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Insects in the city: identifying the drivers influencing urban pollinator communities and the services they provide.

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Abstract

Pollinating insects are declining due to habitat loss and climate change, threatening the pollination of crops and wild plants. Pollinators and the pollination services they provide may be particularly vulnerable in cities, where urban greenspaces provide limited habitat and floral resources. In Chapter 1 of this thesis, I show that there are still substantial knowledge gaps about the effects of heterogeneous urban landscapes on insect pollinator communities, especially for many important non-bee taxa such as hoverflies and moths. This thesis, therefore, aims to test the effects of urbanisation on the biodiversity, the pollen-transport networks, and the pollination service delivery of diurnal and nocturnal pollinators in cities. I use multidisciplinary methods including rigorous biodiversity monitoring, DNA metabarcoding, pollen-limitation experiments, and large-scale manipulation experiments to provide novel insights into the complex multi-level responses to increasing urbanisation. Using a multi-taxon and multi-city approach, I show that across multiple cities, bees, moths, and hoverflies are all negatively responding to increasing areas of impervious surfaces surrounding urban horticultural sites (Chapter 2). Then in Chapter 3, using metabarcoding of pollen loads of bees and moths I show there were striking negative effects of increasing urbanisation on the pollen-transport networks of both taxa. The results from Chapter 4 suggests that the consequences of reduced landscape-scale floral resources with increased urban intensity is driving increased competition among pollinating insects for pollen or nectar resources. Using a model crop, I demonstrate increased pollination service delivery in highly urban areas compared to less urban areas. Finally, using large-scale manipulations of supplemental nesting and floral resources, I reveal that implementing common conservation practices of planting flower patches does not mitigate the negative influences of urbanisation (Chapter 5). Collectively, all these results highlight the critical importance of understanding the factors that impact urban pollinators, and demonstrate the implications for ecosystem service provision in cities, management of urban greenspaces, and the conservation of urban wildlife.

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COVID-19 statement

Due to the COVID-19 pandemic, I had to change the scope of a two-year experiment that started in February 2020 (Chapters 4 and 5). Resulting in a reduction in the scope of this experiment by 25-50%. Loss of data collection in 2020 meant increased data collection in 2021, and due to changes in allotment availability and further restrictions, I was unable to obtain the exact same sites for the two-year field experiment outlined in Chapter 5. I had also secured NERC Environmental Omics Facility funding to run a full-time molecular lab work, this work was planned to run from October 2020 - April 2021 but had to be pushed to five months later. In addition, I faced delays as I was unable to process samples from 2019's intensive field season as I could not access lab space and a microscope for invertebrate ID. Considering these losses and delays, the Grantham Centre for Sustainable Futures extended my funding for 3-months to mitigate this.

Declaration and co-author contributions:

In this thesis format, each data chapter (Chapter 2- Chapter 5) are presented as stand-alone research papers. At the time of submission, only Chapter 3 has been submitted and is currently under review in *Ecology Letters*. Chapter 2 is planned for submission in *Nature Ecology and Evolution*; Chapter 4 is planned for submission in *Journal of Applied Ecology* and Chapter 5; is planned for submission in *Biological Conservation*. Below I outline my contributions to each chapter:

- Chapter 2:
Conceptualisation, fieldwork, insect identification, formal analysis, data curation, visualisation, writing the original draft, review and editing.
- Chapter 3:
Conceptualisation, co-authored molecular lab work funding, field-work, insect identification, molecular lab work, bioinformatics analysis, formal analysis, data curation, visualisation, writing the original draft, review and editing.
- Chapter 4:
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Contributed to study design, supervision, review and editing (Chapter 1-6)

Co-authored molecular lab work funding (Chapter 3)

Fieldwork/ experimental setup (Chapter 4 and 5)

Dr. Jill L. Edmondson.

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Introduction

Insects underpin the functioning of our natural ecosystems through processes such as soil formation, nutrient cycling, carbon storage, and pollination. Pollination by animals is critical for the reproductive success of up to 87.5% of flowering plants (Ollerton et al., 2011). Without pollination, there would be catastrophic knock-on effects for other species (Kearns et al., 1998). The animal transfer of pollen grains could therefore be considered one of the most important ecological insect-plant interactions. Though there are vertebrate pollinators, the majority of animal pollination is mediated by a very diverse group of invertebrates; insects (Arthropoda: Insecta). To date, there are ca. 350,000 known insect pollinator species that interact with ca. 352,000 species of flowering plants (Paton et al., 2008; Ollerton et al., 2011). Most pollinating insects belong to four insect orders: Lepidoptera (butterflies and moths; species n = 141,600), Coleoptera (beetles; species n = 77,300), Hymenoptera (bees and wasps; species n = 70,000) and Diptera (true flies; species n = 55,000). To date, there are relatively few comparative studies that include members from all these orders. In this thesis I aim to assess the relative roles of divergent insect pollinators and focus on three groups of insects (Figure 1.1) including nocturnal moths (Lepidoptera) to address the knowledge gaps about the role moths play in pollination, hoverflies (Syrphidae: Diptera) as their taxonomy and role in pollination are well established compared to other non-syrphid flies and bees (Anthophilla: Hymenoptera) which are the most widely recognised pollinators.

While this thesis focuses on moths (Lepidoptera), flies (Diptera), and bees (Hymenoptera), it's important to note that non-bee Hymenoptera, non-syrphidae Diptera, and butterflies also play significant roles in pollination. For example, some non-bee Hymenoptera, such as wasps and ants, can also act as pollinators for certain plant species (e.g. Weiblen et al., 2001). Similarly, non-syrphidae Diptera, such as tachinid flies, can also serve as important pollinators in some ecosystems (e.g. Kaiser-Bunbury et al., 2011). Butterflies are also important pollinators for certain plant

species, particularly those with deep floral tubes that are inaccessible to many other insect groups (Barrios et al., 2016).

1.1 Pollinators in the Anthropocene

Currently, we are experiencing rapid, global environmental change driven by anthropogenic pressures. The tight interlinkages between human and natural processes have been shaped by the human modulation of ecosystems for millennia (Ellis, 2015), and as a result, “nature” as we know it is a result of historical interwoven human-nature dynamics. Continuous human population growth and industrial development have led to increased unsustainable consumption of natural resources. We are now presented with human pressure on planetary dynamics and nature that is greater than ever before, to the extent that it is comparable to major geological forces. The geological epoch we live in is thus called the Anthropocene (Zalasiewicz et al., 2011). The direct human exploitation of animal and plant populations, habitat destruction, and indirect alterations to ecosystem function due to climate change have resulted in interrelated environmental pressures that threaten global biodiversity and by extension, the provision of crucial ecosystem services.

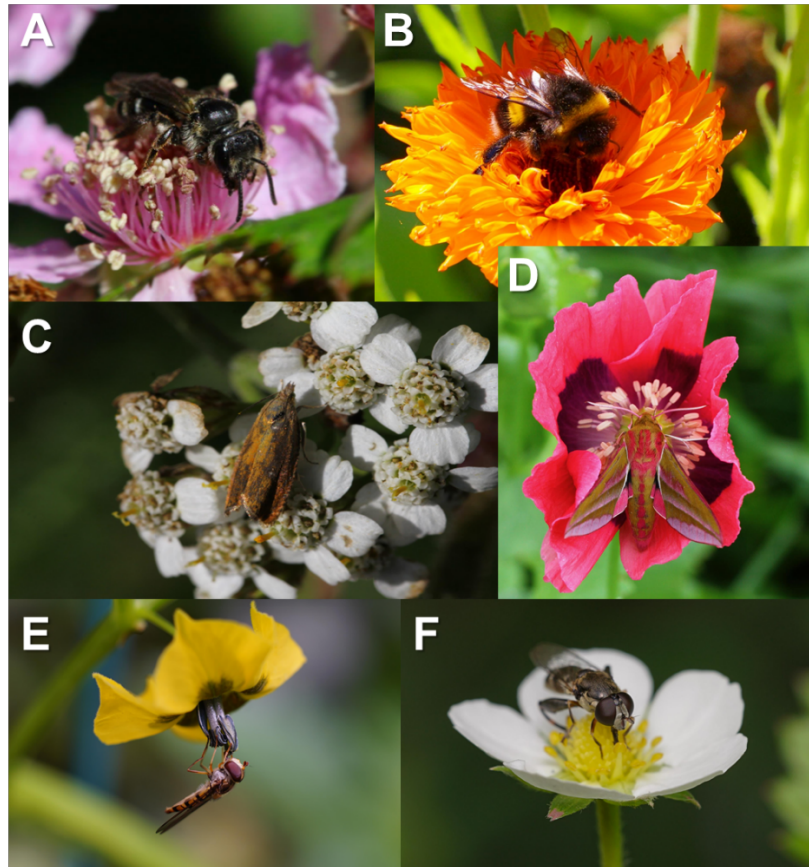


Figure 1. 1 Example of pollinators belonging to Hymenoptera (A-B), Lepidoptera (C-D), and Dipetera (E-F). A) Mining bee (*Andrena* sp.); B) Buff-tailed bumblebee, (*Bombus terrestris* agg.); C) micro-moth, (*Lathronympha strigana*); D) Elephant hawkmoth (*Deilephila elpenor*); E) Hoverfly (*Episyrphus* sp.), F) Hoverfly (*Syrirta pipiens*). Photo credit (A-D) Emilie Ellis; (E and F) Stuart Campbell.

Insect pollination is a high-profile example of a vulnerable ecosystem service due to the close link and dependency humans have on pollination services for global crop production. The loss of pollinator diversity and abundance has been discussed in a number of studies and reviews, for example, Biesmeijer et al. (2006), Potts et al. (2010) and Ollerton (2017). Although highly interlinked and related, the primary drivers of these declines have been identified as land-use change, climate change and the introduction of invasive species (Wagner et al., 2021a). Research suggests an overall pattern of decline (though with variation in sensitivity to the various drivers of change) in the abundance and diversity in all of the ‘big four’ pollinating insect orders, including

bees (Potts et al., 2010; Ollerton et al., 2011; Lintott et al., 2014), flies (Biesmeijer et al., 2006) and moths (Fox et al., 2021; Wagner et al., 2021b).

Understanding pollinator-plant interactions is critical for maintaining healthy ecosystems, and network approaches have become increasingly important in this field of study. Network approaches are important tools for understanding the complex relationships between pollinators and plants and for developing effective strategies for ecosystem management and conservation. By examining the complex interactions between pollinators and plants, researchers can gain insights into the drivers of declines in particular taxa and identify potential strategies for ecosystem management (Devoto et al., 2011; Banza et al., 2015; Banza et al., 2019). One of the key insights gained from network analysis is the importance of diverse host plants in supporting healthy pollinator communities. Different pollinator taxa have different requirements for adult and larval feeding, and access to a variety of host plants is critical for maintaining biodiversity. For example, specialist species that rely on few larval host plants, such as many nocturnal Lepidoptera, may be particularly vulnerable to declines in plant diversity (Banza et al., 2015). In contrast, generalist species like many bees may be more resilient due to their ability to use a wider variety of plants.

1.2 The role of bees, moths and hoverflies in pollination:

Until recently, managed bees have been a primary focus of pollinator research. The honeybee, *Apis mellifera* (Hymenoptera: Apidae) is the most frequently used managed pollinator in modified agricultural systems and has subsequently been perceived as the most important pollinator due to its versatility and direct benefits to human food production (Ollerton, 2017). However, the global reliance on a single domesticated pollinator species is a risky strategy in light of global environmental change. Conserving biodiversity is vital for the functioning of our ecosystems by increasing functional redundancy, and communities with more species performing similar functions (i.e. pollination) are buffered from losses of any given species (Naeem, 1998).

