or <https://registry.nbnatlas.org/public/show/dr922>
- Highland Biological Recording Group ([Year downloaded: 2026]). HBRG Insects Dataset Vol 1. Occurrence dataset accessed through the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email records@hbrg.org.uk, or <https://registry.nbnatlas.org/public/show/dr965>
- Scottish Wildlife Trust ([Year downloaded: 2026]). Survey and monitoring records for Scottish Wildlife Trust reserves from reserve convenors and Trust volunteers - Unassessed data. Occurrence dataset on the NBN Atlas (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr767>
- Records provided by Buglife, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email scotland@buglife.org.uk, or <https://registry.nbnatlas.org/public/show/dp1>
- Records provided by The Wildlife Information Centre, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email info@wildlifeinformation.co.uk, or <https://registry.nbnatlas.org/public/show/dp43>
- Records provided by Scottish Wildlife Trust, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email

kedata@scottishwildlifetrust.org.uk, or
<https://registry.nbnatlas.org/public/show/dp2>

- TWIC Site Surveys (2010 - present) (2020) (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC)). For more information: <https://registry.nbnatlas.org/public/show/dr2010>
- Records provided by Caledonian Conservation, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email info@caledonianconservation.co.uk, or <https://registry.nbnatlas.org/public/show/dp4>
- Records provided by Highland Biological Recording Group, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: email chair@hbrg.org.uk, or <https://registry.nbnatlas.org/public/show/dp7>
- North Ayrshire Countryside Ranger Service ([Year downloaded: 2026]). Species within North Ayrshire from 1984 - Present. Occurrence dataset on the NBN Atlas (Open Government Licence (OGL) OGL). For more information: email rangerservice@north-ayrshire.gov.uk, or <https://registry.nbnatlas.org/public/show/dr1160>
- Records provided by Glasgow Museums Biological Records Centre, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: <https://registry.nbnatlas.org/public/show/dp160>
- Buglife ([Year downloaded: 2026]). Invertebrate records from sites that are mainly across Scotland. Occurrence record dataset on the NBN Atlas (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC) CC-BY-NC). For more information: <https://registry.nbnatlas.org/public/show/dr1363>
- Lothian Wildlife Information Centre surveys (Invertebrates - general), TWIC (2020) (Creative Commons, with Attribution, Non-commercial v4.0 (CC-BY-NC)). For more information: <https://registry.nbnatlas.org/public/show/dr2199>
- Natural History Museum (2023). Data Portal query on 1 resources <https://doi.org/10.5519/qd.i4tk4lrk> (Creative Commons Zero v1.0 (CC0) CC0-1.0). For more information: email data@nhm.ac.uk, or <https://registry.nbnatlas.org/public/show/dr2677>
- Caledonian Conservation ([Year downloaded: 2026]). SNH Invertebrate Site Condition Monitoring of Invertebrate Assemblages at ten SSSIs, 2011-12. Occurrence dataset on the NBN Atlas (Open Government Licence (OGL) CC-BY). For more information: email chris.cathrine@caledonianconservation.co.uk, or <https://registry.nbnatlas.org/public/show/dr1325>

- Records provided by Dipterists Forum, accessed through NBN Atlas website. (). For more information: email showersjohn@gmail.com, or <https://registry.nbnatlas.org/public/show/dp172>
- Commissioned surveys and staff surveys and reports for Scottish Wildlife Trust reserves - Unassessed data, SWT (2020) (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: email kedata@scottishwildlifetrust.org.uk, or <https://registry.nbnatlas.org/public/show/dr793>
- Records provided by UK Pollinator Monitoring Scheme, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: <https://registry.nbnatlas.org/public/show/dp296>
- Records provided by North Ayrshire Countryside Ranger Service, accessed through NBN Atlas website. ([Year downloaded: 2026]). For more information: <https://registry.nbnatlas.org/public/show/dp153>
- Highland Biological Recording Group ([Year downloaded: 2026]). HBRG P.F. Entwistle Colln and Notebooks Dataset (Creative Commons with Attribution 4.0 (CC-BY) CC-BY). For more information: <https://registry.nbnatlas.org/public/show/dr875>

S.2- Urban species list

Table E.1: A species list of bees and hoverflies recorded in our 17 sample sites across the six-month sampling period. Abundance of each species is shown, as well as the synonyms used in the open tree of life database (Hinchliff et al., 2015) and from the open database on traits and phylogenetic data of European pollinators (Michez et al., 2023).

Species	Synonym	Group	Abundance
<i>Apis mellifera</i>		Bees	660
<i>Andrena bicolor</i>		Bees	25
<i>Andrena denticulata</i>		Bees	6
<i>Andrena haemorrhoa</i>		Bees	6
<i>Andrena scotica</i>	<i>Andrena carantonica</i>	Bees	9
<i>Andrena subopaca</i>		Bees	3
<i>Anthophora furcata</i>		Bees	12
<i>Anthophora plumipes</i>		Bees	18
<i>Bombus hortorum</i>		Bees	95
<i>Bombus hypnorum</i>		Bees	356
<i>Bombus lapidarius</i>		Bees	101
<i>Bombus lucorum</i>		Bees	920
<i>Bombus pascuorum</i>		Bees	1681
<i>Bombus pratorum</i>		Bees	415

<i>Bombus sylvestris</i>		Bees	7
<i>Colletes daviesanus</i>		Bees	63
<i>Halictus rubicundus</i>		Bees	5
<i>Hylaeus communis</i>		Bees	2
<i>Hylaeus hyalinatus</i>		Bees	26
<i>Lasioglossum albipes</i>		Bees	3
<i>Lasioglossum calceatum</i>		Bees	9
<i>Lasioglossum cupromicans</i>		Bees	2
<i>Lasioglossum fratellum</i>		Bees	7
<i>Lasioglossum smeathmanellum</i>		Bees	81
<i>Osmia bicornis</i>		Bees	47
<i>Osmia caerulescens</i>		Bees	3
<i>Megachile centuncularis</i>		Bees	41
<i>Megachile willughbiella</i>		Bees	7
<i>Sphecodes geoffrellus</i>		Bees	2
<i>Baccha elongata</i>		Hoverflies	13
<i>Cheilosia albitarsis</i>		Hoverflies	1
<i>Cheilosia bergenstammi</i>		Hoverflies	8
<i>Cheilosia illustrata</i>		Hoverflies	1
<i>Cheilosia latifrons</i>		Hoverflies	1
<i>Cheilosia proxima</i>		Hoverflies	2
<i>Cheilosia vernalis</i>		Hoverflies	3
<i>Chrysogaster solstitialis</i>		Hoverflies	3
<i>Chrysotoxum festivum</i>		Hoverflies	1
<i>Dasysyrphus albostrigatus</i>		Hoverflies	8
<i>Dasysyrphus tricinctus</i>		Hoverflies	2
<i>Dasysyrphus venustus</i>		Hoverflies	2
<i>Didea fasciata</i>		Hoverflies	2
<i>Epistrophe eligans</i>		Hoverflies	16
<i>Epistrophe grossulariae</i>		Hoverflies	39
<i>Episyrphus balteatus</i>		Hoverflies	214
<i>Eristalis pertinax</i>		Hoverflies	339
<i>Eristalis arbustorum</i>		Hoverflies	25
<i>Eristalis horticola</i>		Hoverflies	4
<i>Eristalis intricaria</i>		Hoverflies	12
<i>Eristalis nemorum</i>		Hoverflies	5

<i>Eristalis tenax</i>		Hoverflies	61
<i>Eumerus funeralis</i>		Hoverflies	2
<i>Eupeodes bucculatus</i>		Hoverflies	1
<i>Eupeodes corollae</i>		Hoverflies	38
<i>Eupeodes latifasciatus</i>		Hoverflies	9
<i>Eupeodes luniger</i>		Hoverflies	26
<i>Ferdinandea cuprea</i>		Hoverflies	2
<i>Helophilus pendulus</i>		Hoverflies	78
<i>Leucozona glaucia</i>		Hoverflies	3
<i>Merodon equestris</i>		Hoverflies	32
<i>Melangyna lasiophthalma</i>		Hoverflies	1
<i>Melanostoma mellinum</i>		Hoverflies	9
<i>Melanostoma scalare</i>		Hoverflies	231
<i>Meliscaeva auricollis</i>		Hoverflies	61
<i>Meliscaeva cinctella</i>		Hoverflies	18
<i>Mallota florea</i>		Hoverflies	51
<i>Neoascia podagrica</i>		Hoverflies	61
<i>Neoascia tenur</i>		Hoverflies	4
<i>Parasyrphus punctulatus</i>		Hoverflies	1
<i>Pipizella viduata</i>		Hoverflies	1
<i>Platycheirus albimanus</i>		Hoverflies	335
<i>Platycheirus scutatus</i>		Hoverflies	8
<i>Scaeva pyrastris</i>		Hoverflies	17
<i>Sericomyia silentis</i>		Hoverflies	1
<i>Sphaerophoria scripta</i>		Hoverflies	37
<i>Syritta pipiens</i>		Hoverflies	232
<i>Syrphus ribesii</i>		Hoverflies	190
<i>Syrphus torvus</i>		Hoverflies	7
<i>Syrphus vitripennis</i>		Hoverflies	51
<i>Volucella bombylans</i>		Hoverflies	1
<i>Volucella pellucens</i>		Hoverflies	5
<i>Xylota segnis</i>		Hoverflies	3

S.3- NBN Atlas urban species

Table E.2: Urban pollinator species collated from the NBN Atlas from records within Glasgow city council and the 5km buffer surrounding the council boundary. The table shows pollinator species and their corresponding traits. Body size (continuous or -1=small, 0=medium, 1=large), Phenology star coded as an ordinal factor relating to the month a species is first

active. Polylectic, Oligolectic, Parasitice, above ground and below ground are all code as 1=yes, 0=no.

Pollinator	Body size	Phenology start	Polylectic	Oligolectic	Above ground	Below ground	Cleptoparas
<i>Andrena barbilabris</i>	2.32	3	1	0	0	1	0
<i>Andrena bicolor</i>	2.01	3	1	0	0	1	0
<i>Andrena carantonica</i>	2.86	3	1	0	0	1	0
<i>Andrena clarkella</i>	2.97	3	0	1	0	1	0
<i>Andrena denticulata</i>	2.86	3	1	0	0	1	0
<i>Andrena fulva</i>	2.72	3	1	0	0	1	0
<i>Andrena haemorrhoa</i>	2.49	3	1	0	0	1	0
<i>Andrena lapponica</i>	2.54	4	1	0	0	1	0
<i>Andrena ruficrus</i>	2.07	3	0	1	0	1	0
<i>Apis mellifera</i>	3.01	1	1	0	1	0	0
<i>Bombus bohemicus</i>	4.86	1	0	0	0	0	1
<i>Bombus campestris</i>	4.66	1	0	0	0	0	1
<i>Bombus hortorum</i>	4.54	1	1	0	1	0	0
<i>Bombus hypnorum</i>	4.07	1	1	0	1	0	0
<i>Bombus jonellus</i>	5.07	1	1	0	1	0	0
<i>Bombus lapidarius</i>	4.28	1	1	0	0	1	0
<i>Bombus lucorum</i>	4.28	1	1	0	0	1	0
<i>Bombus monticola</i>	4.03	1	1	0	0	1	0
<i>Bombus pascuorum</i>	3.91	1	1	0	1	0	0
<i>Bombus pratorum</i>	4.03	1	1	0	1	0	0
<i>Bombus sylvestris</i>	4.33	1	1	0	0	0	1
<i>Colletes daviesanus</i>	2.41	6	0	1	0	1	0
<i>Halictus rubicundus</i>	2.1	1	1	0	0	1	0
<i>Lasioglossum albipes</i>	1.59	1	1	0	0	1	0
<i>Lasioglossum calceatum</i>	1.77	1	1	0	0	1	0
<i>Megachile centuncularis</i>	2.72	5	1	0	0	1	0
<i>Megachile willughbiella</i>	3.41	4	1	0	0	1	0
<i>Nomada leucophthalma</i>	1.76	3	0	0	0	0	1
<i>Nomada marshamella</i>	2.23	3	0	0	0	0	1
<i>Nomada ruficornis</i>	1.79	4	0	0	0	0	1