The conservation of wild pollinators increases biodiversity, thus enhancing the ecological stability of pollination services in face of the growing anthropogenic disturbance. Furthermore, there is now strong evidence that non-managed bees (henceforth referred to as wild bees), hoverflies, and other taxa provide the majority of pollination services (Breeze et al., 2011); in fact, the domestic honeybee can in some contexts play only a supporting role in pollination (Smith and Saunders, 2016). Compared to honeybees, visits from wild pollinators can be at least as efficient and effective (Rader et al., 2009), and in some cases even more so (Garibaldi et al., 2013). For example, bumblebees (*Bombus* spp.) are an important group of wild pollinators. In addition to their importance for crop pollination, bumblebees also play a critical role in maintaining biodiversity and ecosystem functioning. They can pollinate a wide variety of wildflowers and other plants, and their foraging behaviour can influence plant community composition and distribution (Breeze et al., 2011; Smith and Saunders, 2016; Rader et al., 2016).

Solitary bees also play a critical role in pollination (Winfrey et al., 2008; Brittain et al., 2013; Garibaldi et al., 2013). There are over 20,000 species of solitary bees worldwide, and they can be either ground-nesting or cavity-nesting. Ground-nesting bees, such as *Andrena* and *Halictus* species, are important pollinators of a wide range of crops, including blueberries, cherries, and almonds (Galli et al., 2009). These bees are active early in the spring and can often tolerate cooler temperatures than honeybees, making them valuable pollinators for crops that bloom early in the season (Greenleaf and Kremen, 2006). Cavity-nesting bees, such as mason bees and leafcutter bees, are also important pollinators for crops such as apples, pears, and cherries (Matsumoto and Maejima, 2010; Sheffield et al., 2008).

Integrating non-bees into agricultural cropping systems also has the potential to boost pollination and promote other important benefits such as pest management (Rader et al., 2020). Hoverflies (Diptera: Syrphidae), for example, are the most effective pollinators within the Diptera order and at a larval stage are predators of important crop pests such as aphids (Pekas et al., 2020). Overall, the conservation of wild

pollinators is essential for maintaining ecological stability and ensuring the pollination services needed for many crops

Moths are the most diverse group of pollinating insects, with more than 123,000 species of flower visitors yet they are the most frequently overlooked insect group in the pollinator literature. This is primarily driven by the nocturnal or crepuscular behaviour of moths, which makes observational studies difficult compared to diurnal bees for example (Macgregor et al., 2019). In the small pool of moth focussed research it has been shown that they are pollinators of at least 289 plant species, although this is likely an underestimate (Hahn and Bruhl, 2016). Many moths, like butterflies, are generalist nectarivores as adults (Macgregor et al., 2015). Consequently, moth-flower interactions at a community level are highly complex and diverse (Hahn and Bruhl, 2016; Macgregor et al., 2019; Walton et al., 2020; Buxton et al., 2022) and have been shown to substantially increase pollination success in generalist flowers (Knop et al., 2017; Alison et al., 2022). However, moths are also one of the most sensitive pollinator groups to environmental change, in the UK for example their populations have decreased by up to 33% (Fox et al., 2021) indicating that it is critical we understand their role in pollination.

1.4 Urban expansion

The proportion of humans living in cities has increased from 3% in 1700 to >50% in 2008 (United Nations, 2017) and by 2050 it is predicted that 70% of the world's population will live in urban areas (UNDESA, 2018), resulting in the 'first urban century' (Hall and Pfeiffer, 2013). This global growth in urban populations has resulted in a rapid increase in urban land use (Bren d'Amour et al., 2017). The process of urban expansion has been identified as a key driver of insect declines, as it is accompanied by a shift from agricultural, semi-natural, or natural landscapes into complex urban ecosystems with areas of hard impervious surfaces. This can drive biodiversity loss through reduced species richness and biotic homogenisation by habitat fragmentation, loss and disturbance (McKinney, 2006; Wagner et al., 2021a).

However, the effect of urbanisation on animal and plant communities is varied (Saari et al., 2016). This is due to the extensive network of greenspaces interwoven with the impervious surfaces in cities. In some countries that have little remaining natural habitat left, e.g. the U.K., expansion of urban land generally occurs in areas of modified agricultural landscapes (UKCEH, 2020). As a result, numerous studies have shown that the greenspace within urban areas can act as a refuge for some insect groups (such as bees) when compared to their agricultural counterparts (Baldock et al., 2015; Hall et al., 2016). This perhaps could be seen as an opportunity to create and develop urban areas in ecologically friendly ways to mitigate pollinator losses in urban areas. Understanding the ecological processes occurring in these complex environments is crucial to give us the opportunity to inform urban expansion, the development of new cities, or to manage current cities in a sustainable way such as greenspace configurations and types.

1.5 Urbanisation gradients within cities:

Cities are complex and heterogeneous systems, characterized by a matrix of human-made impervious sealed surfaces (greyspace) and greenspaces that vary in their management and the ecological habitats they provide (e.g., gardens, parks, allotments). The intensity of urban landuse also varies throughout a city, with higher proportions of impervious greyspace in urban centres compared to suburban areas. There are complex effects of increasing urbanisation on animal and plant communities, and current research aims to identify causes and remedies to urban biodiversity declines (Marluff et al., 2001; McKinney 2008). Urban land-use intensity gradients provide opportunities to understand the landscape composition drivers that can support urban insect communities. One of the most common methods for measuring urbanisation gradients is through a landscape ecology approach, where the density of greyspace is used as a measure of urban intensity (McIntyre et al., 2000). This is considered a broad approach which provides a common context for urban ecology studies throughout the world (McDonnell and Hahs, 2008) whilst capturing reasonably high amounts of variability in the patterns of urbanisation (Hahs and McDonnell, 2006).

1.6 Pollinators in cities

The greenspaces within urban environments have been shown to differ in their value for pollinators, with urban gardens and allotments (areas of urban horticulture) acting as floral and insect pollinator hotspots compared to other greenspaces (Baldock et al., 2019). However, along an urbanisation gradient (increasing impervious surfaces) these greenspaces are become increasingly interwoven with impervious surfaces, which limits the availability of these vital resources (McKinney, 2008). Consequently, it has been shown that the ability to utilise urban greenspaces is highly trait and scale specific, with some traits benefiting insects in urban environments and others being detrimental (Wenzel et al., 2020). Therefore, the extent to which pollinator biodiversity is impacted by urbanisation, as for other anthropogenic impacts such as agricultural intensification, is predicted to be highly dependent on the intensity and heterogeneity of land-use, the spatial scale of investigation, and the taxonomic group studied (McKinney et al. 2008).

To date increasing impervious surfaces along urbanisation gradients have been shown to be linked with changes in pollinator community composition (Bates et al., 2011; Fortel et al., 2014). However, the directions of these changes are not consistent, research outcomes are extremely mixed and contradictory with solid evidence for positive and negative, as well neutral impacts. Wenzel et al. (2020) reviewed 141 studies examining how pollinators respond to increasing urbanisation and found 37% were positively affected by urbanisation, 24% of the studies showed negative effects of urbanisation and 39% found no evidence that urbanisation was influencing pollinator communities. Of these studies there was a heavy bias towards bees as the investigated taxa (70% of studies). Other pollinator groups like flies and moths received considerably less attention.

Bees, moths and hoverflies vary considerably in their life cycles and resource requirements throughout their larval and adult stages both within and across orders. Understanding the divergent life-history traits and subsequent resource requirements of these insect groups is an important step in conserving their populations and the pollination services they provide. Generally, bees depend entirely on floral resources

for both larval and adult stages while most flies and other non-bee flower visitors do not. The adults of hoverflies and moths primarily use floral resources (mostly nectar), but their larval lifestyles are widely variable, even within families (Rader et al., 2020). These variations in resource dependency translate into different responses to environmental pressures.

Variation in life history and larval habit may explain in part the differential sensitivity of insects to environmental change, but this is relatively poorly understood. Bees, for example have been shown to be less sensitive to the effects of urbanisation compared to hoverflies, but highly sensitive to agricultural areas due to the neonicotinoid insecticides and floral resource limitations (Theodorou et al., 2020). Hoverflies show the opposite responses, favouring agricultural over urban areas (Baldock et al., 2015; Theodorou et al., 2020; Verboven et al., 2014), most likely due to changes in the availability of non-floral resources needed by many hoverfly species' larval stages, for example, stagnant ponds (Rader et al., 2020). Moths, to our knowledge, have never been included in research that also investigates diurnal pollinator groups' responses to urbanisation. The relative responses of moths compared to other insect taxa are therefore unknown. However, as a community, they have been shown negatively be influenced by light pollution (MacGregor et al., 2015) and are positively correlated with increased habitat structure (such as more shrubs and trees) in urban areas (Bates et al., 2014; Ellis and Wilkinson, 2021). The habitat quality requirements of non-bee pollinators, especially moths, remain largely unknown and there is a need to evaluate the life history needs of diverse taxa and assess how they vary in time and across habitat quality gradients.

1.7 Opportunities in cities

Within urban areas, greenspaces are highly managed and vary in the resources they provide based on individual management decisions (e.g. homeowner, park manager). Increasing concern over pollinator declines amongst the general public and policymakers has started to shape greenspace management through bottom-up approaches (e.g. 'No-mow may' (Plant Life) and 'Gardening for Wildlife' (RSPB)) and top-down policy measures (see Hall et al., 2017). Improved habitat quality through

increased plant richness and complexity of the vegetation using wildlife-friendly garden management techniques can benefit urban pollinator communities (Muratet and Fontaine, 2015). Supplementing floral resources has also become a focus of pollinator conservation efforts in urban and agricultural areas. Planting either a perennial native seed mix or a non-native annual mix in greenspace areas greatly increases the nectar and pollen resources (Potts et al., 2016) and has been shown to benefit bee communities (Simao et al., 2018; Griffiths-Lee et al., 2022). However, the benefits of these additions for non-bee pollinators are rarely tested.

1.8 Urban horticulture:

Converting homogenous greenspace such as lawns (which have limited ecological value) into heterogeneous and diverse greenspace could improve the overall sustainability of cities (e.g., Baldock et al., 2019; Grafius et al., 2020). For example, allotments (urban green spaces which are composed of plots of land rented by an individual or household for growing fruits and vegetables) represent a large-scale multi-faceted opportunity for city-wide benefits. Evidence suggests that if allotments were to expand into redundant greenspace, food production could increase to feed 12% of a city (Edmondson et al., 2020). The expansion of allotments can add resilience to urban areas through the facilitation of fundamental ecosystem services such as increased biodiversity (Lin et al., 2015), increase refuge for pollinators (Baldock et al., 2019), carbon storage (Edmondson et al., 2014; Dobson et al., 2021a) and health and wellbeing benefits to urban human populations (Dobson et al., 2021b).

Furthermore, urban horticulture is increasingly recognised as being a component of transformed urban food systems that contribute to food security (Mbow et al., 2019). Globally, it is estimated that 15–20 % of global food production already takes place in or near urban areas (Armar-Klemesu, 2000), and worldwide, approximately 800 million people earn their daily livelihood as urban farmers (Wenzel et al., 20210). The food production from urban horticulture, like conventional agriculture, is considerably dependent on insect pollination. Nevertheless, the ability of urban pollinators to provide pollination services in these urban systems is understudied. The underlying mechanisms that influence insect pollination in allotments needs to be understood to

provide informed management plans for the creation of new allotments that are applicable to other greenspaces and also to manage existing allotments to optimise their role in supporting biodiversity and crop production.

For this reason, this research was conducted in urban horticultural sites (allotments) which represent a unique context to examine urban pollinators, their pollination networks and their pollination services for several practical reasons: first, they have relatively high insect and plant diversity), second, they directly benefit from insect pollination through increased food production; and third, they exist along urbanisation gradients which allow us to investigate how heterogeneous urban greenspaces sustain pollinator-plant interactions.

1.9 Knowledge gaps and thesis aims:

The overarching aim of my thesis was to assess how urbanisation gradients influence the biodiversity, plant visitation patterns and pollination services of diurnal and nocturnal insect pollinators. I used multi-disciplinary approaches to assess insect biodiversity using traditional insect sampling methods, molecular methods to construct insect pollen-transport networks and finally experimental pollination techniques to disentangle the drivers influencing pollinating insect communities, urban insect-plant interactions and pollination service delivery. My research was based around three broad themes:

1.9.1 Insect communities:

Despite a surge in urban pollinator research the mechanisms shaping urban pollinator communities, especially non-bee pollinators remain unclear, for two key reasons. First, many studies consider only subsets of potential pollinators in isolation (typically bees, hoverflies or butterflies) rather than undertaking more inclusive sampling. Studies directly comparing diurnal and nocturnal community responses are completely lacking. Secondly, most studies have limited replication, collecting data from a small number of sites, often in a single city. A more complete understanding of urban plant-pollinator biology is required for effective pollinator conservation. To achieve this, data needs to be collected at a much larger scale using a well-replicated experimental design and include multiple scales and pollinator groups.

In Chapter 2 I present a multicity assessment of both nocturnal and diurnal pollinator groups (moths, bees and hoverflies) in twenty-four allotment sites in three cities sampled over an eight-month period throughout the growing season. I quantified the landscape composition surrounding the sites on multiple scales to identify the most important drivers shaping pollinator communities in the U.K. This study aimed to test, for the first time, (i) how both diurnal and nocturnal pollinators respond to increasing urbanisation intensity; (ii) assess the relative sensitivity of three insect groups to urbanisation, and determine whether city-specific variation in land use influences pollinator diversity

1.9.2 Insect-plant interactions:

Pollinator communities are maintained through complex interactions with diverse plant species, and an ecological network approach can inform ecosystem management for pollinators (e.g. Devoto et al., 2011; Banza et al., 2015) by revealing the drivers of taxon-specific declines. However, direct comparisons of diurnal and nocturnal pollination networks are rarely attempted (Devoto et al., 2011; Walton et al., 2020). Consequently, little is known about how greenspace management techniques affect nocturnal pollinators, or whether there are trade-offs between moth- and bee-beneficial interventions.

In Chapter 3 I use DNA metabarcoding to analyse the pollen loads of bees and moths in urban agroecosystems with the aims to (i) analyse plant communities visited by bees and moths, highlighting taxon-specific differences and similarities in host plant visitation; (ii) construct bipartite pollen-transport networks to compare structural differences of moth and bee visitation patterns; (iii) assess the effect of urbanisation on pollen transport by each insect group.

1.9.3 Resource provisioning and pollination services:

The impact of floral additions on pollinators and the pollination services they provide has been well-studied in agricultural contexts where the impact is generally positive

(Haaland et al., 2011; but see Wood et al. 2015). However, despite the rapid expansion of urban areas, fewer studies have been conducted in cities, where the impact of floral additions at different scales remains unclear. Despite their vulnerability to urbanisation, non-bee pollinators are very rarely assessed when examining the benefits of habitat restoration or floral resource supplementation. Due to their non-floral resource requirements, it is likely that the addition of floral resources may not have the same benefits which have been shown in bee communities (Moquet et al., 2018). Additionally, another popular urban habitat addition is the addition of 'bee hotels', which are artificial trap nests with tube cavities that supplement nesting resources for cavity-nesting bees and wasps (Maclvor, 2017). However, despite the clear interlinked dependence on both floral and nesting resources, the effects both these habitat supplementations have on bee communities are rarely empirically tested.

In Chapters 4 and 5 I ran a two-year large-scale manipulation experiment where I added supplemental floral resources (patches of nectar-rich flowers) and nesting resources (trap nests for cavity-nesting bees) and measured subsequent changes to pollination services. In Chapter 4 my aims were to test how enhancing habitat quality can (i) influence bee and non-bee pollinator diversity and abundance, (ii) improve pollination services (crop yields) and finally (iii) assess the differences in visitation patterns of different groups of insect pollinators. In Chapter 5 I monitored bee and wasp uptake of trap nests over two years with two main aims: (i) identify the landscape level drivers affecting trap-nest colonisation and (ii) test if the local additions of floral resources can modulate the effects of urbanisation.

Multi-city study reveals negative effects of urbanisation on moths, hoverflies and bees.

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Abstract:

Insect diversity is declining globally due to land-use change. Urbanisation may be a key driver of insect declines, but the effects of urban densification on insect pollinator communities within complex urban landscapes remain poorly understood, particularly for important non-bee pollinators such as flies and moths. We assessed the impacts of urban densification on non-managed, wild bee, hoverfly and moth diversity and abundance along replicate urbanisation gradients in three cities. There were consistent negative effects of increasing greyspace on the species richness of bees, hoverflies and moths in all cities, suggesting that divergent insect groups are declining due to the abiotic stress or limited resources of urban environments. Landscape mapping indicates that these effects are driven in part by the reduction of semi-natural habitat and tree cover with increasing greyspace, suggesting that urban insect conservation depends on the preservation of these habitats in cities. Finally, we show that moths and hoverflies are particularly sensitive to urbanisation, and we highlight the importance of including these frequently overlooked insect groups when assessing the biodiversity impacts of environmental change.

Introduction:

Pollinating insects are vital for the reproduction of 60-90% of plant species worldwide and have been deemed critical for 35% of crop species (Klein et al., 2007; Klatt et al., 2013; Rader et al., 2016). Significant declines in the abundance and diversity of a wide range of insect taxa are commonly reported (Potts et al., 2010), including butterflies

(van Strien et al., 2019), bees (Potts et al., 2010; Ollerton et al., 2011; Lintott et al., 2014) and moths (Fox et al., 2021; Wagner et al. 2021b), raising concerns about the pollination services underpinning natural and managed ecosystems. Climate change, habitat fragmentation and loss, and degradation of habitat quality have been proposed as some of the main drivers of insect declines (Hallmann et al., 2017).

Urbanisation may be a key driver of insect declines (Wagner et al., 2021a) but the effects of urban densification on insect pollinator communities remain poorly understood for most insect taxa. Urban expansion causes biodiversity loss in the form of reduced species richness and biotic homogenisation through habitat fragmentation, loss and disturbance (McKinney, 2006; Seto et al. 2012). Urban areas are expanding and are expected to triple from 2000 to 2030 (Seto et al., 2012) and as land-use for urbanisation increases, an improved understanding of the ecological processes driving urban species diversity is an important prerequisite to developing ecologically sustainable cities.

The extent to which pollinator biodiversity is impacted by urbanisation, is predicted to be highly dependent on the intensity and heterogeneity of land-use, spatial scale, and the taxonomic group studied (McKinney, 2008). While many studies have contrasted 'urban' and 'rural' areas (Theodorou et al., 2020) cities are composed of complex habitat mosaics, with non-linear gradients of urban intensity. Understanding this complexity requires the identification of the local scale-dependent mechanisms and processes that drive ecological interactions. Within cities, the value of different greenspaces for urban pollinators can vary due to different land-uses and subsequent resource provision. For example, home gardens and allotments (community horticultural gardens) have been shown to act as urban pollinator diversity hotspots due to their high proportions of floral and nesting resources compared to other greenspaces such as parkland (Baldock et al., 2019). However, the suitability of urban greenspaces can be highly taxon-specific (Wenzel et al., 2020). For example, Lepidoptera have different adult and larval resource requirements and thus may be less resilient to urbanisation compared to bees (Theodorou et al., 2020).

Despite the considerable body of pollinator research (Baldock et al., 2020; Wenzel et al., 2020) the mechanisms shaping urban pollinator communities, especially non-bee

pollinators, remain unclear, for three key reasons. First, many studies consider only subsets of potential pollinators in isolation (typically bees, hoverflies, or butterflies) rather than undertaking more inclusive sampling (but see Bates et al., 2014; Baldock et al., 2019; Theodorou et al., 2020). Second, there have been relatively few studies relating local diversity to the landscape composition surrounding the study system, in order to assess whether taxa differ in their resilience to urbanisation. Finally, most studies have sampled single cities, which can vary significantly in habitat availability and composition of the urban fabric, thus obscuring generalisation about the factors supporting pollinating insects.

We assessed both nocturnal and diurnal pollinator groups (moths, bees and hoverflies) along urbanisation gradients in three cities. The aims of this study were to test, for the first time, 1) how both diurnal and nocturnal pollinators respond to increasing urbanisation intensity; 2) assess the relative sensitivity of three insect orders (Lepidoptera, Hymenoptera and Diptera) to urbanisation; and 3) determine whether city-specific variation in land use influences pollinator diversity. We predicted that increasing urbanisation would lead to lower pollinator diversity and abundance, with more negative impacts on moths and flies due to their more complex resource requirements.

Methods

Study system:

This study was carried out in greenspaces used for urban horticulture (allotments). Allotments are urban green spaces comprising plots of land rented by individuals or households for growing fruits and vegetables. They directly benefit from insect pollination through increased food production and they exist along urbanisation gradients which allow us to investigate how changes in landscape composition surrounding these urban greenspaces affect their ability to sustain diverse pollinator communities.

Study area description:

Three UK cities were selected for this study, Leeds, Leicester, and Sheffield which are good representatives of U.K. city structure (see Grafius et al., 2019; Figure 2.1; Table 2.1). Within each city, eight allotment sites were selected along a gradient of urbanisation from the city centre to the edge of the administrative boundary (Supplementary Methods S1; Supplementary Material Figure S2.1 and Table S2.0). Preliminary analysis showed distance from the city centre was indeed a good proxy for increasing urbanisation, explaining 77% of the variation in greyspace surrounding our sites (at a 1000m buffer; $F_{(2,24)} = 13.98$, $df = 2$, $p < 0.00001$; Supplementary Material Figure S2.2). Within each city, the eight sites were at least 2 km apart; however, Leicester, a small city (only 14km wide), had some sites that were closer together (minimum distance of 1 km). Although the dispersal abilities of some insect taxa are greater than the distance between sites, the disturbed nature of urban environments, such as habitat fragmentation and topographic barriers (e.g., buildings), means they have high degrees of independence.

Table 2. 1 Size and total area of greyspace of three cities in the U.K.

City	Size (km ²)	Area of greyspace (km ²)	
Leeds	579	101	(17%)
Leicester	73	61	(83%)
Sheffield	368	123	(33%)

Insect sampling:

We measured the abundance and species richness of three groups of flying insect pollinators: diurnal hoverflies (Diptera: Syrphidae) and bees (Hymenoptera: Anthophila), and nocturnal moths (Lepidoptera). We sampled insects for six months (May-October 2019) using a robust combination of biodiversity monitoring methods, including Malaise traps sweep netting, and light trapping (See Supplementary Methods S2 for more details). The combination of techniques minimizes potential biases of each method (e.g., taxonomic bias, see Campbell and Hanula, 2007; Thompson et al., 2021).