<i>Osmia bicornis</i>	3.08	3	1	0	0	1	0
<i>Baccha elongata</i>	0	2					
<i>Cheilosia albitarsis</i>	0	2					
<i>Cheilosia bergenstammi</i>	0	2					
<i>Cheilosia illustrata</i>	0	2					
<i>Cheilosia pagana</i>	-1	2					
<i>Cheilosia variabilis</i>	0	2					
<i>Chrysogaster solstitialis</i>	0	2					
<i>Chrysotoxum bicinctum</i>	0	3					
<i>Chrysotoxum festivum</i>	0	2					
<i>Dasysyrphus albostrigatus</i>	0	2					
<i>Dasysyrphus tricinctus</i>	0	2					
<i>Dasysyrphus venustus</i>	0	2					
<i>Didea fasciata</i>	1	2					
<i>Epistrophe eligans</i>	0	1					
<i>Epistrophe grossulariae</i>	1	2					
<i>Episyrphus balteatus</i>	0	1					
<i>Eristalis arbustorum</i>	0	2					
<i>Eristalis horticola</i>	1	3					
<i>Eristalis intricaria</i>	1	2					
<i>Eristalis nemorum</i>	1	2					
<i>Eristalis pertinax</i>	0	1					
<i>Eristalis similis</i>	1	1					
<i>Eristalis tenax</i>	1	1					
<i>Eupeodes corollae</i>	-1	2					
<i>Eupeodes latifasciatus</i>	-1	2					
<i>Eupeodes luniger</i>	0	2					
<i>Helophilus pendulus</i>	0	2					
<i>Helophilus trivittatus</i>	1	2					
<i>Lejogaster metallina</i>	-1	2					
<i>Leucozona glauca</i>	1	2					
<i>Leucozona laternaria</i>	0	3					
<i>Leucozona lucorum</i>	1	3					
<i>Melanostoma mellinum</i>	-1	2					

<i>Melanostoma scalare</i>	0	1					
<i>Meliscaeva auricollis</i>	0	1					
<i>Meliscaeva cinctella</i>	0	2					
<i>Merodon equestris</i>	1	2					
<i>Myathropa florea</i>	1	2					
<i>Parasyrphus punctulatus</i>	-1	2					
<i>Platycheirus albimanus</i>	0	2					
<i>Platycheirus clypeatus agg.</i>	0	2					
<i>Platycheirus granditarsus</i>	0	2					
<i>Platycheirus manicatus</i>	0	2					
<i>Platycheirus rosarum</i>	0	2					
<i>Platycheirus scutatus</i>	0	2					
<i>Portevinia maculata</i>	0	2					
<i>Rhingia campestris</i>	0	2					
<i>Scaeva pyrastris</i>	1	1					
<i>Sericomyia lappona</i>	1	2					
<i>Sericomyia silentis</i>	1	2					
<i>Sericomyia superbiens</i>	1	4					
<i>Sphaerophoria philanthus</i>	0	2					
<i>Sphaerophoria scripta</i>	0	2					
<i>Syrirta pipiens</i>	0	1					
<i>Syrphus ribesii</i>	1	2					
<i>Syrphus torvus</i>	1	1					
<i>Syrphus vitripennis</i>	0	2					
<i>Volucella bombylans</i>	1	2					
<i>Volucella pellucens</i>	1	2					
<i>Xylota segnis</i>	1	2					
<i>Xylota sylvarum</i>	1	2					

S.4- HMSC model comparisons

Table E.3: Model WAIC scores, for bee and hoverfly HMSC models, with environmental variable removed from each model.

Community	Model	WAIC
Hoverflies	Floral richness+ Floral abundance+ Green space size+ Surrounding green space+ Site type+ % abundance native + % richness native + Month	7.94
Hoverflies	Floral richness+ Floral abundance+ Green space size+ Surrounding green space+ Site type+ % abundance native + Month	7.93
Hoverflies	Floral richness+ Floral abundance+ Green space size+ Surrounding green space+ Site type + Month	7.92
Hoverflies	Floral richness+ Floral abundance+ Green space size+ Surrounding green space + Month	7.92
Hoverflies	Floral richness+ Floral abundance+ Green space size + Month	7.93
Hoverflies	Floral richness+ Floral abundance + Month	7.94
Hoverflies	Floral richness + Month	7.93
Hoverflies	Month	8.03
Bees	Floral richness+ Floral abundance+ Green space size+ Surrounding green space+ Site type+ % abundance native + % richness native + Month	5.47
Bees	Floral richness+ Floral abundance+ Green space size+ Surrounding green space+ Site type+ % abundance native + Month	5.15
Bees	Floral richness+ Floral abundance+ Green space	5.48

	size+ Surrounding green space+ Site type + Month	
Bees	Floral richness+ Floral abundance+ Green space size+ Site type + Month	5.47
Bees	Floral richness+ Floral abundance+ Month	5.47
Bees	Floral richness+ Floral abundance + Month	5.47
Bees	Floral richness + Month	5.49
Bees	Month	5.79

S.5- Regional species list

Table E.4: Regional species list for bees and hoverflies, as the result of co-occurrence analysis in a 30km buffer around our core study area. Species synonyms used in the trait database are also noted.

Species	Synonym	Group
<i>Andrena barbilabris</i>		Bees
<i>Andrena bicolor</i>		Bees
<i>Andrena chrysosceles</i>		Bees
<i>Andrena cineraria</i>		Bees
<i>Andrena clarkella</i>		Bees
<i>Andrena coitana</i>		Bees
<i>Andrena denticulata</i>		Bees
<i>Andrena fulva</i>		Bees
<i>Andrena haemorrhoa</i>		Bees
<i>Andrena helvola</i>		Bees
<i>Andrena lapponica</i>		Bees
<i>Andrena ruficrus</i>		Bees
<i>Andrena scotica</i>		Bees
<i>Andrena tarsata</i>		Bees
<i>Anthophora furcata</i>		Bees
<i>Anthophora plumipes</i>		Bees
<i>Apis mellifera</i>		Bees
<i>Bombus barbutellus</i>		Bees
<i>Bombus bohemicus</i>		Bees
<i>Bombus campestris</i>		Bees

<i>Bombus hortorum</i>		Bees
<i>Bombus hypnorum</i>		Bees
<i>Bombus jonellus</i>		Bees
<i>Bombus lapidarius</i>		Bees
<i>Bombus lucorum</i>		Bees
<i>Bombus monticola</i>		Bees
<i>Bombus pascuorum</i>		Bees
<i>Bombus pratorum</i>		Bees
<i>Bombus soroeensis</i>		Bees
<i>Bombus sylvestris</i>		Bees
<i>Bombus vestalis</i>		Bees
<i>Colletes daviesanus</i>		Bees
<i>Colletes succinctus</i>		Bees
<i>Halictus rubicundus</i>		Bees
<i>Hylaeus hyalinatus</i>		Bees
<i>Lasioglossum albipes</i>		Bees
<i>Lasioglossum calceatum</i>		Bees
<i>Lasioglossum fratellum</i>		Bees
<i>Lasioglossum villosulum</i>		Bees
<i>Megachile centuncularis</i>		Bees
<i>Megachile versicolor</i>		Bees
<i>Megachile willughbiella</i>		Bees
<i>Nomada flavoguttata</i>		Bees
<i>Nomada leucophthalma</i>		Bees
<i>Nomada marshamella</i>		Bees
<i>Nomada panzeri</i>		Bees
<i>Osmia bicornis</i>		Bees
<i>Sphecodes geoffrellus</i>		Bees
<i>Sphecodes monilicornis</i>		Bees
<i>Anasimyia lineata</i>	<i>Eurimyia lineata</i>	Hoverflies
<i>Baccha elongata</i>		Hoverflies
<i>Chalcosyrphus nemorum</i>		Hoverflies
<i>Cheilosia albipila</i>		Hoverflies
<i>Cheilosia albitarsis</i>		Hoverflies

<i>Cheilosia bergenstammi</i>		Hoverflies
<i>Cheilosia fraterna</i>		Hoverflies
<i>Cheilosia grossa</i>		Hoverflies
<i>Cheilosia illustrata</i>		Hoverflies
<i>Cheilosia impressa</i>		Hoverflies
<i>Cheilosia lasiopa</i>		Hoverflies
<i>Cheilosia pagana</i>	<i>Cheilosia paganus</i>	Hoverflies
<i>Cheilosia proxima</i>		Hoverflies
<i>Cheilosia variabilis</i>		Hoverflies
<i>Chrysogaster solstitialis</i>		Hoverflies
<i>Chrysotoxum arcuatum</i>		Hoverflies
<i>Chrysotoxum bicinctum</i>		Hoverflies
<i>Chrysotoxum cautum</i>		Hoverflies
<i>Chrysotoxum festivum</i>		Hoverflies
<i>Criorhina floccosa</i>		Hoverflies
<i>Dasysyrphus albostratus</i>		Hoverflies
<i>Dasysyrphus venustus</i>		Hoverflies
<i>Epistrophe eligans</i>		Hoverflies
<i>Epistrophe grossulariae</i>		Hoverflies
<i>Episyrphus balteatus</i>		Hoverflies
<i>Eriozona syrphoides</i>		Hoverflies
<i>Eristalinus sepulchralis</i>		Hoverflies
<i>Eristalis abusiva</i>		Hoverflies
<i>Eristalis arbustorum</i>		Hoverflies
<i>Eristalis horticola</i>		Hoverflies
<i>Eristalis intricaria</i>		Hoverflies
<i>Eristalis nemorum</i>		Hoverflies
<i>Eristalis pertinax</i>		Hoverflies
<i>Eristalis rupium</i>		Hoverflies
<i>Eristalis tenax</i>		Hoverflies
<i>Eupeodes corollae</i>		Hoverflies
<i>Eupeodes latifasciatus</i>		Hoverflies
<i>Eupeodes luniger</i>		Hoverflies
<i>Ferdinandea cuprea</i>		Hoverflies