Malaise traps: These flight intercept traps are time- and cost-effective and have been shown to be well-suited for comparative studies of the flying arthropod fauna at a large geographical scale (Diserud et al., 2013). Twenty-four Malaise traps (NHBS code) (one per site) were simultaneously deployed for the first seven days of each month between the beginning of May-October 2019. The Malaise traps were set up close to the centre of the allotment along a natural insect flight path (i.e. perpendicular to the main path through the allotment). The sample bottles were filled one-third with 100% non-toxic propylene glycol.

Timed transects: diurnal bees and hoverflies were collected at each site at three time points during the season (early summer = May; midsummer = June; late summer = September) by timed line-transects through the main path of the site and also on individually managed plots (Supplementary Methods S2). Site transects consisted of a fixed time of thirty minutes along the main path running through the allotment. For plot-level transects, three individually managed plots (spread across the site) were sampled for a fixed time of 10 minutes per plot (Supplementary Methods S2).

Light traps: nocturnal moths were sampled on calm, warm nights (paired with each diurnal collection) using a 12-volt portable Heath Trap equipped with a 15W actinic bulb (NHBS product code SK22). All sites within each city (n=8) were sampled from dusk until dawn on the same night and all cities were sampled within 5 days of each other and during the same week as the diurnal collections at each sampling point.

Local, landscape and city scale variables:

To determine the main environmental drivers shaping insect biodiversity along an urbanisation gradient, we gathered a series of local (site) and landscape-level variables that are potentially related to insect pollinators. We measured two allotment site-level variables: 1) Site cultivation: allotment site land cover was measured using surveys conducted at a site level where the individual plots within the site were given a score between 0-5 based on the cover of cultivated ground on their plot (zero being completely unused, 5 being 100% managed with no unkempt areas). A site-level overall cultivation score was then calculated. 2) Allotment site size (m²) was extracted

from the OS Greenspaces layer in Mastermap in a geographic information system (GIS) (ArcGIS version 10.7.1; see Supplementary Methods S1).

Landscape variables were quantified at three spatial scales surrounding each site: circular buffers (with the centre of the site being the centre point of the circle) with radii of 250 m, 500 m, and 1000 m were drawn, using ArcGIS. Land cover in each buffer was extracted from OS Mastermap and tree canopy cover was extracted from the National Tree Map (Bluesky ©). The land cover characteristics we extracted at a landscape scale were (i) area of greyspace cover (building, roads, and impervious surfaces), (ii) area of semi-natural cover (scrub, grassland and shrubs), (iii) the area of gardens and (iv) area of tree canopy.

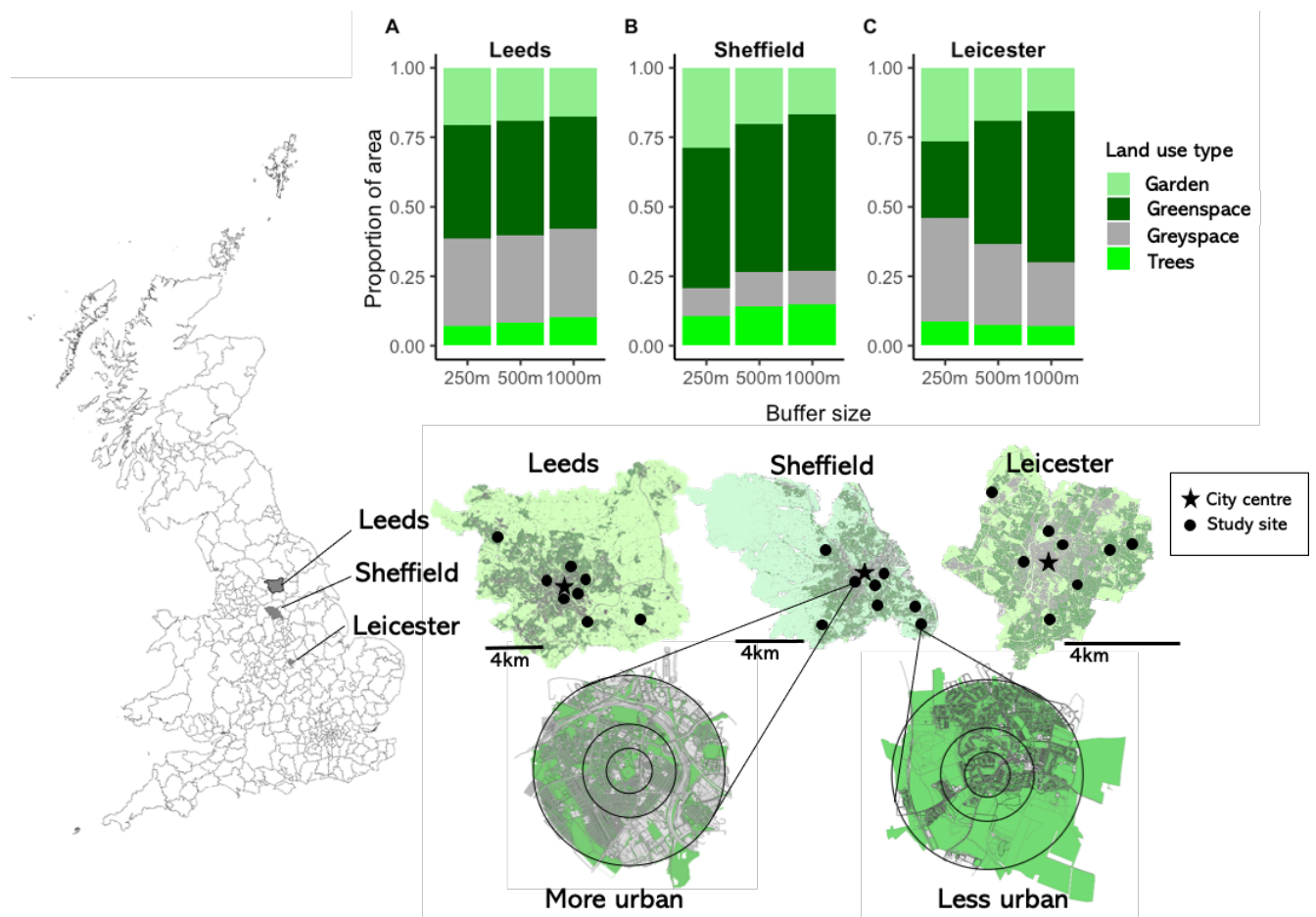


Figure 2. 1 Landscape composition of Leeds, Sheffield and Leicester. Left the city locations within the UK. Top right, the proportion of area of garden, greenspace, greyspace and trees surrounding eight allotment sites across A) Leeds, B) Sheffield, C) Leicester, at three different scales surrounding the site;

250m, 500m and 1000m. Middle right, maps of Leeds, Sheffield and Leicester showing their greenspace (green) and greyspace (grey) areas and the site locations (black dots). Bottom right, examples of highly urban and least urban (left-right) along the urbanisation gradients in Sheffield. Circles within the map depict buffers at which landscape composition was measured; 250m, 500m and 1000m.

Data analysis:

All analyses were done in R version 4.12 (R Core Team, 2022).

Insect data was aggregated across the season and sampling method to gain an insight into the overall abundance and species richness of bees, moths and hoverflies in each site. These were all subsequently analysed as the response variable in our models (outlined below).

Generalised linear mixed effect models (lme4::glmer, Bates et al., 2015) and generalised linear models (glm) were used to identify how local and landscape variables affected insect communities. We had two approaches to the analysis. Our first approach was to test how insect communities respond to total landscape gradients, which involved aggregating data for all cities in the analysis. The rationale for this analysis was due to the variation in the range of urbanisation gradients each city captured (Figure 2.2). The sites collectively (n = 24) characterised a well-represented gradient of landscape proportion of greyspace cover spanning from 6-63%. We first tested total the response of total insect communities (aggregated by site) along landscape habitat gradients (habitat variables: (i) area of greyspace cover (building, roads, and impervious surfaces), (ii) area of semi-natural cover (scrub, grassland and shrubs), (iii) the area of gardens and (iv) area of tree canopy).

*measure of total insect diversity ~ habitat variable + Site size +
Site cultivation*

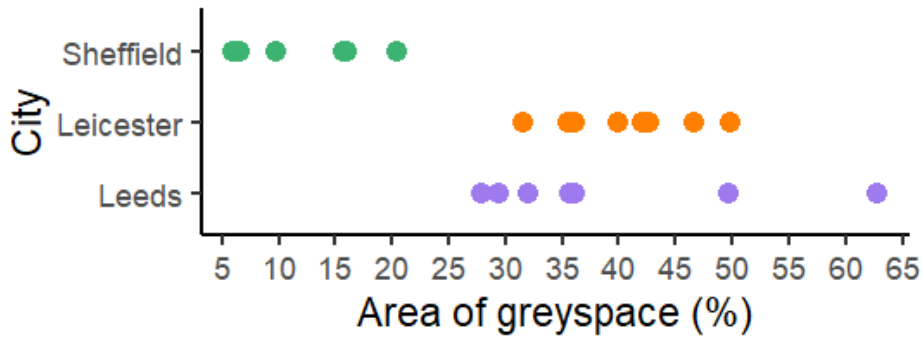


Figure 2. 2 Allotments sites (points) plotted based on the proportion of greyspace in the 250m surrounding the sites. The variation in the urbanisation gradient captured across Leeds, Leicester and Sheffield.

Our second approach accounted for insect taxa across city and their interactions. Specifically, to test how insect communities respond to landscape composition and if these responses varied across insect taxa and city (while correcting for local covariates):

$$\begin{aligned}
 \textit{measure of insect diversity} &\sim \textit{City} + \textit{Insect taxon} + \textit{habitat variable} \\
 &+ (\textit{City} * \textit{Insect taxa}) + (\textit{habitat variable} * \textit{Insect taxa}) \\
 &+ (\textit{City} * \textit{environmental variable}) + \textit{Site size} \\
 &+ \textit{Site cultivation} + .(1|\textit{Site}).
 \end{aligned}$$

As the environmental explanatory variables were proportions of land-use (area of greyspace, semi-natural area, tree canopy and gardens) in the same area, they were highly correlated, therefore they were analysed separately. The second approach of analysis was carried out again but with insect abundance included as an explanatory model term when testing the influence landscape has on species richness. This was to account for the differences in abundances found across sites. All models followed Gaussian fit except for the abundance data which was fitted with Poisson distribution. When models were fitted with Poisson distribution assumptions, they were tested for overdispersion using DHARMA::testDispersion (Hartig, 2022). Overdispersion corrections (observational random effects) were added to ensure models were not overdispersed. All residual diagnostics were examined using the DHARMA package.

To test if the cities differed based on the landscape composition surrounding the sites (area of greyspace, tree canopies, gardens and semi-natural habitat) and insect community structure, we performed multivariate analysis using the ‘vegan’ package. Landscape composition across cities was compared based on the largest scale (1000m). Non-metric multidimensional scaling (NMDS) was used to visualise the sites and how they cluster based on their 1) landscape composition and 2) insect community composition. The differences between the cities were tested using an analysis of similarities (ANOSIM).