<i>Helophilus pendulus</i>		Hoverflies
<i>Helophilus trivittatus</i>		Hoverflies
<i>Leucozona glaucia</i>		Hoverflies
<i>Leucozona laternaria</i>		Hoverflies
<i>Leucozona lucorum</i>		Hoverflies
<i>Melangyna cincta</i>	<i>Fagisyrphus cinctus</i>	Hoverflies
<i>Melangyna compositarum</i>		Hoverflies
<i>Melangyna compositarum/labiatarum</i>		Hoverflies
<i>Melangyna labiatarum</i>		Hoverflies
<i>Melangyna lasiophthalma</i>		Hoverflies
<i>Melangyna umbellatarum</i>		Hoverflies
<i>Melanogaster hirtella</i>		Hoverflies
<i>Melanostoma mellinum</i>		Hoverflies
<i>Melanostoma scalare</i>		Hoverflies
<i>Meliscaeva auricollis</i>		Hoverflies
<i>Meliscaeva cinctella</i>		Hoverflies
<i>Merodon equestris</i>		Hoverflies
<i>Myathropa florea</i>		Hoverflies
<i>Neoascia geniculata</i>		Hoverflies
<i>Neoascia meticulosa</i>		Hoverflies
<i>Neoascia podagrica</i>		Hoverflies
<i>Neoascia tenur</i>		Hoverflies
<i>Orthonevra nobilis</i>		Hoverflies
<i>Parasyrphus punctulatus</i>		Hoverflies
<i>Parhelophilus versicolor</i>		Hoverflies
<i>Pipiza luteitarsis</i>		Hoverflies
<i>Pipiza noctiluca</i>		Hoverflies
<i>Platycheirus albimanus</i>		Hoverflies
<i>Platycheirus ambiguus</i>		Hoverflies
<i>Platycheirus angustatus</i>		Hoverflies
<i>Platycheirus clypeatus</i>		Hoverflies
<i>Platycheirus europaeus</i>		Hoverflies
<i>Platycheirus fulviventris</i>		Hoverflies

<i>Platycheirus granditarsus</i>	<i>Pyrophaena granditarsa</i>	Hoverflies
<i>Platycheirus manicatus</i>		Hoverflies
<i>Platycheirus peltatus</i> agg.		Hoverflies
<i>Platycheirus ramsarensis</i>		Hoverflies
<i>Platycheirus rosarum</i>	<i>Pyrophaena rosarum</i>	Hoverflies
<i>Platycheirus scambus</i>		Hoverflies
<i>Platycheirus scutatus</i>		Hoverflies
<i>Rhingia campestris</i>		Hoverflies
<i>Riponnensia splendens</i>		Hoverflies
<i>Scaeva pyrastris</i>		Hoverflies
<i>Sericomyia lappona</i>		Hoverflies
<i>Sericomyia silentis</i>		Hoverflies
<i>Sericomyia superbiens</i>		Hoverflies
<i>Sphaerophoria</i>		Hoverflies
<i>Sphaerophoria interrupta</i>		Hoverflies
<i>Sphegina clunipes</i>		Hoverflies
<i>Sphegina sibirica</i>		Hoverflies
<i>Syritta pipiens</i>		Hoverflies
<i>Syrphus ribesii</i>		Hoverflies
<i>Syrphus torvus</i>		Hoverflies
<i>Syrphus vitripennis</i>		Hoverflies
<i>Trichopsomyia flavitarsis</i>		Hoverflies
<i>Volucella bombylans</i>		Hoverflies
<i>Volucella pellucens</i>		Hoverflies
<i>Xylota segnis</i>		Hoverflies
<i>Xylota sylvarum</i>		Hoverflies

List of References

- Abrego, N., Ovaskainen, O. (Eds.), 2020. Introduction to Community Ecology: Theory and Methods, in: Joint Species Distribution Modelling: With Applications in R, Ecology, Biodiversity and Conservation. Cambridge University Press, Cambridge, pp. 1–50. <https://doi.org/10.1017/9781108591720.002>
- Aizen, M.A., Morales, C.L., Morales, J.M., 2008. Invasive Mutualists Erode Native Pollination Webs. *PLOS Biol.* 6, e31. <https://doi.org/10.1371/journal.pbio.0060031>
- Aizen, M.A., Sabatino, M., Tylianakis, J.M., 2012. Specialization and Rarity Predict Nonrandom Loss of Interactions from Mutualist Networks. *Science* 335, 1486–1489. <https://doi.org/10.1126/science.1215320>
- Albrecht, M., Schmid, B., Hautier, Y., Müller, C.B., 2012. Diverse pollinator communities enhance plant reproductive success. *Proc. R. Soc. B Biol. Sci.* 279, 4845–4852. <https://doi.org/10.1098/rspb.2012.1621>
- Amado De Santis, A.A., Lomáscolo, S.B., Chacoff, N.P., 2023. Effects of urbanization on the structure of plant-flower visitor network at the local and landscape levels in the northern Argentinian Yungas forest. *Front. Sustain. Cities* 5. <https://doi.org/10.3389/frsc.2023.1086076>
- Ayers, A.C., Rehan, S.M., 2021. Supporting Bees in Cities: How Bees Are Influenced by Local and Landscape Features. *Insects* 12, 128. <https://doi.org/10.3390/insects12020128>
- Baldock, K.C., 2020. Opportunities and threats for pollinator conservation in global towns and cities. *Curr. Opin. Insect Sci., Ecology • Parasites/Parasitoids/Biological control* 38, 63–71. <https://doi.org/10.1016/j.cois.2020.01.006>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Morse, H., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Staniczenko, P.P.A., Stone, G.N., Vaughan, I.P., Memmott, J., 2019. A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nat. Ecol. Evol.* 3, 363–373. <https://doi.org/10.1038/s41559-018-0769-y>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P., Memmott, J., 2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proc. R. Soc. B Biol. Sci.* 282, 20142849. <https://doi.org/10.1098/rspb.2014.2849>
- Banaszak-Cibicka, W., Twerd, L., Fliszkiewicz, M., Giejdasz, K., Langowska, A., 2018. City parks vs. natural areas - is it possible to preserve a natural level of bee richness and abundance in a city park? *Urban Ecosyst.* 21, 599–613. <https://doi.org/10.1007/s11252-018-0756-8>
- Banaszak-Cibicka, W., Żmihorski, M., 2012. Wild bees along an urban gradient: winners and losers. *J. Insect Conserv.* 16, 331–343. <https://doi.org/10.1007/s10841-011-9419-2>
- Banerjee, P., Stewart, K.A., Antognazza, C.M., Bunholi, I.V., Deiner, K., Barnes, M.A., Saha, S., Verdier, H., Doi, H., Maity, J.P., Chan, M.W.Y., Chen, C.Y., 2022. Plant–animal interactions in the era of environmental DNA (eDNA)—A review. *Environ. DNA* 4, 987–999. <https://doi.org/10.1002/edn3.308>

- Barrett, M., Fischer, B., 2024. Ethical issues in lethal insect monitoring. *Curr. Opin. Insect Sci.* 66, 101279. <https://doi.org/10.1016/j.cois.2024.101279>
- Bascompte, J., Jordano, P., Melián, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci.* 100, 9383–9387. <https://doi.org/10.1073/pnas.1633576100>
- Bascompte, J., Scheffer, M., 2023. The Resilience of Plant–Pollinator Networks. *Annu. Rev. Entomol.* 68, 363–380. <https://doi.org/10.1146/annurev-ento-120120-102424>
- Basilio, A.M., Medan, D., Torretta, J.P., Bartoloni, N.J., 2006. A year-long plant-pollinator network. *Austral Ecol.* 31, 975–983. <https://doi.org/10.1111/j.1442-9993.2006.01666.x>
- Bates, A.J., Sadler, J.P., Fairbrass, A.J., Falk, S.J., Hale, J.D., Matthews, T.J., 2011. Changing Bee and Hoverfly Pollinator Assemblages along an Urban-Rural Gradient. *PLOS ONE* 6, e23459. <https://doi.org/10.1371/journal.pone.0023459>
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *J. Stat. Softw.* 67, 1–48. <https://doi.org/10.18637/jss.v067.i01>
- Bennett, A.B., Lovell, S., 2019. Landscape and local site variables differentially influence pollinators and pollination services in urban agricultural sites. *PLOS ONE* 14, e0212034. <https://doi.org/10.1371/journal.pone.0212034>
- Bersier, L.-F., Banašek-Richter, C., Cattin, M.-F., 2002. Quantitative Descriptors of Food-Web Matrices. *Ecology* 83, 2394–2407. [https://doi.org/10.1890/0012-9658\(2002\)083%5B2394:QDOFWM%5D2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083%5B2394:QDOFWM%5D2.0.CO;2)
- Biella, P., Tommasi, N., Guzzetti, L., Pioltelli, E., Labra, M., Galimberti, A., 2022. City climate and landscape structure shape pollinators, nectar and transported pollen along a gradient of urbanization. *J. Appl. Ecol.* 59, 1586–1595. <https://doi.org/10.1111/1365-2664.14168>
- Bille, R.A., Jensen, K.E., Buitenwerf, R., 2023. Global patterns in urban green space are strongly linked to human development and population density. *Urban For. Urban Green.* 86, 127980. <https://doi.org/10.1016/j.ufug.2023.127980>
- Birdshire, K.R., Carper, A.L., Briles, C.E., 2020. Bee community response to local and landscape factors along an urban-rural gradient. *Urban Ecosyst.* 23, 689–702. <https://doi.org/10.1007/s11252-020-00956-w>
- Blaauw, B.R., Isaacs, R., 2014. Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *J. Appl. Ecol.* 51, 890–898. <https://doi.org/10.1111/1365-2664.12257>
- Blareau, E., Gabard, C., Riva, C., Dajoz, I., Requier, F., 2025. Automated 24-h surveys of flower-visiting communities reveal temporal complementarities and overlaps among strawberry pollinators. *Glob. Ecol. Conserv.* 62, e03727. <https://doi.org/10.1016/j.gecco.2025.e03727>
- Blüthgen, N., Fründ, J., Vázquez, D.P., Menzel, F., 2008. What Do Interaction Network Metrics tell Us About Specialization and Biological Traits. *Ecology* 89, 3387–3399. <https://doi.org/10.1890/07-2121.1>
- Blüthgen, Nico, Menzel, F., Blüthgen, Nils, 2006. Measuring specialization in species interaction networks. *BMC Ecol.* 6, 9. <https://doi.org/10.1186/1472-6785-6-9>

- Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I., Öckinger, E., 2010. Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. B Biol. Sci.* 277, 2075–2082. <https://doi.org/10.1098/rspb.2009.2221>
- Bottero, I., Dominik, C., Schweiger, O., Albrecht, M., Attridge, E., Brown, M.J.F., Cini, E., Costa, C., De la Rúa, P., de Miranda, J.R., Di Prisco, G., Dzul Uuh, D., Hodge, S., Ivarsson, K., Knauer, A.C., Klein, A.-M., Mänd, M., Martínez-López, V., Medrzycki, P., Pereira-Peixoto, H., Potts, S., Raimets, R., Rundlöf, M., Schwarz, J.M., Senapathi, D., Tamburini, G., Talaván, E.T., Stout, J.C., 2023. Impact of landscape configuration and composition on pollinator communities across different European biogeographic regions. *Front. Ecol. Evol.* 11. <https://doi.org/10.3389/fevo.2023.1128228>
- Bozdogan, H., 1987. Model selection and Akaike's Information Criterion (AIC): The general theory and its analytical extensions. *Psychometrika* 52, 345–370. <https://doi.org/10.1007/BF02294361>
- Bracken, A.M., Nelli, L., Cao Pinna, L., Corbett, A., McLeod, R., Dominoni, D.M., McCafferty, D.J., 2026. Designing nature networks for cities: combining multi-species modelling approaches. *Landsc. Ecol.* 41, 56. <https://doi.org/10.1007/s10980-026-02315-0>
- Braman, S.K., Griffin, B., 2022. Opportunities for and Impediments to Pollinator Conservation in Urban Settings: A Review. *J. Integr. Pest Manag.* 13. <https://doi.org/10.1093/jipm/pmac004>
- Brasil, S.N.R., George, M., Rehan, S.M., 2024. Functional traits of wild bees in response to urbanization. *J. Insect Conserv.* 28, 127–139. <https://doi.org/10.1007/s10841-023-00528-1>
- Breeze, T.D., Bailey, A.P., Balcombe, K.G., Brereton, T., Comont, R., Edwards, M., Garratt, M.P., Harvey, M., Hawes, C., Isaac, N., Jitlal, M., Jones, C.M., Kunin, W.E., Lee, P., Morris, R.K.A., Musgrove, A., O'Connor, R.S., Peyton, J., Potts, S.G., Roberts, S.P.M., Roy, D.B., Roy, H.E., Tang, C.Q., Vanbergen, A.J., Carvell, C., 2021. Pollinator monitoring more than pays for itself. *J. Appl. Ecol.* 58, 44–57. <https://doi.org/10.1111/1365-2664.13755>
- Brooks, M., Kristensen, K., van Benthem, K., Magnusson, A., Berg, C., Nielsen, A., Skaug, H., Maechler, M., Bolker, B., 2017. glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. *R J.* 9, 378–400. <https://doi.org/doi:10.32614/RJ-2017-066>
- Brosi, B.J., Niezgodá, K., Briggs, H.M., 2017. Experimental species removals impact the architecture of pollination networks. *Biol. Lett.* 13, 20170243. <https://doi.org/10.1098/rsbl.2017.0243>
- 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. *Landsc. Urban Plan.* 196, 103731. <https://doi.org/10.1016/j.landurbplan.2019.103731>
- Burdine, J.D., McCluney, K.E., 2019a. Interactive effects of urbanization and local habitat characteristics influence bee communities and flower visitation rates. *Oecologia* 190, 715–723. <https://doi.org/10.1007/s00442-019-04416-x>
- Burdine, J.D., McCluney, K.E., 2019b. Differential sensitivity of bees to urbanization-driven changes in body temperature and water content. *Sci. Rep.* 9. <https://doi.org/10.1038/s41598-018-38338-0>

- Campbell, A.J., Wilby, A., Sutton, P., Wäckers, F.L., 2017. Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop? A case study from UK cider apple orchards. *Agric. Ecosyst. Environ.* 239, 20–29. <https://doi.org/10.1016/j.agee.2017.01.005>
- Chacoff, N.P., Vázquez, D.P., Lomáscolo, S.B., Stevani, E.L., Dorado, J., Padrón, B., 2012. Evaluating sampling completeness in a desert plant–pollinator network. *J. Anim. Ecol.* 81, 190–200. <https://doi.org/10.1111/j.1365-2656.2011.01883.x>
- Chapman, R.E., Bourke, A.F.G., 2001. The influence of sociality on the conservation biology of social insects. *Ecol. Lett.* 4, 650–662. <https://doi.org/10.1046/j.1461-0248.2001.00253.x>
- Chapman, S., Watson, J.E.M., Salazar, A., Thatcher, M., McAlpine, C.A., 2017. The impact of urbanization and climate change on urban temperatures: a systematic review. *Landsc. Ecol.* 32, 1921–1935. <https://doi.org/10.1007/s10980-017-0561-4>
- Chittka, L., Thomson, J.D., Waser, N.M., 1999. Flower Constancy, Insect Psychology, and Plant Evolution. *Naturwissenschaften* 86, 361–377. <https://doi.org/10.1007/s001140050636>
- Chrobock, T., Winiger, P., Fischer, M., van Kleunen, M., 2013. The cobblers stick to their lasts: pollinators prefer native over alien plant species in a multi-species experiment. *Biol. Invasions* 15, 2577–2588. <https://doi.org/10.1007/s10530-013-0474-3>
- Church, E.K., Wilson, K.A., Loder, J., Dean, A.J., 2025. From citizen science experiences to stewardship action: The importance of both nature and social experiences. *Mar. Policy* 173, 106537. <https://doi.org/10.1016/j.marpol.2024.106537>
- CitiesWithNature, 2024. Berlin Urban Nature Pact.
- CMS, 2020. Improving Ways of Addressing Connectivity in the Conservation of Migratory Species, Resolution 12.26 (REV.COP13), Gandhinagar, India. UNEP/CMS/COP13/CRP 26.4.4.
- Colom, P., Tejeda, A., Bonelli, S., Fontaine, B., Kuussaari, M., Maes, D., Mestdagh, X., Munguira, M.L., Musche, M., Pettersson, L.B., Roy, D., Rüdisser, J., Šašić, M., Schmucki, R., Stefanescu, C., Titeux, N., Settele, J., van Swaay, C., Gordillo, J., Melero, Y., 2026. The Interplay of Climate Change, Urbanisation, and Species Traits Shapes European Butterfly Population Trends. *Glob. Ecol. Biogeogr.* 35, e70204. <https://doi.org/10.1111/geb.70204>
- Connor, E.F., McCoy, E.D., 2013. *Species–Area Relationships*, 2nd ed. Academic Press.
- da Cunha-Silva, R.R., Barreto, E., Almeida-Neto, M., 2025. Urbanization influences the structure of plant–insect pollination networks through changes in pollinator species richness. *Arthropod-Plant Interact.* 19, 50. <https://doi.org/10.1007/s11829-025-10156-y>
- Daniels, B., Jedamski, J., Ottermanns, R., Ross-Nickoll, M., 2020. A “plan bee” for cities: Pollinator diversity and plant-pollinator interactions in urban green spaces. *PLOS ONE* 15, e0235492. <https://doi.org/10.1371/journal.pone.0235492>
- Deguines, N., Julliard, R., de Flores, M., Fontaine, C., 2016. Functional homogenization of flower visitor communities with urbanization. *Ecol. Evol.* 6, 1967–1976. <https://doi.org/10.1002/ece3.2009>

- Delisle, Z.J., Flaherty, E.A., Nobbe, M.R., Wzientek, C.M., Swihart, R.K., 2021. Next-Generation Camera Trapping: Systematic Review of Historic Trends Suggests Keys to Expanded Research Applications in Ecology and Conservation. *Front. Ecol. Evol.* 9. <https://doi.org/10.3389/fevo.2021.617996>
- Department for Environment, Food & Rural Affairs (Defra), 2014. The National Pollinator Strategy: For bees and other pollinators in England.
- Desaegher, J., Nadot, S., Dajoz, I., Colas, B., 2017. Buzz in Paris: flower production and plant–pollinator interactions in plants from contrasted urban and rural origins. *Genetica* 145, 513–523. <https://doi.org/10.1007/s10709-017-9993-7>
- Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W., Venail, P., Villéger, S., Mouquet, N., 2010. Defining and measuring ecological specialization. *J. Appl. Ecol.* 47, 15–25. <https://doi.org/10.1111/j.1365-2664.2009.01744.x>
- Díaz-Calafat, J., Jaume-Ramis, S., Soacha, K., Álvarez, A., Piera, J., 2024. Revealing biases in insect observations: A comparative analysis between academic and citizen science data. *PLOS ONE* 19, e0305757. <https://doi.org/10.1371/journal.pone.0305757>
- Dickinson, J.L., Shirk, J., Bonter, D., Bonney, R., Crain, R.L., Martin, J., Phillips, T., Purcell, K., 2012. The current state of citizen science as a tool for ecological research and public engagement. *Front. Ecol. Environ.* 10, 291–297. <https://doi.org/10.1890/110236>
- Dietzel, S., Rojas-Botero, S., Kollmann, J., Fischer, C., 2023. Enhanced urban roadside vegetation increases pollinator abundance whereas landscape characteristics drive pollination. *Ecol. Indic.* 147, 109980. <https://doi.org/10.1016/j.ecolind.2023.109980>
- Dorado, J., Vázquez, D.P., Stevani, E.L., Chacoff, N.P., 2011. Rareness and specialization in plant–pollinator networks. *Ecology* 92, 19–25. <https://doi.org/10.1890/10-0794.1>
- Dormann, C.F., 2011. How to be a specialist? Quantifying specialisation in pollination networks. *Netw. Biol.* 1, 1. <https://doi.org/10.0000/issn-2220-8879-networkbiology-2011-v1-0001>
- Dormann, C.F., Frund, J., Bluthgen, N., Gruber, B., 2009. Indices, Graphs and Null Models: Analyzing Bipartite Ecological Networks. *Open Ecol. J.* 2, 7–24. <https://doi.org/10.2174/1874213000902010007>
- Dormann, C.F., Fründ, J., Schaefer, H.M., 2017. Identifying Causes of Patterns in Ecological Networks: Opportunities and Limitations. *Annu. Rev. Ecol. Evol. Syst.* 48, 559–584. <https://doi.org/10.1146/annurev-ecolsys-110316-022928>
- Dormann, C.F., Gruber, B., Fründ, J., 2008. Introducing the bipartite Package: Analysing Ecological Networks 8.
- Drinkwater, E., Robinson, E.J.H., Hart, A.G., 2019. Keeping invertebrate research ethical in a landscape of shifting public opinion. *Methods Ecol. Evol.* 10, 1265–1273. <https://doi.org/10.1111/2041-210X.13208>
- Droissart, V., Azandi, L., Onguene, E.R., Savignac, M., Smith, T.B., Deblauwe, V., 2021. PICT: A low-cost, modular, open-source camera trap system to study plant–insect interactions. *Methods Ecol. Evol.* 12, 1389–1396. <https://doi.org/10.1111/2041-210X.13618>
- Dylewski, Ł., Maćkowiak, Ł., Banaszak-Cibicka, W., 2020. Linking pollinators and city flora: How vegetation composition and environmental features shapes pollinators

- composition in urban environment. *Urban For. Urban Green.* 56, 126795. <https://doi.org/10.1016/j.ufug.2020.126795>
- Dylewski, Ł., Maćkowiak, Ł., Banaszak-Cibicka, W., 2019. Are all urban green spaces a favourable habitat for pollinator communities? Bees, butterflies and hoverflies in different urban green areas. *Ecol. Entomol.* 44, 678–689. <https://doi.org/10.1111/een.12744>
- Ebeling, A., Klein, A.-M., Tschardtke, T., 2011. Plant–flower visitor interaction webs: Temporal stability and pollinator specialization increases along an experimental plant diversity gradient. *Basic Appl. Ecol.* 12, 300–309. <https://doi.org/10.1016/j.baae.2011.04.005>
- Eckhart, V., Rushing, N., Hart, G., Hansen, J., 2006. Frequency–dependent pollinator foraging in polymorphic *Clarkia xantiana* ssp. *xantiana* populations: implications for flower colour evolution and pollinator interactions. *Oikos* 112, 412–421. <https://doi.org/10.1111/j.0030-1299.2006.14289.x>
- Egerer, M., Cecala, J.M., Cohen, H., 2020. Wild Bee Conservation within Urban Gardens and Nurseries: Effects of Local and Landscape Management. *Sustainability* 12, 293. <https://doi.org/10.3390/su12010293>
- Eggenberger, H., Frey, D., Pellissier, L., Ghazoul, J., Fontana, S., Moretti, M., 2019. Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *J. Anim. Ecol.* 88, 1522–1533. <https://doi.org/10.1111/1365-2656.13051>
- Elle, E., Elwell, S.L., Gielens, G.A., 2012. The use of pollination networks in conservation. This article is part of a Special Issue entitled “Pollination biology research in Canada: Perspectives on a mutualism at different scales”. *Botany* 90, 525–534. <https://doi.org/10.1139/b11-111>
- Erickson, E., Adam, S., Russo, L., Wojcik, V., Patch, H.M., Grozinger, C.M., 2020. More Than Meets the Eye? The Role of Annual Ornamental Flowers in Supporting Pollinators. *Environ. Entomol.* 49, 178–188. <https://doi.org/10.1093/ee/nvz133>
- European Union, 2020. Mapping Guide v6.2 for a European Urban Atlas.
- Falk, S., Lewington, R., 2018. Field Guide to the Bees of Great Britain and Ireland (Bloomsbury Wildlife Guides). Bloomsbury Wildlife.
- Ferreira, P.A., Boscolo, D., Viana, B.F., 2013. What do we know about the effects of landscape changes on plant–pollinator interaction networks? *Ecol. Indic., Linking landscape structure and biodiversity* 31, 35–40. <https://doi.org/10.1016/j.ecolind.2012.07.025>
- Fischer, L.K., Eichfeld, J., Kowarik, I., Buchholz, S., 2016. Disentangling urban habitat and matrix effects on wild bee species. *PeerJ* 4, e2729. <https://doi.org/10.7717/peerj.2729>
- Fisogni, A., Hautekèete, N., Piquot, Y., Brun, M., Vanappelghem, C., Michez, D., Massol, F., 2020. Urbanization drives an early spring for plants but not for pollinators. *Oikos* 129, 1681–1691. <https://doi.org/10.1111/oik.07274>
- Fisogni, A., Hautekèete, N., Piquot, Y., Brun, M., Vanappelghem, C., Ohlmann, M., Franchomme, M., Hinnewinkel, C., Massol, F., 2022. Seasonal trajectories of plant–pollinator interaction networks differ following phenological mismatches along an