Results:

Insect communities:

In total, we collected 10,799 insects belonging to 322 species. Hoverflies were the most abundant accounting for 42% of the total abundance, and moths accounted for 49% of the total species richness (Table 2.2; Species lists Supplementary Material Tables S2.1-S2.3).

Table 2. 2 Total insect community data

Taxa	Abundance	Species richness
Bees	3333	60
Hoverflies	4589	106
Moths	2877	157
Total	10,799	322

The overall city-scale landscape composition differed considerably across city. When cities were analysed at a city level, Leeds had the lowest proportion of greyspace (17%) and Leicester had the highest (83%) (Table 2.1). Analysis of similarity (ANOSIM) show all cities were significantly different ($p < 0.05$; Supplementary Material Figure S2.3).

We found that insect species richness ($F_{(4,40)} = 3.92$, $p = 0.007$) and abundance ($\chi^2 = 19.9$, $df = 4$, $p < 0.001$; Figure 2.3), differed among cities and this appeared to be driven by significantly lower moth abundance and species richness in Leeds, compared to

the other cities (Figure 2.3). However, NMDS plots showed that there were no significant differences in hoverfly (ANOSIM $R^2 = 0.088$, $p = 0.082$), moth (ANOSIM $R^2 = 0.076$, $p = 0.12$) or bee (ANOSIM $R^2 = 0.03$, $p = 0.28$) community composition when comparing cities (Supplementary Material Figure S2.4).

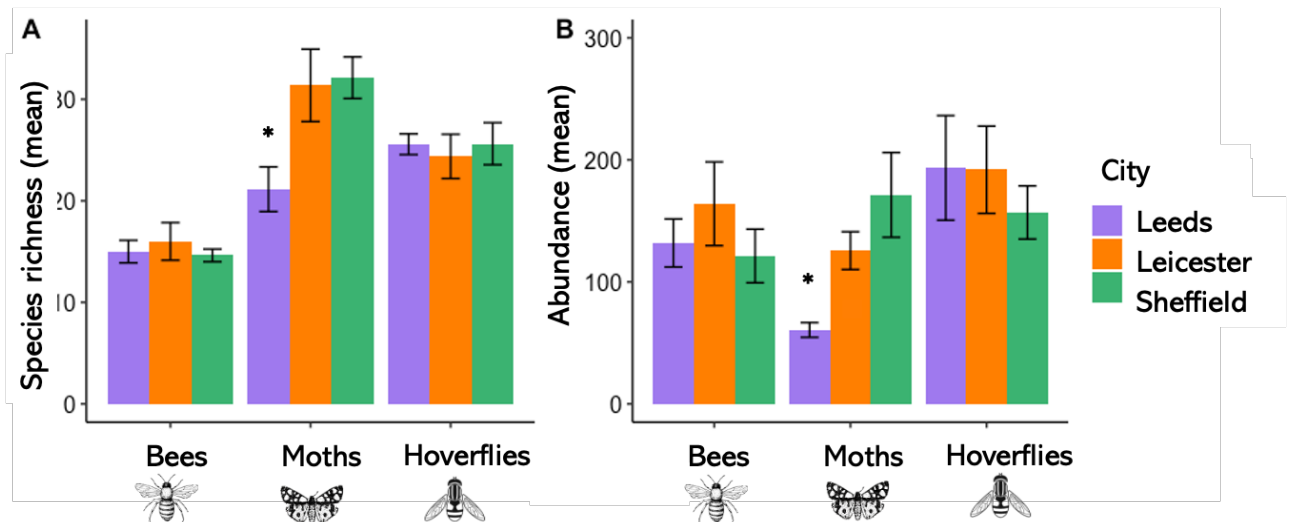


Figure 2. 3 The mean a) abundance and b) species richness of bees, moths and hoverflies in three cities (averaged by eight sites in each city). Bars are standard error bars. Stars depict significantly lower mean abundance and species richness of moths in Leeds compared to Leicester and Sheffield.

Urbanisation gradients:

Across all our analyses, we found that sites with lower proportions of surrounding greyspace (less urban) supported higher, abundance and species richness of bees, moths, and hoverflies and that this is driven by the reduction in the area of tree canopy and semi-natural habitat as urbanisation increased. When city was excluded, we show that total insect species richness was strongly negatively affected by increasing area of greyspace (Figure 2.4A) and this pattern was seen at 250m ($F_{(1,19)} = 8.23$, $p = 0.009$), 500m ($F_{(1,19)} = 5.10$, $p = 0.036$), 1000m ($F_{(1,19)} = 6.025$, $p = 0.024$). This pattern was not shown when the abundance of insects was tested at 250m ($F_{(1,19)} = 2.19$, $p = 0.16$: Figure 2.4B) nor at any other scale tested (Supplementary Material Table S2.4).

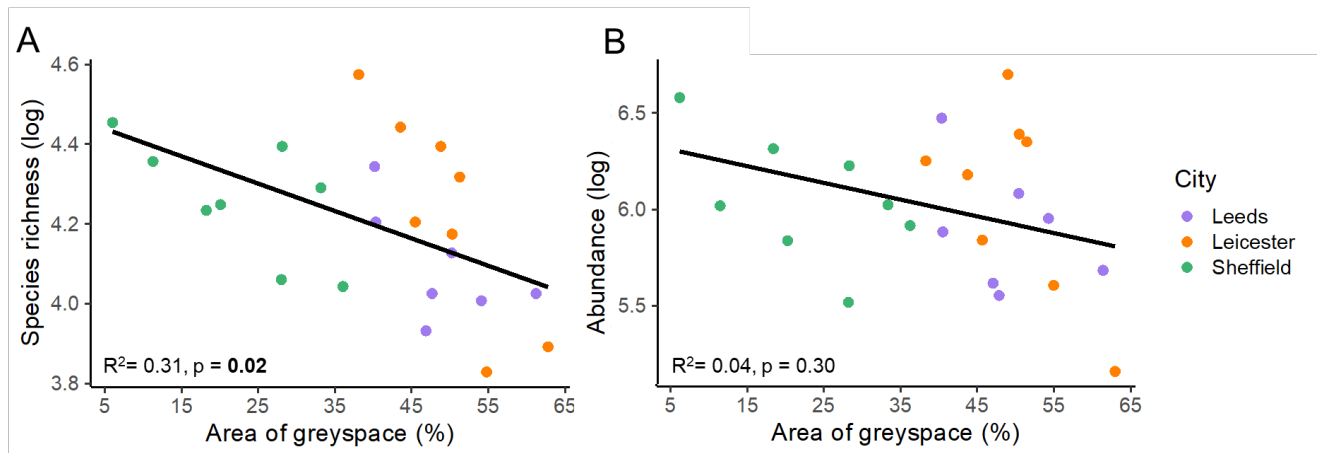


Figure 2. 4 Pollinating insect community responses to the increasing area of greyspace (%) surrounding urban horticultural sites in Leeds, Leicester and Sheffield. A) Total species richness and B) total abundance of bees, moths and hoverflies collected in 24 allotment sites in three cities. Lines fitted are generalised linear model prediction testing insect species richness and abundance along an urbanisation gradient and p values derived from analysis of variance type II.

When all cities were included in the analysis, we found consistent patterns of decline across the three cities and insect groups (Figure 2.5A). The negative effects of urbanisation were clearest at a scale of 250 m where insect species richness was declining as urbanisation increased ($F_{(1,17)} = 10.86$; $p = 0.005$; Figure 2.5A). There was some evidence of insect species richness declines were city specific but only at 500 m ($F_{(2,17)} = 5.28$, $p = 0.048$), where only Leicester had significant declines of species richness as area of greyspace increased (Supplementary Material Figure S2.5). There were significant insect taxa x urbanisation interactions when the abundance of insects was analysed ($F_{(2,40)} = 4.13$, $p = 0.023$; Figure 2.5B). Post-hoc tests showed that the abundance of moths ($p = 0.007$) and hoverflies ($p = 0.045$) declined as urbanisation increased but bees were not influenced ($p = 0.80$; Supplementary Material Table S2.5). The overall patterns of decline were also observed when insect abundance was included in the models (Supplementary Material 2 Figure S2.7, Table S2.6).

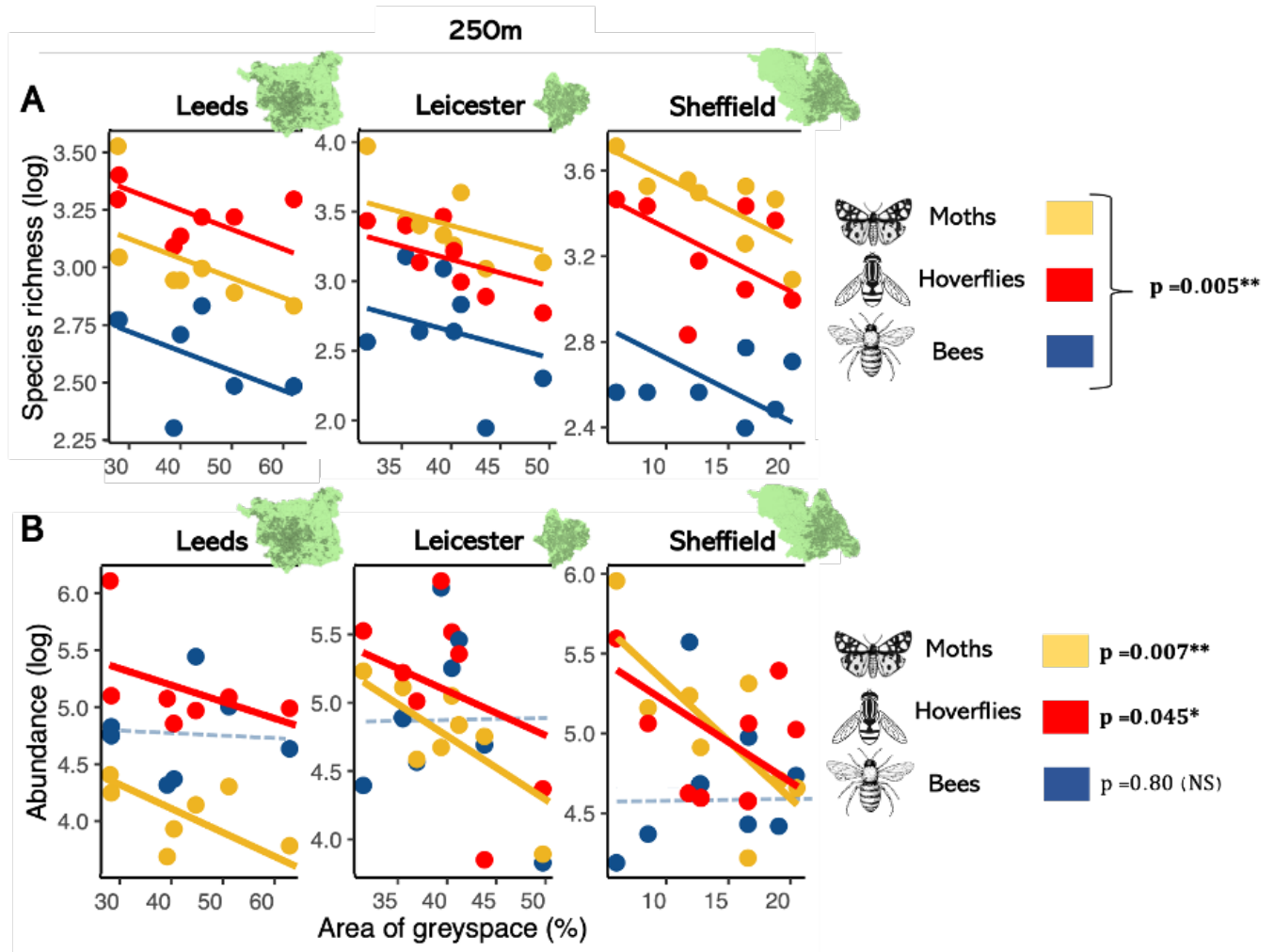





Figure 2. 5 A) Insect species richness of moths hoverflies and bees decreases as area of greyspace surrounding allotment sites (250m) increases in three cities. Lines show model predictions with no significant interactions of city:urbanisation or insect:urbanisation. B) Insect abundance of moths and hoverflies decreases as area of greyspace surrounding allotment sites increases, lines show no significant interaction with city:urbanisation but a significant insect:urbanisation interaction where bee abundance was not significant (Supplementary Material Table S2.5).