- urbanization gradient. *Landsc. Urban Plan.* 226, 104512. <https://doi.org/10.1016/j.landurbplan.2022.104512>
- Fortel, L., Henry, M., Guilbaud, L., Guirao, A.L., Kuhlmann, M., Mouret, H., Rollin, O., Vaissi re, B.E., 2014. Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. *PLoS ONE* 9, e104679. <https://doi.org/10.1371/journal.pone.0104679>
- Fournier, B., Frey, D., Moretti, M., 2020. The origin of urban communities: From the regional species pool to community assemblages in city. *J. Biogeogr.* 47, 615–629. <https://doi.org/10.1111/jbi.13772>
- Fowler, R.E., Rotheray, E.L., Goulson, D., 2016. Floral abundance and resource quality influence pollinator choice. *Insect Conserv. Divers.* 9, 481–494. <https://doi.org/10.1111/icad.12197>
- Fronhofer, E.A., Liebig, J., Mitesser, O., Poethke, H.J., 2018. Eusociality outcompetes egalitarian and solitary strategies when resources are limited and reproduction is costly. *Ecol. Evol.* 8, 12953–12964. <https://doi.org/10.1002/ece3.4737>
- Fukase, J., 2016. INCREASED POLLINATOR ACTIVITY IN URBAN GARDENS WITH MORE NATIVE FLORA. *Appl. Ecol. Environ. Res.* 14, 297–310. https://doi.org/10.15666/aeer/1401_297310
- Gallai, N., Garibaldi, L.A., Li, X., Breeze, T.D., Esp rito Santo, M.M., Rodriguez Fernandez, J., Kelbessa, E., Salles, J.M., Sandhu, H.S., Veldtman, R., 2016. Chapter 4: Economic valuation of pollinator gains and losses. In IPBES (2016): The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. S.G. Potts, V. L. Imperatriz-Fonseca, and H. T. Ngo (eds.). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany.
- Gao, Y., Xue, X., Qin, G., Li, K., Liu, J., Zhang, Y., Li, X., 2024. Application of machine learning in automatic image identification of insects - a review. *Ecol. Inform.* 80, 102539. <https://doi.org/10.1016/j.ecoinf.2024.102539>
- Garc a, Y., Gim enez-Benavides, L., Iriondo, J.M., Lara-Romero, C., M endez, M., Morente-L pez, J., Santamar a, S., 2024. Addition of nocturnal pollinators modifies the structure of pollination networks. *Sci. Rep.* 14, 1226. <https://doi.org/10.1038/s41598-023-49944-y>
- Gathof, A.K., Grossmann, A.J., Herrmann, J., Buchholz, S., 2022. Who can pass the urban filter? A multi-taxon approach to disentangle pollinator trait–environmental relationships. *Oecologia* 199, 165–179. <https://doi.org/10.1007/s00442-022-05174-z>
- Gentili, R., Quaglini, L.A., Galasso, G., Montagnani, C., Caronni, S., Cardarelli, E., Citterio, S., 2024. Urban refugia sheltering biodiversity across world cities. *Urban Ecosyst.* 27, 219–230. <https://doi.org/10.1007/s11252-023-01432-x>
- Gerner, E.E., Sargent, R.D., 2022. Local plant richness predicts bee abundance and diversity in a study of urban residential yards. *Basic Appl. Ecol.* 58, 64–73. <https://doi.org/10.1016/j.baae.2021.11.004>

- Geslin, B., Gauzens, B., Thébault, E., Dajoz, I., 2013. Plant Pollinator Networks along a Gradient of Urbanisation. *PLOS ONE* 8, e63421. <https://doi.org/10.1371/journal.pone.0063421>
- Geslin, B., Le Féon, V., Folschweiller, M., Flacher, F., Carmignac, D., Motard, E., Perret, S., Dajoz, I., 2016. The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. *Ecol. Evol.* 6, 6599–6615. <https://doi.org/10.1002/ece3.2374>
- Glasgow City Council, n.d. Allotments. URL <https://www.glasgow.gov.uk/allotments>
- Glasgow City Council, n.d. Glasgow Pollinator Plan 2017-2027.
- Glaum, P., Wood, T.J., Morris, J.R., Valdovinos, F.S., 2021. Phenology and flowering overlap drive specialisation in plant–pollinator networks. *Ecol. Lett.* 24, 2648–2659. <https://doi.org/10.1111/ele.13884>
- Gómez-Baggethun, E., Gren, Å., Barton, D.N., Langemeyer, J., McPhearson, T., O’Farrell, P., Andersson, E., Hamstead, Z., Kremer, P., 2013. Urban Ecosystem Services, in: Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P.J., McDonald, R.I., Parnell, S., Schewenius, M., Sendstad, M., Seto, K.C., Wilkinson, C. (Eds.), *Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities: A Global Assessment*. Springer Netherlands, Dordrecht, pp. 175–251. https://doi.org/10.1007/978-94-007-7088-1_11
- Gómez-Martínez, C., González-Estévez, M.A., Cursach, J., Lázaro, A., 2022. Pollinator richness, pollination networks, and diet adjustment along local and landscape gradients of resource diversity. *Ecol. Appl.* 32, e2634. <https://doi.org/10.1002/eap.2634>
- Gordon, S.C.C., Kerr, J.T., 2025. A comparative analysis of metacommunities reveals contrasting drivers of alpha and beta diversity in urban butterflies. *J. Urban Ecol.* 11, juaf006. <https://doi.org/10.1093/jue/juaf006>
- Graf, L.V., Meyer, F.S., Jeronimo, F.F., Gonçalves, R.B., 2024. Urbanization as a driver of changes in mutualistic networks between bees and plants. *Urban Ecosyst.* 28, 30. <https://doi.org/10.1007/s11252-024-01639-6>
- Graffigna, S., González-Vaquero, R.A., Torretta, J.P., Marrero, H.J., 2024. Importance of urban green areas’ connectivity for the conservation of pollinators. *Urban Ecosyst.* 27, 417–426. <https://doi.org/10.1007/s11252-023-01457-2>
- Grass, I., Jauker, B., Steffan-Dewenter, I., Tschardtke, T., Jauker, F., 2018. Past and potential future effects of habitat fragmentation on structure and stability of plant–pollinator and host–parasitoid networks. *Nat. Ecol. Evol.* 2, 1408–1417. <https://doi.org/10.1038/s41559-018-0631-2>
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee Foraging Ranges and Their Relationship to Body Size. *Oecologia* 153, 9.
- Griffiths-Lee, J., Nicholls, E., Goulson, D., 2022. Sown mini-meadows increase pollinator diversity in gardens. *J. Insect Conserv.* 26, 299–314. <https://doi.org/10.1007/s10841-022-00387-2>
- Griffiths-Lee, J., Nicholls, E., Goulson, D., 2020. Companion planting to attract pollinators increases the yield and quality of strawberry fruit in gardens and allotments. *Ecol. Entomol.* 45, 1025–1034. <https://doi.org/10.1111/een.12880>

- Grilli, J., Rogers, T., Allesina, S., 2016. Modularity and stability in ecological communities. *Nat. Commun.* 7, 12031. <https://doi.org/10.1038/ncomms12031>
- Grossmann, A.J., Herrmann, J., Buchholz, S., Gathof, A.K., 2023. Dry grassland within the urban matrix acts as favourable habitat for different pollinators including endangered species. *Insect Conserv. Divers.* 16, 97–109. <https://doi.org/10.1111/icad.12607>
- Guenat, S., Kunin, W.E., Dougill, A.J., Dallimer, M., 2019. Effects of urbanisation and management practices on pollinators in tropical Africa. *J. Appl. Ecol.* 56, 214–224. <https://doi.org/10.1111/1365-2664.13270>
- Haase, D., Gaeva, D., 2023. Allotments for all? Social–environmental values of urban gardens for gardeners and the public in cities: The example of Berlin, Germany. *People Nat.* 5, 1207–1219. <https://doi.org/10.1002/pan3.10488>
- Hahn, M., Brühl, C.A., 2016. The secret pollinators: an overview of moth pollination with a focus on Europe and North America. *Arthropod-Plant Interact.* 10, 21–28. <https://doi.org/10.1007/s11829-016-9414-3>
- Hamblin, A.L., Youngsteadt, E., Frank, S.D., 2018. Wild bee abundance declines with urban warming, regardless of floral density. *Urban Ecosyst.* 21, 419–428. <https://doi.org/10.1007/s11252-018-0731-4>
- Harrison, T., Gibbs, J., Winfree, R., 2018. Forest bees are replaced in agricultural and urban landscapes by native species with different phenologies and life-history traits. *Glob. Change Biol.* 24, 287–296. <https://doi.org/10.1111/gcb.13921>
- Harrison, T., Winfree, R., 2015. Urban drivers of plant-pollinator interactions. *Funct. Ecol.* 29, 879–888. <https://doi.org/10.1111/1365-2435.12486>
- Hartig, F., 2024. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models.
- Hegland, S.J., Dunne, J., Nielsen, A., Memmott, J., 2010. How to monitor ecological communities cost-efficiently: The example of plant–pollinator networks. *Biol. Conserv.* 143, 2092–2101. <https://doi.org/10.1016/j.biocon.2010.05.018>
- Herrmann, J., Buchholz, S., Theodorou, P., 2023. The degree of urbanisation reduces wild bee and butterfly diversity and alters the patterns of flower-visitation in urban dry grasslands. *Sci. Rep.* 13, 2702. <https://doi.org/10.1038/s41598-023-29275-8>
- Hicks, D.M., Ouvrard, P., Baldock, K.C.R., Baude, M., Goddard, M.A., Kunin, W.E., Mitschunas, N., Memmott, J., Morse, H., Nikolitsi, M., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Sinclair, F., Westbury, D.B., Stone, G.N., 2016. Food for Pollinators: Quantifying the Nectar and Pollen Resources of Urban Flower Meadows. *PLOS ONE* 11, e0158117. <https://doi.org/10.1371/journal.pone.0158117>
- Hinchliff, C.E., Smith, S.A., Allman, J.F., Burleigh, J.G., Chaudhary, R., Coghill, L.M., Crandall, K.A., Deng, J., Drew, B.T., Gazis, R., Gude, K., Hibbett, D.S., Katz, L.A., Laughinghouse, H.D., McTavish, E.J., Midford, P.E., Owen, C.L., Ree, R.H., Rees, J.A., Soltis, D.E., Williams, T., Cranston, K.A., 2015. Synthesis of phylogeny and taxonomy into a comprehensive tree of life. *Proc. Natl. Acad. Sci.* 112, 12764–12769. <https://doi.org/10.1073/pnas.1423041112>
- Hinners, S.J., Kearns, C.A., Wessman, C.A., 2012. Roles of scale, matrix, and native habitat in supporting a diverse suburban pollinator assemblage. *Ecol. Appl.* 22, 1923–1935. <https://doi.org/10.1890/11-1590.1>

- Høye, T.T., Montagna, M., Oteman, B., Roy, D.B., 2025. Emerging technologies for pollinator monitoring. *Curr. Opin. Insect Sci.* 69, 101367. <https://doi.org/10.1016/j.cois.2025.101367>
- Hua, L., Zhang, X., Nie, Q., Sun, F., Tang, L., Hua, L., Zhang, X., Nie, Q., Sun, F., Tang, L., 2020. The Impacts of the Expansion of Urban Impervious Surfaces on Urban Heat Islands in a Coastal City in China. *Sustainability* 12. <https://doi.org/10.3390/su12020475>
- Jimenez, M.P., DeVille, N.V., Elliott, E.G., Schiff, J.E., Wilt, G.E., Hart, J.E., James, P., 2021. Associations between Nature Exposure and Health: A Review of the Evidence. *Int. J. Environ. Res. Public Health* 18, 4790. <https://doi.org/10.3390/ijerph18094790>
- Johnston, A., Matechou, E., Dennis, E.B., 2023. Outstanding challenges and future directions for biodiversity monitoring using citizen science data. *Methods Ecol. Evol.* 14, 103–116. <https://doi.org/10.1111/2041-210X.13834>
- Kaiser-Bunbury, C.N., Blüthgen, N., 2015. Integrating network ecology with applied conservation: a synthesis and guide to implementation. *AoB PLANTS* 7, plv076. <https://doi.org/10.1093/aobpla/plv076>
- Kendall, L.K., Mola, J.M., Portman, Z.M., Cariveau, D.P., Smith, H.G., Bartomeus, I., 2022. The potential and realized foraging movements of bees are differentially determined by body size and sociality. *Ecology* 103, e3809. <https://doi.org/10.1002/ecy.3809>
- 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. *Proc. R. Soc. B Biol. Sci.* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Knop, E., Gerpe, C., Ryser, R., Hofmann, F., Menz, M.H.M., Trösch, S., Ursenbacher, S., Zoller, L., Fontaine, C., 2018. Rush hours in flower visitors over a day–night cycle. *Insect Conserv. Divers.* 11, 267–275. <https://doi.org/10.1111/icad.12277>
- Knop, E., Zoller, L., Ryser, R., Gerpe, C., Hörler, M., Fontaine, C., 2017. Artificial light at night as a new threat to pollination. *Nature* 548, 206–209. <https://doi.org/10.1038/nature23288>
- Kovács-Hostyánszki, A., Piross, I.S., Shebl, M.A., 2022. Non-native plant species integrate well into plant-pollinator networks in a diverse man-made flowering plant community. *Urban Ecosyst.* 25, 1491–1502. <https://doi.org/10.1007/s11252-022-01242-7>
- Kritsky, G., 2017. Beekeeping from Antiquity Through the Middle Ages. *Annu. Rev. Entomol.* 62, 249–264. <https://doi.org/10.1146/annurev-ento-031616-035115>
- Kuussaari, M., Toivonen, M., Heliölä, J., Pöyry, J., Mellado, J., Ekroos, J., Hyyryläinen, V., Vähä-Piikkiö, I., Tiainen, J., 2021. Butterfly species' responses to urbanization: differing effects of human population density and built-up area. *Urban Ecosyst.* 24, 515–527. <https://doi.org/10.1007/s11252-020-01055-6>
- Kwartnik-Pruc, A., Droj, G., 2023. The Role of Allotments and Community Gardens and the Challenges Facing Their Development in Urban Environments—A Literature Review. *Land* 12, 325. <https://doi.org/10.3390/land12020325>
- Lanner, J., Kratschmer, S., Petrović, B., Gaulhofer, F., Meimberg, H., Pachinger, B., 2020. City dwelling wild bees: how communal gardens promote species richness. *Urban Ecosyst.* 23, 271–288. <https://doi.org/10.1007/s11252-019-00902-5>

- Li, G., Fang, C., Li, Y., Wang, Z., Sun, S., He, S., Qi, W., Bao, C., Ma, H., Fan, Y., Feng, Y., Liu, X., 2022. Global impacts of future urban expansion on terrestrial vertebrate diversity. *Nat. Commun.* 13, 1628. <https://doi.org/10.1038/s41467-022-29324-2>
- Liang, H., He, Y.-D., Theodorou, P., Yang, C.-F., 2023. The effects of urbanization on pollinators and pollination: A meta-analysis. *Ecol. Lett.* 26, 1629–1642. <https://doi.org/10.1111/ele.14277>
- Liao, Z., Shen, X., Zhang, J., Zhu, M., Deng, Z., Liu, F., Huang, Z.Y., Zhang, Y., 2025. Vegetation coverage and land imperviousness in urban area jointly affect hymenopteran pollinator diversity and spatial pattern. *Ecol. Indic.* 178, 114116. <https://doi.org/10.1016/j.ecolind.2025.114116>
- Llodrà-Llabrés, J., Cariñanos, P., 2022. Enhancing pollination ecosystem service in urban green areas: An opportunity for the conservation of pollinators. *Urban For. Urban Green.* 74, 127621. <https://doi.org/10.1016/j.ufug.2022.127621>
- Loram, A., Tratalos, J., Warren, P.H., Gaston, K.J., 2007. Urban domestic gardens (X): the extent & structure of the resource in five major cities. *Landsc. Ecol.* 22, 601–615. <https://doi.org/10.1007/s10980-006-9051-9>
- Lowenstein, D.M., Matteson, K.C., Minor, E.S., 2019. Evaluating the dependence of urban pollinators on ornamental, non-native, and ‘weedy’ floral resources. *Urban Ecosyst.* 22, 293–302. <https://doi.org/10.1007/s11252-018-0817-z>
- Lüdecke, D., Mattan, S., Shachar, B., Patil, I., Waggoner, W., Makowski, D., 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. *J. Open Source Softw.* 6, 3139. <https://doi.org/10.21105/joss.03139>
- Luder, K., Knop, E., Menz, M.H.M., 2018. Contrasting responses in community structure and phenology of migratory and non-migratory pollinators to urbanization. *Divers. Distrib.* 24, 919–927. <https://doi.org/10.1111/ddi.12735>
- MacInnis, G., Normandin, E., Ziter, C.D., 2023. Decline in wild bee species richness associated with honey bee (*Apis mellifera* L.) abundance in an urban ecosystem. *PeerJ* 11, e14699. <https://doi.org/10.7717/peerj.14699>
- Manning, I., Zoller, L., Resasco, J., 2025. Impacts of sampling effort on seasonal plant-pollinator interaction turnover over eight years. *Oecologia* 207, 131. <https://doi.org/10.1007/s00442-025-05771-8>
- Martini, M., Kaul, E., Miller, R., Gibbs, J., Bobiwash, K., 2025. Non-native plants in road verges attract pollinators despite associated declines in native flowers. *Glob. Ecol. Conserv.* 58, e03489. <https://doi.org/10.1016/j.gecco.2025.e03489>
- Martins, K.T., Gonzalez, A., Lechowicz, M.J., 2017. Patterns of pollinator turnover and increasing diversity associated with urban habitats. *Urban Ecosyst.* 20, 1359–1371. <https://doi.org/10.1007/s11252-017-0688-8>
- Matteson, K.C., Ascher, J.S., Langellotto, G.A., 2008. Bee Richness and Abundance in New York City Urban Gardens. *Ann. Entomol. Soc. Am.* 101, 140–150. [https://doi.org/10.1603/0013-8746\(2008\)101%5B140:BRAAIN%5D2.0.CO;2](https://doi.org/10.1603/0013-8746(2008)101%5B140:BRAAIN%5D2.0.CO;2)
- Matteson, K.C., Langellotto, G.A., 2010. Determinates of inner city butterfly and bee species richness. *Urban Ecosyst.* 13, 333–347. <https://doi.org/10.1007/s11252-010-0122-y>

- McCune, F., Normandin, É., Mazerolle, M.J., Fournier, V., 2020. Response of wild bee communities to beekeeping, urbanization, and flower availability. *Urban Ecosyst.* 23, 39–54. <https://doi.org/10.1007/s11252-019-00909-y>
- McDonald, R.I., Marcotullio, P.J., Güneralp, B., 2013. Urbanization and Global Trends in Biodiversity and Ecosystem Services, in: Elmqvist, T., Fragkias, M., Goodness, J., Güneralp, B., Marcotullio, P.J., McDonald, R.I., Parnell, S., Schewenius, M., Sendstad, M., Seto, K.C., Wilkinson, C. (Eds.), *Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities: A Global Assessment*. Springer Netherlands, Dordrecht, pp. 31–52. https://doi.org/10.1007/978-94-007-7088-1_3
- McKinney, M.L., 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst.* 11, 161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Memmott, J., 1999. The structure of a plant-pollinator food web. *Ecol. Lett.* 2, 276–280. <https://doi.org/10.1046/j.1461-0248.1999.00087.x>
- Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B Biol. Sci.* 271, 2605–2611. <https://doi.org/10.1098/rspb.2004.2909>
- Merckx, T., Kaiser, A., Van Dyck, H., 2018. Increased body size along urbanization gradients at both community and intraspecific level in macro-moths. *Glob. Change Biol.* 24, 3837–3848. <https://doi.org/10.1111/gcb.14151>
- Michez, D., Vujić, A., Sentil, A., 2023. Open database on traits and phylogenetic data on European pollinators. <https://doi.org/https://doi.org/10.5281/zenodo.8300431>
- Michonneau, F., Brown, J.W., Winter, D.J., 2016. rotl: an R package to interact with the Open Tree of Life data. *Methods Ecol. Evol.* 7. <https://doi.org/doi:10.1111/2041-210X.12593>
- Miguet, P., Fahrig, L., Lavigne, C., 2017. How to quantify a distance-dependent landscape effect on a biological response. *Methods Ecol. Evol.* 8, 1717–1724. <https://doi.org/10.1111/2041-210X.12830>
- Miguez, N.G., Mason, B.M., Qiu, J., Cao, H., Callaghan, C.T., 2025. Urban greenspaces benefit both human utility and biodiversity. *Urban For. Urban Green.* 107, 128791. <https://doi.org/10.1016/j.ufug.2025.128791>
- Mohajerani, A., Bakaric, J., Jeffrey-Bailey, T., 2017. The urban heat island effect, its causes, and mitigation, with reference to the thermal properties of asphalt concrete. *J. Environ. Manage.* 197, 522–538. <https://doi.org/10.1016/j.jenvman.2017.03.095>
- Moll, R.J., Cepek, J.D., Lorch, P.D., Dennis, P.M., Tans, E., Robison, T., Millspaugh, J.J., Montgomery, R.A., 2019. What does urbanization actually mean? A framework for urban metrics in wildlife research. *J. Appl. Ecol.* 56, 1289–1300. <https://doi.org/10.1111/1365-2664.13358>
- Naqvi, Q., Wolff, P.J., Molano-Flores, B., Sperry, J.H., 2022. Camera traps are an effective tool for monitoring insect–plant interactions. *Ecol. Evol.* 12, e8962. <https://doi.org/10.1002/ece3.8962>
- NatureScot., 2022. Landscape Indicator.
- NatureScot, 2017. Pollinator Strategy for Scotland 2017-2027.
- NBN Trust, 2026. The National Biodiversity Network (NBN) Atlas.