Greenspaces:

When city was excluded from the analysis, there were positive effects of increasing tree canopy and semi-natural habitat on insect species richness at multiple scales (Figure 2.6). We found positive effects of area semi-natural habitat on the total species richness of our sites when analysed at 500 m and 1000 m (Figure 2.6). Total species richness was positively associated with increasing the area of tree canopy at 500 m

($F_{(1,21)} = 5.34, p = 0.031$). The only evidence of a positive effect of semi-natural habitat on the abundance of insects was found at the largest 1000 m scale (Supplementary Material Figure S2.6, $F_{(1,21)} = 7.33, p = 0.006$).

Total species richness

Land use type	Buffer scale		
	250m	500m	1000m
Tree canopy 	NS $F_{(1,21)} = 4.08; p = 0.05$	* $F_{(1,21)} = 5.35; p = 0.03$	NS $F_{(1,21)} = 2.67; p = 0.12$
Semi-natural habitat 	NS $F_{(1,21)} = 2.7; p = 0.11$	** $F_{(1,21)} = 9.6; p = 0.005$	** $F_{(1,21)} = 9.3; p = 0.006$
Gardens 	NS $F_{(1,21)} = 0.05; p = 0.82$	NS $F_{(1,21)} = 1.4; p = 0.25$	NS $F_{(1,21)} = 1.3; p = 0.26$

	Positive effect
	Not significant $p > 0.05$

Figure 2. 6 The effect of increasing area of tree canopy, area of semi-natural greenspaces and area of gardens on the total species richness of bees, moths and hoverflies across the three cities. Landscape composition was measured at three buffer scales surrounding sites of urban horticulture (250m, 500m, 1000m). Colours of cells indicate positive response (or non-significant) effects tested using Anova type II of generalized linear models.

When greenspace composition was analysed across cities and insect taxa, the responses were varied and scale-dependent (see summary in Figure 2.7). There was a significant insect species richness x area of tree canopy interaction at 250m ($F_{(2,42)} = 4.67, p = 0.014$). Moths were the only insect taxa that responded positively at the 250 m scale, and were distinct from other taxa in their positive response to tree cover ($F_{(1,30)} = 6.49, p = 0.016$) (Figure 2.7). At the larger scales, the species richness of all three insect groups responded positively to increasing areas of semi-natural habitat (Figure 2.7). The area of gardens had no detectable effect on the insect communities across all our analyses. These patterns were largely influenced by insect abundance as seen when insect abundance was included in the models there was a loss of significant tree canopy effects (Supplementary Material 2 Figure S2.7, Table S2.6).

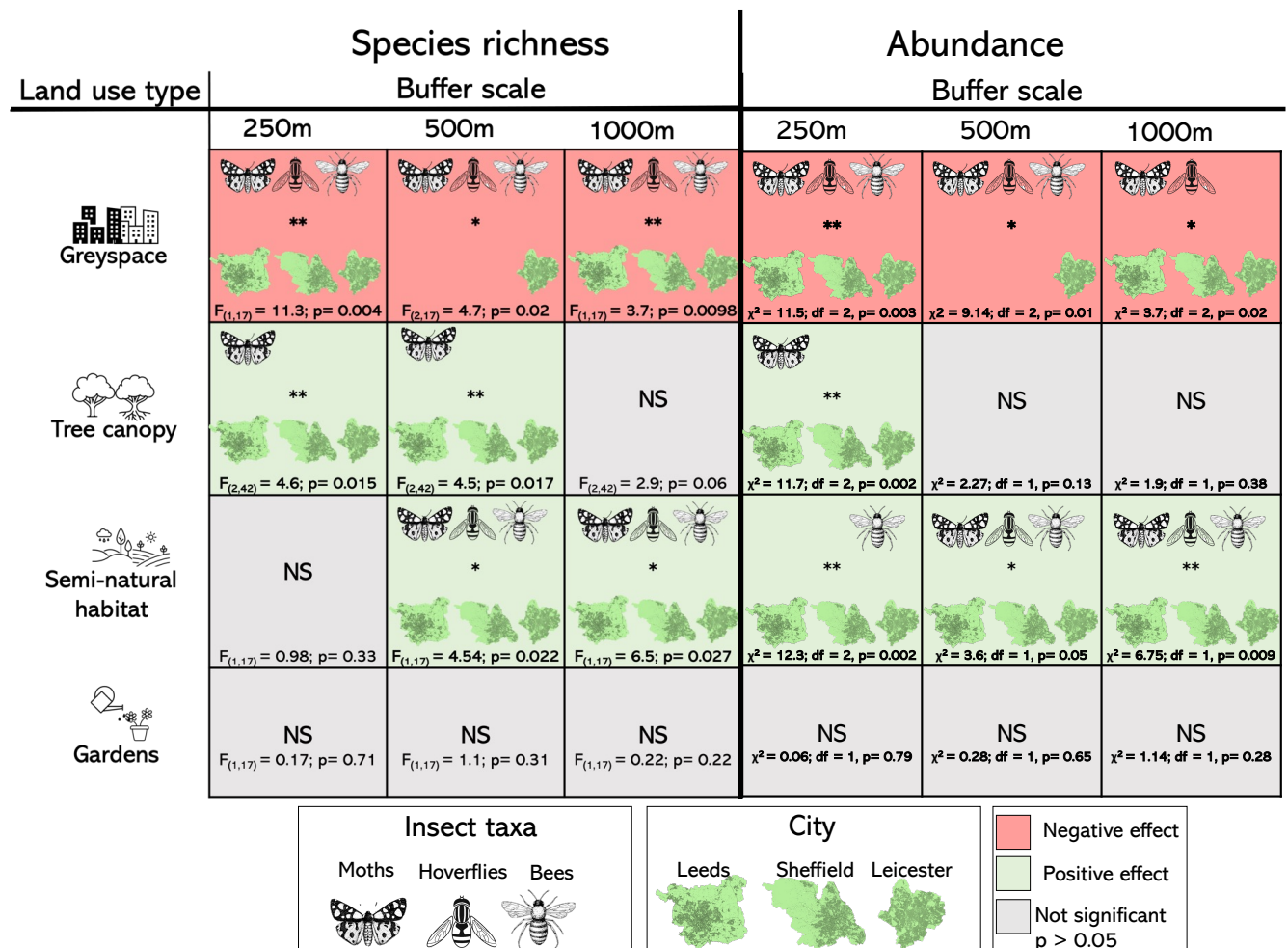


Figure 2. 7 Disentangling the landscape drivers of insect communities in urban agroecosystems across multiple scales. The effect of area of greyspace, area of tree canopy, area of semi-natural greenspaces and area of gardens on the species richness and abundance of bees, moths and hoverflies across the three cities. Landscape composition was measured at three scales surrounding sites of urban horticulture (250m, 500m, 1000m). Colours of cells indicate positive or negative response (or non-significant) effects tested using anova type II of generalized linear mixed effect models. Icons of insect taxa and city indicate if there were significant interactions between the environmental variable and insect taxa/ city.

Discussion:

Our results demonstrate significant negative impacts of increasing urbanisation on the species richness of three divergent insect groups, including both nocturnal and diurnal taxa. There were consistent negative effects of increasing greyspace in all three cities,

with a 57% decline in species richness from our least urban site (greyspace proportion 5%) compared to our most urban site (greyspace proportion 65%) indicating that for every 10% increase of greyspace there is almost 10% decline in species richness. Urban areas continue to rapidly expand, and they are predicted to triple in land cover by 2030 (Seto et al., 2013). The geographic and taxonomic generality of our findings suggests that these changes will lead contribute significantly to declines in a wide range of pollinating insects, with significant implications for the future of pollination ecosystem services in cities.

While there were relatively similar declines of all taxa (Figure 2.5A), there was evidence that moths and flies may be disproportionately affected by urbanisation compared to bees. There are several potentially non-exclusive mechanisms for this heightened sensitivity. First, unlike bees, moths and flies are dependent on non-floral resources to complete the larval component of their lifecycles. These insects may therefore be more sensitive to urbanisation due to more specific larval host plant and prey requirements (Groenendijk and Ellis, 2011; Rader et al., 2020). Our result shows that moths may benefit from increased tree cover (Figure 2.7) or semi-natural habitat. Urban city trees add structural complexity to urban habitat and may benefit urban moth assemblages (Ellis and Wilkinson, 2020) potentially by increasing the availability of day-time roosting locations, larval host plants (Bates et al., 2014), or adult food sources (Ellis et al., *in review*). Finally, moths have been shown to be more sensitive to pollution, which covaries positively with urban intensity (Azam et al., 2016) and has the potential to undermine both adult and larval life stages. Adult moths are negatively affected by light pollution, which may disrupt reproduction, dispersal and foraging (Macgregor et al., 2015; Merckx et al., 2018; Boyes et al., 2021), and moth larvae are negatively affected by air pollution, which reduces host plant quality (Campbell and Vallano, 2018). The potential for multiple urban stressors to affect both adult and larval life stages may be a significant factor in the nocturnal moth declines we document in this study.

In contrast to moths, bee abundance results suggest that bees may be more resilient to urbanisation compared to moths and hoverflies (Figure 2.5B). This may be due in part to the fact that bees feed on floral resources as both adults and larvae, (e.g., Wilson and Jamieson 2019; Gerner and Sargent, 2022). Allotments have been shown

to contain the highest abundance of both floral resources and insect pollinators compared to other greenspaces (Baldock et al., 2019; Borysiak et al., 2017). They contain a relatively high diversity of crop and wild flowering plants that could provide sufficient floral resources for adult bees and their offspring. The evidence that bees are resilient to urbanisation has been observed previously (Cane et al., 2006; Banaszak-Cibicka and Zmihorski, 2012; Hinners et al., 2012; Cardoso and Gonçalves, 2018; Wilson and Jamieson, 2019) and also when compared to other diurnal taxa such as hoverflies (Verboven et al., 2014; Theodorou et al., 2020). Diet breadth has been shown to be a pivotal trait when predicting pollinator resilience to urbanisation (Banasza-Cibicka and Zmihorski, 2012; Wray and Elle, 2015) and studies that have shown positive effects of urbanisation on pollinators appear to be driven by high abundance of generalist (e.g. bumble bees and halictid bees) and managed bee species (i.e., domesticated honeybees) (e.g. Bennet and Lovell, 2019). The sociality behaviour of the bees in our dataset (88% of all bees collected) permits behavioural and ecological flexibility that might also facilitate survival in urbanised environments (Banasza-Cibicka and Zmihorski, 2012). Our finding that urbanisation is driving down bee diversity (Figure 2.5A) but not abundance (Figure 2.5B) is consistent with a shift to more generalist-dominated bee communities, which may have significant implications for pollination services. For example, in a follow-on study we have shown that the negative impacts of urbanisation on bee diversity led to declines in the pollination of experimental plants (Ellis et al., *in prep(b)*).