- Neumann, A.E., Conitz, F., Karlebowski, S., Sturm, U., Schmack, J.M., Egerer, M., 2024. Flower richness is key to pollinator abundance: The role of garden features in cities. *Basic Appl. Ecol.* 79, 102–113. <https://doi.org/10.1016/j.baae.2024.06.004>
- Nicholls, E., Griffiths-Lee, J., Basu, P., Chatterjee, S., Goulson, D., 2023. Crop–pollinator interactions in urban and peri-urban farms in the United Kingdom. *PLANTS PEOPLE PLANET* 5, 759–775. <https://doi.org/10.1002/ppp3.10376>
- Normandin, É., Vereecken, N.J., Buddle, C.M., Fournier, V., 2017. Taxonomic and functional trait diversity of wild bees in different urban settings. *PeerJ* 5, e3051. <https://doi.org/10.7717/peerj.3051>
- Nowak, D.J., Greenfield, E.J., 2020. The increase of impervious cover and decrease of tree cover within urban areas globally (2012–2017). *Urban For. Urban Green.* 49, 126638. <https://doi.org/10.1016/j.ufug.2020.126638>
- Nuissl, H., Siedentop, S., 2021. Urbanisation and Land Use Change, in: Weith, T., Barkmann, T., Gaasch, N., Rogga, S., Strauß, C., Zscheischler, J. (Eds.), *Sustainable Land Management in a European Context: A Co-Design Approach*. Springer International Publishing, Cham, pp. 75–99. https://doi.org/10.1007/978-3-030-50841-8_5
- Office for National Statistics (ONS), 2023. UK natural capital: urban accounts.
- Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, p, O’Hara, R., Solymos, P., Stevens, M., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Drand, S., Evangelista, H., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M., Lahti, L., McGlinn, D., Ouellette, M., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C., Weedon, J., 2024. *vegan: Community Ecology Package_*. R package version 2.6-8.
- Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O’Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Ribeiro Cunha, E., Smith, T., Stier, A., Ter Braak, C.J.F., Weedon, J., Borman, T., 2001. *vegan: Community Ecology Package*. <https://doi.org/10.32614/CRAN.package.vegan>
- Olesen, J.M., Bascompte, J., Dupont, Y.L., Jordano, P., 2007. The modularity of pollination networks. *Proc. Natl. Acad. Sci. U. S. A.* 104, 19891–19896. <https://doi.org/10.1073/pnas.0706375104>
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Olsson, R.L., Brousil, M.R., Clark, R.E., Baine, Q., Crowder, D.W., 2021. Interactions between plants and pollinators across urban and rural farming landscapes. *Food Webs* 27, e00194. <https://doi.org/10.1016/j.fooweb.2021.e00194>
- Ordnance Survey (GB), 2025. OS MasterMap Greenspace [SHAPE geospatial data].
- Paradis, E., Schliep, K., 2019. ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics* 35, 526–528. <https://doi.org/doi:10.1093/bioinformatics/bty633>
- Pardee, G.L., Philpott, S.M., 2014. Native plants are the bee’s knees: local and landscape predictors of bee richness and abundance in backyard gardens. *Urban Ecosyst.* 17, 641–659. <https://doi.org/10.1007/s11252-014-0349-0>

- Paudel, S., States, S.L., 2023. Urban green spaces and sustainability: Exploring the ecosystem services and disservices of grassy lawns versus floral meadows. *Urban For. Urban Green*. 84, 127932. <https://doi.org/10.1016/j.ufug.2023.127932>
- Philpott, S.M., Pardee, G., Hsu, J., Kulikowski, A.J., Bichier, P., Liere, H., Lin, B.B., Jha, S., 2025. Floral richness shapes plant-pollinator networks in urban agroecosystems. *Basic Appl. Ecol.* 88, 114–127. <https://doi.org/10.1016/j.baae.2025.10.004>
- Pinto, L.V., Inácio, M., Ferreira, C.S.S., Ferreira, A.D., Pereira, P., 2022. Ecosystem services and well-being dimensions related to urban green spaces – A systematic review. *Sustain. Cities Soc.* 85, 104072. <https://doi.org/10.1016/j.scs.2022.104072>
- Plant, E., Dunkley, R., Dominoni, D.M., McCafferty, D.J., 2025. Supporting pollinators in urban gardens: floral richness and abundance influence flower visitor interactions regardless of the surrounding landscape. *Urban Ecosyst.* 28, 235. <https://doi.org/10.1007/s11252-025-01848-7>
- Plowright, R.C., Lavery, T.M., 1984. The Ecology and Sociobiology of Bumble Bees. *Annu. Rev. Entomol.* 29, 175–199. <https://doi.org/10.1146/annurev.en.29.010184.001135>
- Plummer, K.E., Dadam, D., Brereton, T., Dennis, E.B., Massimino, D., Risely, K., Siriwardena, G.M., Toms, M.P., 2024. Trends in butterfly populations in UK gardens—New evidence from citizen science monitoring. *Insect Conserv. Divers.* 17, 345–357. <https://doi.org/10.1111/icad.12645>
- Poole, O., Costa, A., Kaiser-Bunbury, C.N., Shaw, R.F., 2025. Pollinators respond positively to urban green space enhancements using wild and ornamental flowers. *Insect Conserv. Divers.* 18, 16–28. <https://doi.org/10.1111/icad.12779>
- Porto, R.G., de Almeida, R.F., Cruz-Neto, O., Tabarelli, M., Viana, B.F., Peres, C.A., Lopes, A.V., 2020. Pollination ecosystem services: A comprehensive review of economic values, research funding and policy actions. *Food Secur.* 12, 1425–1442. <https://doi.org/10.1007/s12571-020-01043-w>
- Prendergast, K.S., Ollerton, J., 2022. Spatial and temporal scale of analysis alter conclusions about the effects of urbanisation on plant–pollinator networks. *Arthropod-Plant Interact.* 16. <https://doi.org/10.1007/s11829-022-09925-w>
- Prendergast, K.S., Ollerton, J., 2021. Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens. *Urban Ecosyst.* 24, 973–987. <https://doi.org/10.1007/s11252-020-01089-w>
- Proesmans, W., Felten, E., Laurent, E., Albrecht, M., Cyrille, N., Labonté, A., Maurer, C., Paxton, R., Schweiger, O., Szentgyörgyi, H., Vanbergen, A.J., 2024. Urbanisation and agricultural intensification modulate plant–pollinator network structure and robustness. *Funct. Ecol.* 38, 628–641. <https://doi.org/10.1111/1365-2435.14503>
- QGIS Development Team, 2026. QGIS Geographic Information System.
- R version 4.5.2, 2025. . [Not] Part in a Rumble.
- Reeher, P., Lanterman Novotny, J., Mitchell, R.J., 2020. Urban bumble bees are unaffected by the proportion of intensely developed land within urban environments of the industrial Midwestern USA. *Urban Ecosyst.* 23, 703–711. <https://doi.org/10.1007/s11252-020-00965-9>

- Ren, P., Si, X., Ding, P., 2022. Stable species and interactions in plant–pollinator networks deviate from core position in fragmented habitats. *Ecography* 2022, e06102. <https://doi.org/10.1111/ecog.06102>
- Renaud, E., Baudry, E., Bessa-Gomes, C., 2020. Influence of taxonomic resolution on mutualistic network properties. *Ecol. Evol.* 10, 3248–3259. <https://doi.org/10.1002/ece3.6060>
- Resasco, J., Chacoff, N.P., Vázquez, D.P., 2021. Plant–pollinator interactions between generalists persist over time and space. *Ecology* 102, e03359. <https://doi.org/10.1002/ecy.3359>
- Ritchie, A.D., Ruppel, R., Jha, S., 2016. Generalist Behavior Describes Pollen Foraging for Perceived Oligolectic and Polylectic Bees. *Environ. Entomol.* 45, 909–919. <https://doi.org/10.1093/ee/nvw032>
- Rivera-Hutinel, A., Bustamante, R.O., Marín, V.H., Medel, R., 2012. Effects of sampling completeness on the structure of plant–pollinator networks. *Ecology* 93, 1593–1603. <https://doi.org/10.1890/11-1803.1>
- Ropars, L., Dajoz, I., Fontaine, C., Muratet, A., Geslin, B., 2019a. Wild pollinator activity negatively related to honey bee colony densities in urban context. *PLOS ONE* 14, e0222316. <https://doi.org/10.1371/journal.pone.0222316>
- Ropars, L., Dajoz, I., Fontaine, C., Muratet, A., Geslin, B., 2019b. Wild pollinator activity negatively related to honey bee colony densities in urban context. *PLOS ONE* 14, e0222316. <https://doi.org/10.1371/journal.pone.0222316>
- Rose, F., O'Reilly, C., 2006. *The Wild Flower Key (Revised Edition)- How to identify wild plants, trees shrubs in Britain and Ireland.* Warne, Rev Ed.
- Roy, H.E., Baxter, E., Saunders, A., Pocock, M.J.O., 2016. Focal Plant Observations as a Standardised Method for Pollinator Monitoring: Opportunities and Limitations for Mass Participation Citizen Science. *PLOS ONE* 11, e0150794. <https://doi.org/10.1371/journal.pone.0150794>
- Salisbury, A., Armitage, J., Bostock, H., Perry, J., Tatchell, M., Thompson, K., 2015. EDITOR'S CHOICE: Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species? *J. Appl. Ecol.* 52, 1156–1164. <https://doi.org/10.1111/1365-2664.12499>
- Sánchez-Bayo, F., Wyckhuys, K.A.G., 2019. Worldwide decline of the entomofauna: A review of its drivers. *Biol. Conserv.* 232, 8–27. <https://doi.org/10.1016/j.biocon.2019.01.020>
- Schmack, J.M., Egerer, M., 2023. Floral richness and seasonality influences bee and non-bee flower interactions in urban community gardens. *Urban Ecosyst.* 26, 1099–1112. <https://doi.org/10.1007/s11252-023-01353-9>
- Scottish Government, 2023. National Planning Framework 4 (NPF4).
- Seitz, N., vanEngelsdorp, D., Leonhardt, S.D., 2020. Are native and non-native pollinator friendly plants equally valuable for native wild bee communities? *Ecol. Evol.* 10, 12838–12850. <https://doi.org/10.1002/ece3.6826>
- Serra-Marin, P.E., Solé-Ribalta, A., Lana, A., Borge-Holthoefer, J., Hervías-Parejo, S., Traveset, A., 2025. Comparative assessment of automated and manual monitoring in

- comprehensive plant–pollinator communities. *Methods Ecol. Evol.* 16, 2960–2978. <https://doi.org/10.1111/2041-210X.70165>
- Silva, D., Jack, 2021. Life History and the Transitions to Eusociality in the Hymenoptera. *Front. Ecol. Evol.* 9. <https://doi.org/10.3389/fevo.2021.727124>
- Silva, V.H.D., Gomes, I.N., Bosenbecker, C., Junker, R.R., Maruyama, P.K., 2025. One for all, all for one? Pollinator groups differ in diversity and specialization of interactions across urban green spaces. *Landsc. Urban Plan.* 259, 105361. <https://doi.org/10.1016/j.landurbplan.2025.105361>
- Silva, V.H.D., Gomes, I.N., Cardoso, J.C.F., Bosenbecker, C., Silva, J.L.S., Cruz-Neto, O., Oliveira, W., Stewart, A.B., Lopes, A.V., Maruyama, P.K., 2023. Diverse urban pollinators and where to find them. *Biol. Conserv.* 281, 110036. <https://doi.org/10.1016/j.biocon.2023.110036>
- Simao, M.-C.M., Matthijs, J., Perfecto, I., 2018. Experimental small-scale flower patches increase species density but not abundance of small urban bees. *J. Appl. Ecol.* 55, 1759–1768. <https://doi.org/10.1111/1365-2664.13085>
- Sirohi, M.H., Jackson, J., Ollerton, J., 2025. Influence of urban land cover and habitat quality on wild bees. *Urban Ecosyst.* 28, 78. <https://doi.org/10.1007/s11252-025-01687-6>
- Sirohi, M.H., Jackson, J., Ollerton, J., 2022. Plant–bee interactions and resource utilisation in an urban landscape. *Urban Ecosyst.* 25, 1913–1924. <https://doi.org/10.1007/s11252-022-01290-z>
- Sittinger, M., Uhler, J., Pink, M., Herz, A., 2024. Insect detect: An open-source DIY camera trap for automated insect monitoring. *PLOS ONE* 19, e0295474. <https://doi.org/10.1371/journal.pone.0295474>
- Sivakoff, F.S., Prajzner, S.P., Gardiner, M.M., 2018. Unique Bee Communities within Vacant Lots and Urban Farms Result from Variation in Surrounding Urbanization Intensity. *Sustainability* 10. <https://doi.org/10.3390/su10061926>
- Smith, T.J., Saunders, M.E., 2016. Honey bees: the queens of mass media, despite minority rule among insect pollinators. *Insect Conserv. Divers.* 9, 384–390. <https://doi.org/10.1111/icad.12178>
- Souza, C.S., Maruyama, P.K., Aoki, C., Sigrist, M.R., Raizer, J., Gross, C.L., de Araujo, A.C., 2018. Temporal variation in plant–pollinator networks from seasonal tropical environments: Higher specialization when resources are scarce. *J. Ecol.* 106, 2409–2420. <https://doi.org/10.1111/1365-2745.12978>
- Spiesman, B.J., Inouye, B.D., 2013. Habitat loss alters the architecture of plant–pollinator interaction networks. *Ecology* 94, 2688–2696. <https://doi.org/10.1890/13-0977.1>
- Staab, M., Pereira-Peixoto, M.H., Klein, A.-M., 2020. Exotic garden plants partly substitute for native plants as resources for pollinators when native plants become seasonally scarce. *Oecologia* 194, 465–480. <https://doi.org/10.1007/s00442-020-04785-8>
- Ştefan, V., Stark, T., Wurm, M., Taubenböck, H., Knight, T.M., 2025a. Successes and limitations of pretrained YOLO detectors applied to unseen time-lapse images for automated pollinator monitoring. *Sci. Rep.* 15, 30671. <https://doi.org/10.1038/s41598-025-16140-z>
- Ştefan, V., Workman, A., Cobain, J.C., Rakosy, D., Knight, T.M., 2025b. Utilising affordable smartphones and open-source time-lapse photography for pollinator image

- collection and annotation. *J. Pollinat. Ecol.* 38, 1–21. [https://doi.org/10.26786/1920-7603\(2025\)778](https://doi.org/10.26786/1920-7603(2025)778)
- Stewart, A.B., Sritongchuay, T., Teartisup, P., Kaewsomboon, S., Bumrungsri, S., 2018. Habitat and landscape factors influence pollinators in a tropical megacity, Bangkok, Thailand. *PeerJ* 6, e5335. <https://doi.org/10.7717/peerj.5335>
- Stroh, P.A., Walker, K.J., Humphrey, O., Pescott, L., Burkmar, R.J., 2023. *Plant atlas 2020: Mapping changes in the distribution of the British and Irish flora*. Princeton.
- Stubbs, A.E., Falk, S.J., 2002. *British Hoverflies: An Illustrated Identification Guide*. British Entomological & Natural History Society.
- Suni, S., Hall, E., Bahu, E., Hayes, H., 2022. Urbanization increases floral specialization of pollinators. *Ecol. Evol.* 12, e8619. <https://doi.org/10.1002/ece3.8619>
- Tassin de Montaigu, C., Goulson, D., 2024. Factors influencing butterfly and bumblebee richness and abundance in gardens. *Sci. Total Environ.* 908, 167995. <https://doi.org/10.1016/j.scitotenv.2023.167995>
- Tavares-Brancher, K.P., Graf, L.V., Ferreira-Júnior, W.G., Faria, L.D.B., Zenni, R.D., 2024. Plant-pollinator interactions in the neotropics are affected by urbanization and the invasive bee *Apis mellifera*. *J. Insect Conserv.* 28, 251–261. <https://doi.org/10.1007/s10841-024-00547-6>
- Taylor, L., Hochuli, D.F., 2017. Defining greenspace: Multiple uses across multiple disciplines. *Landsc. Urban Plan.* 158, 25–38. <https://doi.org/10.1016/j.landurbplan.2016.09.024>
- Theodorou, P., Albig, K., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T.E., Paxton, R.J., 2017. The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. *Funct. Ecol.* 31, 838–847. <https://doi.org/10.1111/1365-2435.12803>
- Theodorou, P., Baltz, L.M., Paxton, R.J., Soro, A., 2020a. Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. *Evol. Appl.* 14, 53–68. <https://doi.org/10.1111/eva.13087>
- Theodorou, P., Herbst, S.-C., Kahnt, B., Landaverde-González, P., Baltz, L.M., Osterman, J., Paxton, R.J., 2020b. Urban fragmentation leads to lower floral diversity, with knock-on impacts on bee biodiversity. *Sci. Rep.* 10, 21756. <https://doi.org/10.1038/s41598-020-78736-x>
- 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., 2020c. Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat. Commun.* 11, 576. <https://doi.org/10.1038/s41467-020-14496-6>
- Tikhonov, G., Ovaskainen, O., Oksanen, J., de Jonge, M., Opedal, O., Dallas, T., 2025. *Hmsc: Hierarchical Model of Species Communities*.
- Tommasi, N., Biella, P., Guzzetti, L., Lasway, J.V., Njovu, H.K., Tapparo, A., Agostinetto, G., Peters, M.K., Steffan-Dewenter, I., Labra, M., Galimberti, A., 2021. Impact of land use intensification and local features on plants and pollinators in Sub-Saharan smallholder farms. *Agric. Ecosyst. Environ.* 319, 107560. <https://doi.org/10.1016/j.agee.2021.107560>

- Turo, K.J., Spring, M.R., Sivakoff, F.S., Delgado de la flor, Y.A., Gardiner, M.M., 2021. Conservation in post-industrial cities: How does vacant land management and landscape configuration influence urban bees? *J. Appl. Ecol.* 58, 58–69. <https://doi.org/10.1111/1365-2664.13773>
- Tylianakis, J.M., Laliberté, E., Nielsen, A., Bascompte, J., 2010. Conservation of species interaction networks. *Biol. Conserv.*, Conserving complexity: Global change and community-scale interactions 143, 2270–2279. <https://doi.org/10.1016/j.biocon.2009.12.004>
- Udy, K.L., Reininghaus, H., Scherber, C., Tschardtke, T., 2020. Plant–pollinator interactions along an urbanization gradient from cities and villages to farmland landscapes. *Ecosphere* 11, e03020. <https://doi.org/10.1002/ecs2.3020>
- UK Pollinator Monitoring Scheme, 2025. The UK PoMS Annual report 2024. UK Centre for Ecology & Hydrology and Joint Nature Conservation Committee.
- Ulrich, J., Sargent, R.D., 2025. Urban landscapes with more natural greenspace support higher pollinator diversity. *Ecol. Appl.* 35, e70005. <https://doi.org/10.1002/eap.70005>
- United Nations, 2025. World urbanization prospects 2025: summary of results (No. UN DESA/POP/2025/TR/ NO. 12.). New York: United Nations, New York.
- United Nations, 2019. United Nations World Urbanization Prospects: The 2018 Revision.
- Vaughan, I.P., Gotelli, N.J., Memmott, J., Pearson, C.E., Woodward, G., Symondson, W.O.C., 2018. *econullnetr*: An r package using null models to analyse the structure of ecological networks and identify resource selection. *Methods Ecol. Evol.* 9, 728–733. <https://doi.org/10.1111/2041-210X.12907>
- Watanabe, S., 2010. Asymptotic Equivalence of Bayes Cross Validation and Widely Applicable Information Criterion in Singular Learning Theory. *J. Mach. Learn. Res.*
- Wenzel, A., Grass, I., Belavadi, V.V., Tschardtke, T., 2020. How urbanization is driving pollinator diversity and pollination – A systematic review. *Biol. Conserv.* 241, 108321. <https://doi.org/10.1016/j.biocon.2019.108321>
- Wignall, V.R., Brolly, M., Uthoff, C., Norton, K.E., Chipperfield, H.M., Balfour, N.J., Ratnieks, F.L.W., 2020. Exploitative competition and displacement mediated by eusocial bees: experimental evidence in a wild pollinator community. *Behav. Ecol. Sociobiol.* 74, 152. <https://doi.org/10.1007/s00265-020-02924-y>
- Wilson, C.J., Jamieson, M.A., 2019. The effects of urbanization on bee communities depends on floral resource availability and bee functional traits. *PLOS ONE* 14, e0225852. <https://doi.org/10.1371/journal.pone.0225852>
- Wonderlin, N.E., 2024. Distinct diurnal and nocturnal flower visitor communities provide pollination services in urban gardens. *Ecol. Entomol.* 49, 225–234. <https://doi.org/10.1111/een.13296>
- Worthy, S.H., Acorn, J.H., Frost, C.M., 2023. Honey bees (*Apis mellifera*) modify plant–pollinator network structure, but do not alter wild species’ interactions. *PLOS ONE* 18, e0287332. <https://doi.org/10.1371/journal.pone.0287332>
- Wu, C., Li, J., Wang, C., Song, C., Haase, D., Breuste, J., Finka, M., 2021. Estimating the Cooling Effect of Pocket Green Space in High Density Urban Areas in Shanghai, China. *Front. Environ. Sci.* 9.

- Yahaya, M.M., Rodger, J.G., Landi, P., Hui, C., 2024. Emergence of structure in plant–pollinator networks: low floral resource constrains network specialisation. *Oikos* 2024, e10533. <https://doi.org/10.1111/oik.10533>
- Zaninotto, V., Fauviau, A., Dajoz, I., 2023a. Diversity of greenspace design and management impacts pollinator communities in a densely urbanized landscape: the city of Paris, France. *Urban Ecosyst.* 26, 503–515. <https://doi.org/10.1007/s11252-023-01351-x>
- Zaninotto, V., Raynaud, X., Gendreau, E., Kraepiel, Y., Motard, E., Babiar, O., Hansart, A., Hignard, C., Dajoz, I., 2020. Broader phenology of pollinator activity and higher plant reproductive success in an urban habitat compared to a rural one. *Ecol. Evol.* 10, 11607–11621. <https://doi.org/10.1002/ece3.6794>
- Zaninotto, V., Thebault, E., Dajoz, I., 2023b. Native and exotic plants play different roles in urban pollination networks across seasons. *Oecologia* 201, 525–536. <https://doi.org/10.1007/s00442-023-05324-x>
- Zuur, A.F., Ieno, E.N., Walker, N., Saveliev, A.A., Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York.