Our multiscale analysis of the landscape features driving insect declines provides insight into the spatial scales which may be relevant to taxon-specific responses to urbanisation (Concepcion et al., 2015). Our three cities varied considerably in their urbanisation intensity gradients, their total landscape composition and their local landscape configurations (Supplementary Material Figure S2.3). However, there were consistent effects, of landscape composition (Figure 2.7) suggesting that processes occurring within a city are driven by the local scale of landscape configurations (i.e. 250m- 1000m). Nevertheless, at 500m there was evidence that there were stronger negative influences of increasing greyspace in Leicester compared to the other cities. Leicester was the smallest city and had the highest area of greyspace when assessed at a city level, suggesting that city level greyspace is also an important factor to consider when assessing patterns of urban insect communities (as shown in Niemela

et al., 2000). There was also evidence of taxonomic variation in which drivers were more important: Moths were the only insect group to respond positively to increasing area of tree canopy and the only insect group that were influenced at the smaller scale buffer of greenspace. These small-scale responses of moth species richness suggest that they may be more reliant on the landscape matrix surrounding the allotment sites, and particularly surrounding tree cover, compared to bees and hoverflies. Flowering city trees have also been found to play an important role as a floral food source for both bees (Hausmann et al., 2015; Maclvor et al., 2014) and moths (Ellis et al., *in review*). Surrounding tree canopy has also been associated with increased pollination service delivery of urban garden crop yields (McDougall et al., 2022). Finally, we found that bees, hoverflies and moths benefited from higher areas of semi-natural habitat (Figures 2.6 and 2.7) which further highlights the importance of complex habitats, rich in floral, larval host plants and nesting resources.

In contrast to other studies, we found no effect of urban domestic gardens on bees (Gunnarsson and Federsel, 2014). Gardens are typically thought to benefit bees, and garden management (e.g., mowing/pruning frequency) has been shown to be an important factor for bees (del Toro and Ribbons, 2020; Lerman et al., 2018), hoverflies (Garbuzov et al., 2014) and moths (Ellis and Wilkinson, 2021). Urban domestic gardens vary significantly in their management, from completely paved to 'wildlife friendly gardening'. Thus, the lack of a significant effect of gardens in our analysis may be a result of our inability to assess this variation using GIS based tools. However, we note that gardens were not correlated with greyspace, unlike semi-natural habitat and trees. This suggests that the effects of urbanisation on insects is unlikely to have been driven by garden availability in the urban forms comprised by our three cities, and that any benefits of gardens will require further study along explicit urbanisation gradients.

Conclusions:

We provide evidence that increasing urbanisation has striking negative effects on the species richness and abundance of both nocturnal and diurnal pollinators, including bees, moths, and hoverflies. Our results highlight that the appropriate urban planning and stakeholder engagement to provide local floral, nesting, and larval food resources by increasing the cover of semi-natural vegetation and trees could enhance their

values as refuges for species affected by densification of impervious surfaces. Scale-specific responses to urban landscape composition demonstrate that it is also vital to take into account the dispersal abilities and life history trait differences across important non-bee pollinators such as moths and hoverflies when managing these systems for pollinators.

Negative effects of urbanisation on diurnal and nocturnal pollen-transport networks

In review in Ecology Letters

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Abstract

Pollinating insects are declining due to habitat loss and climate change, threatening the pollination of crops and wild plants. Plant-pollinator interactions may be particularly vulnerable in cities, where urban greenspaces provide limited habitat and floral resources. However, the effects of heterogeneous urban landscapes on pollination networks remain poorly understood for many important insect taxa. Here, we use DNA metabarcoding to test the effects of urbanisation on the pollen-transport networks of diurnal and nocturnal pollinators in urban agroecosystems. Diurnal bees and nocturnal moths exhibit substantial divergence in the communities of plants they interact with, indicating distinct, seasonally-dependent urban niches of nocturnal and diurnal pollinators. Despite the different life histories and host ranges of bees and moths, there were striking negative effects of increasing urbanisation on the pollen-transport networks of both taxa, with important implications for insect conservation and urban plant communities. We show that nocturnal moths are an important, but frequently overlooked, component of urban pollen-transport networks for wild flowering plants, horticultural crops and trees, accounting for up to one third of the interactions in this system. In the face of rapidly declining bee and moth populations, our results highlight the critical importance of understanding the factors that impact urban pollinators, with implications for ecosystem service provision in cities, management of urban greenspaces, and the conservation of urban wildlife.

Introduction

Pollinating insect biodiversity is declining due to habitat loss and climate change (Fox et al., 2014; Outhwaite et al., 2020; Wagner et al., 2021a). Declines in bees (Biesmeijer et al., 2006; Potts et al., 2010; Ollerton et al., 2014), flies (Hallmann et al., 2021) and moths (Conrad et al., 2006; Groenendijk and Ellis 2011; Wagner et al., 2021b) have been well-documented, raising concerns about the resilience of key ecosystem services, particularly pollination of food crops (Vanbergen et al., 2013) and wild plants (Ollerton et al., 2011). A range of anthropogenic drivers contribute to pollinating insect declines, however, research on these drivers has focussed predominantly on diurnal bees (Wagner et al., 2021a, Potts et al., 2010; Winfree et al., 2011), and the causes underlying declines of other taxa (e.g., nocturnal moths) with different resource requirements and life histories remain unclear.

A major cause of pollinator decline is the rapid expansion of urban areas, and the concomitant increases in habitat fragmentation and degradation (McKinney 2006; Seto et al., 2012; Wagner et al., 2021a). Urban greenspaces can provide habitat and resources for pollinators (Hall et al., 2017). However, individual greenspaces (e.g., allotment gardens, parks, urban woodlands) are managed for a variety of purposes (e.g., urban horticulture, recreation, gardening), leading to significant variation in habitat heterogeneity and the diversity of native, non-native, and invasive species (Niinemets and Peñuelas, 2008). Consequently, while urban greenspaces can support large numbers of pollinating insects compared with neighbouring agricultural areas (Baldock et al., 2015; Theodorou et al., 2017; Theodorou et al., 2020), they vary in pollinator diversity (Baldock et al., 2019), and the underlying landscape-level drivers of this variation have not been clearly identified. As a result, the suitability of urban areas for different taxonomic groups of pollinators, with potentially divergent responses to urbanisation, remains poorly understood.

Pollinator communities are maintained through complex interactions with diverse plant species, and an ecological network approach can inform ecosystem management for pollinators (Devoto et al., 2011; Banza et al., 2015; Banza et al., 2019) by revealing the drivers of taxon-specific declines. For example, a key constraint on the diversity of insect communities is the availability of diverse host plants that support adult and/or

larval feeding. The sensitivity of different taxa to urbanisation should depend in part on the relative resilience of their plant interaction networks, with specialist species using few larval host plants (i.e., most nocturnal Lepidoptera) predicted to be less resilient compared to generalists (i.e., many bees). However, direct comparisons of diurnal and nocturnal pollination networks are rarely attempted (Devoto et al., 2011; Alison et al., 2020; Walton et al., 2020). This can be due to sampling challenges: wild bees (non-managed Hymenoptera) are a main component of diurnal pollination networks and have been the emphasis of considerable research (Prendergast et al., 2022), due in part to the relative ease of assessing diurnal plant visitation (Macgregor et al., 2015). Conversely, moths (Lepidoptera) are the primary component of temperate nocturnal pollen-transport networks and are globally important pollen vectors for a diverse range of plant taxa (Hahn and Brühl, 2016). However, due to the difficulty of direct nocturnal observation, moth pollination networks remain poorly understood. Consequently, little is known about how different greenspace management tactics affect nocturnal pollinators, or whether there are trade-offs between moth- and bee-beneficial interventions. For example, while bees may benefit from wildflower planting (Wilson and Jamieson, 2019), moth assemblages have been shown to benefit from increasing tree and shrub density (Ellis and Wilkinson, 2021; Bates et al., 2014). Some of the limitations of observation-based pollination networks can be overcome by identification of the pollen on insect bodies (Macgregor et al., 2015), providing insight into landscape-level differences between diurnal and nocturnal networks.

Here, we use a DNA metabarcoding approach to compare the pollen loads of bees and moths in urban agroecosystems. Our aim was to test the relative impact of urbanisation on nocturnal and diurnal pollen-transport networks. The molecular analysis of pollen loads overcomes two major limitations of traditional observational methods: 1) it allows us to analyse nocturnal insect-plant interactions and 2) it allows us examine insect species' foraging patterns on a wider range of plant species than could be directly observed at specific sites or time points.

We focus on urban horticultural sites (allotments), which represent a unique context in which to examine urban pollination networks for several reasons: first, they have relatively high insect and plant diversity (Baldock et al., 2019; Borysiak et al., 2017); second, they directly benefit from insect pollination through increased food production;

and third, they exist along urbanisation gradients which allow us to investigate how heterogeneous urban greenspaces sustain pollinator-plant interactions.

We had three specific objectives: (i) to analyse plant communities visited by bees and moths, highlighting taxon-specific differences and similarities in host plant visitation; (ii) construct bipartite pollen-transport networks to compare structural differences of moth and bee visitation patterns; (iii) assess the effect of urbanisation on pollen transport by each insect group.

Methods

Study system and Surveys

We sampled insects during the growing season (May – September) of 2019 in eight allotment sites along an urbanisation gradient (Figure S3.1). Sites were located between 1.8 km – 12.2 km from the city centre of Leeds, UK (53°47'47.33"N, -1°32'52.26"W) and were 5192 m² – 22639 m², spanning the range of allotment sizes within Leeds (Supplementary Methods S1; Figure S3.2).

To account for seasonal variation, paired samples of bees and moths were collected at each site at three time points during the season (early summer = May; midsummer = June; late summer = September) (Table S3.1). Bees were collected by timed line-transects (20 minutes) through the centre of each site on clear, warm, calm days (Baldock et al., 2019). Each bee was caught in a clean sweep net to prevent species pollen cross-contamination (Pornon et al., 2016). Moths were sampled on calm, warm nights (Bates et al., 2013) using a 12-volt portable Heath Trap (NHBS product code SK22) equipped with a 15W actinic bulb. All sites were sampled from dusk until dawn on the same night for each sampling point. These methods are standard insect sampling approaches, and accurately recover local (α) diversity for these taxa. Individuals were individually euthanised in tubes and retained for pollen extraction (Macgregor et al., 2019). Insects were identified to species; 3% of samples (8 specimens) were identified to genus due to difficulty in identification.

DNA Metabarcoding:

We amplified two plant barcodes: ITS2 (UniPlantF and Uniplant R; Moorhouse-Gann et al., 2018) and *rbcL* (*rbcLa-F*, *rbcL-3CR* primers; Macgregor et al., 2019; Costion et al., 2011). ITS2 is a short nuclear ribosomal region with high species-specificity, and *rbcL* is a longer chromosomal region with lower species-level discrimination but a greater coverage of plant families. Both regions have large GenBank references for UK plant species (Jones et al., 2021).

Protocols for pollen removal, DNA extraction, amplification and sequencing are detailed in Supplementary Information Text S1. In brief, pollen was first removed from either the whole insect (bees) or the excised proboscis (moths); using the proboscis minimises cross-contamination of body pollen in light traps (Macgregor et al., 2019). DNA was successfully extracted using ammonium acetate precipitation from 918 insect pollen loads in total, and pooled by insect species within each site and time point, resulting in 442 samples. Each sample was then separately PCR-amplified using ITS2 and *rbcL* primers, and indexed with i7- and i5-tailed primers in a second PCR, pooled, AMPure-XP bead cleaned, and quantified using qPCR. ITS2 and *rbcL* pools were sequenced separately on an Illumina MiSeq using standard chemistry. Using multiple individuals of each species where possible allowed us to better estimate the species-level visitation patterns, though as in most studies we focus our analysis on aggregated data for bees and moths.

Data analysis:

Bioinformatics:

Unless otherwise stated all analysis was done in R version 4.12 (R Core Team; 2022). Raw MiSeq reads were processed using a pipeline in the R environment with the packages *dada2*, *Biostrings* and *ShortRead* (details available in Table S3.2 and code in Supplementary Information Text S2). In brief, primers were removed using *cutadapt* (Martin 2011), poor quality sequences were removed using *filter* and *trim* functions and an error model was used to dereplicate reads and infer ASVs (amplicon sequence variants) from the cleaned data. Sequences were BLASTed against a hybrid curated database (Hawkins et al., 2015; de Vere et al., 2017): ASVs were BLASTn against the nucleotide database of GenBank as well as the Barcode Wales database (de Vere et

al., 2012) allowing us to obtain lower taxonomic assignments for a wider range of native species, as well as non-native and crop plant species commonly found in urban allotments. Sample-based rarefaction of the sequences was used to examine the read depth of each sample and any samples below 8,000 reads were removed. MEGAN (version 6.21.12) was used to assign species identifications using the Lowest Common Ancestor method (Huson et al., 2016). Assignments higher than genus were not analysed (8% of assignments).

Network construction and statistical analyses:

Using the 'bipartite' package in R (Dormann et al., 2017), we constructed pollen-transport networks. To visualise the networks, we used the 'plotweb' function with a CCA clustering method which clusters insects together based on their similarity of plant visits. To assess how plant communities differed between moth and bee networks, we constructed three networks (one for each time point) and compared the structures of moth and bee networks using standard weighted indices, as follows: to describe network complexity we calculated nestedness (the degree to which specialist species interact with subsets of the species interacting with generalists (Mariani et al., 2019) and linkage density (average number of links per species); to assess the relative insect specialisation we calculated the average number of plant links per pollinator species (insect 'generalisation'). Network level indices were calculated first by site (pooled across time), generating indices for eight pairs (moths and bees) of networks and then by time (pooled across sites, N=3 pairs) which allowed us to examine spatial and temporal changes in network structure. To test the effect of urbanisation on insect community structure and foraging patterns, 48 networks were constructed for each taxon, site and time point and community indices were estimated (number of plant species visited, by taxon (bees vs moths) and by species, insect species richness, insect abundance). These were then related to two standard measures of urbanisation estimated using ArcGIS (version 10.1.7): percentage cover of grey impervious surfaces in the 250m, 500m and 1km area around the allotment site, and each allotment site's distance from the geographic city centre (km) (Supplementary Text S3).

To compare the plant communities foraged on by bees and moths, non-metric multidimensional scaling (NMDS) plots were constructed for each time point, using Bray-Curtis distances. Each insect group's foraged plant community was then statistically compared using analysis of similarities (ANOSIM; Clarke and Green 1988). To test if there were taxon-specific preferences for certain plant functional traits, we used generalised linear models (`car::glm`) to compare the mean visits by bees and moths to different functional groups of plants such as woody perennial vs non-woody herbaceous.

To test how insect species richness, insect abundance, number of plants visited, and the insect generality varied as a function of insect taxon (moth vs bee), time, and their interaction, we fitted generalized linear mixed-effects models (`lme4::glmer`; Bates et al., 2015) and compared insect taxa using contrasts of least-squares means (`emmeans::joint_tests`; Lenth 2018); site was included a random effect. To test how urbanisation affected plant visitation patterns, we used generalized linear models (GLMs) with number and species richness of plants visited per site as dependent variables, and each urbanization measure, time point, and insect taxon as independent variables. For all analyses, model residuals were checked for adherence to model assumptions to avoid overfitting.

Results:

A total of 443 individual moths were caught belonging to 67 species (species list Table S3.3). Pollen was found on 55% of individuals (Table S3.3). Pollen transport by moths was largely driven by macromoths (98% of pollen carrying moths) rather than micromoths (2% of pollen carrying moths), and particularly Noctuidae (70% of Noctuids were carrying pollen). Twenty species of bee belonging to five families were collected. All bees ($n = 475$) were found to be carrying pollen (Table S3.4). Honeybees (*Apis mellifera*) made up over one third of the individuals sampled (169 individuals), while solitary bees accounted for 8% of bee community abundance but 60% of total bee species richness (Table S3.4).

The merged dataset of ITS2 and rbcL yielded 328 plant assignments (Table S3.5), 61% of which were to species level, 39% of which were to genus only. Asteraceae had the largest species diversity ($n=26$; 12% of all species), followed by Brassicaceae (n

= 18 species; 9%) and Rosaceae (13 species, 6%). Of the species assigned, 13% (n=23) were fruit or vegetable crops, 46% were native, 29% were naturalised and 25% were non-native (<https://plantatlas.brc.ac.uk/>). Non-woody angiosperms made up most of the plant community (74% of assignments) and flowering woody angiosperms (trees and shrubs) accounted for 26% of the plant community.

In total, 3375 insect-plant interactions were observed with bees accounting for 2548 of these interactions (75%), and moths 827 (25%). Bees and moths differed significantly in the communities of plants visited; however, a large plant community was shared by both insect groups at each point in the season (shared plants in early summer: 20%; midsummer: 35%; late summer 17%). Bipartite networks of pollen transport of bees and moths at each time indicate distinct higher-level node clustering of bee and moths which became pronounced in midsummer and late summer (Figure 3.1). In midsummer 46% of the visited plants were visited only by bees, while 19% of plants were unique to moths. By late summer, there was greater divergence of foraging preferences, with 61% of plants visited only by bees and 21% of plants visited only by moths (Figure 3.1).

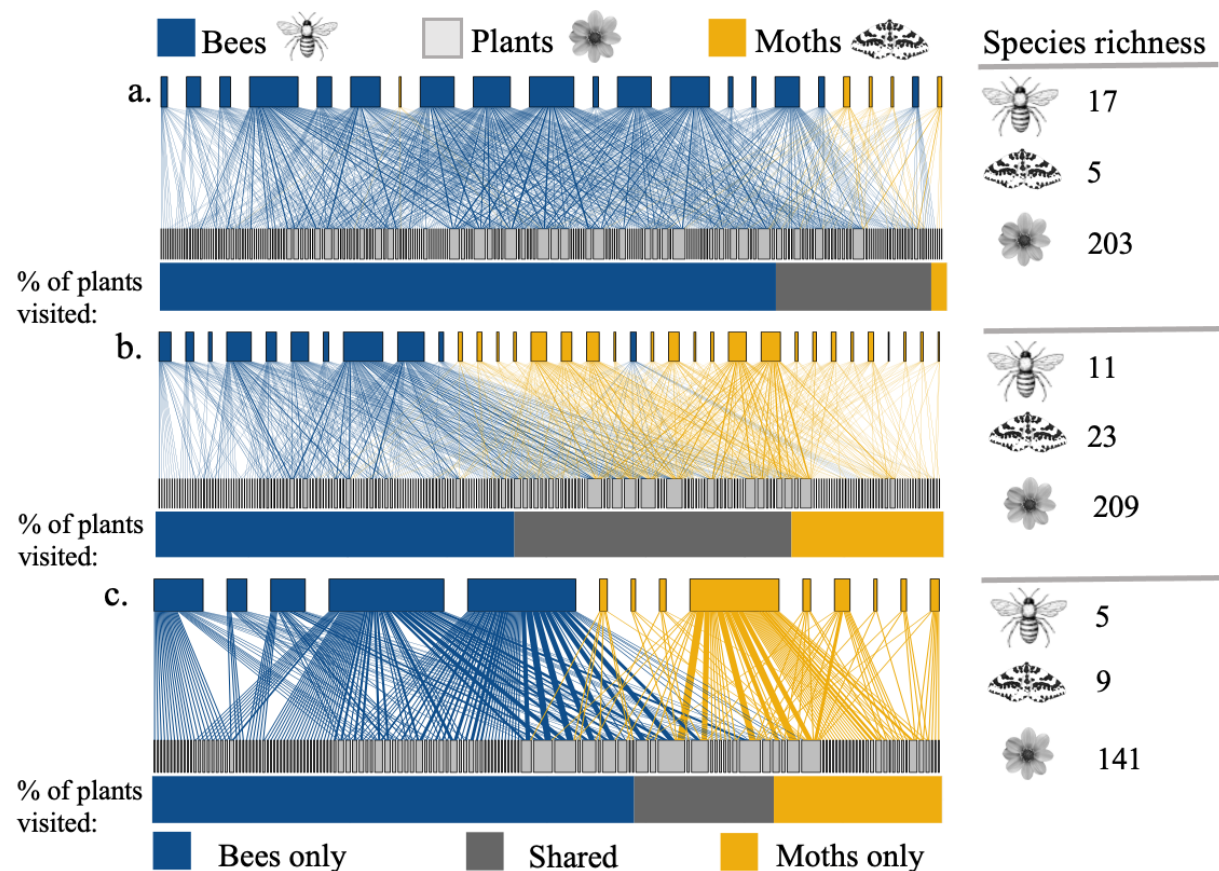


Figure 3.1: Bipartite networks of pollen transport of moth and bees in a) early summer (May), b) midsummer (July), c) end of summer (September). Top nodes of each network (higher level) are individual insect species of bees (blue), and moths (yellow), and bottom nodes of each network (lower level) are individual plant taxonomic assignments. Stacked barcharts indicate the proportion of plants that were visited by each insect group alone and the proportion shared (dark grey) between insect taxa.

Multivariate analyses (NMDS) confirmed that the assemblages of plant species' pollen carried by moths and bees were distinct in early and late summer, but not midsummer (Figure 3.2 (a-c)). The distinctiveness of the pollen assemblages was based on different plant communities over the season, with significant temporal turnover in plant species composition (ANOSIM $R^2 = 0.46$, stress = 0.19, $p < 0.001$; Figure S3.3). *Rubus* spp. (138 visits), *Borago officinalis* (117 visits) and *Urtica dioica* (98 visits) were the most visited when all insect groups were combined and constituted an important component of the plant community shared by bees and moths (Table S3.5). However, diurnal, and nocturnal insects also differed significantly in which plant species were more visited. For example, *Buddleja* spp. was the plant most visited by moths (53 visits) whereas only eight bees were recorded visiting it. On the other hand, *Symphytum* sp. was the second most commonly bee-visited plant (80 visits) compared to only 11 moth visitors. (Table S3.5-S7). Bees visited non-woody annual/biannual flowers more often than woody perennial plants ($F = 85.7$, $df = 1$, $p < 0.0001$). Conversely, moths visited perennial, woody flowering plants (trees and shrubs) as often as annuals ($\chi^2 = 0.02$, $df = 1$, $p = 0.90$)(Table S3.8).

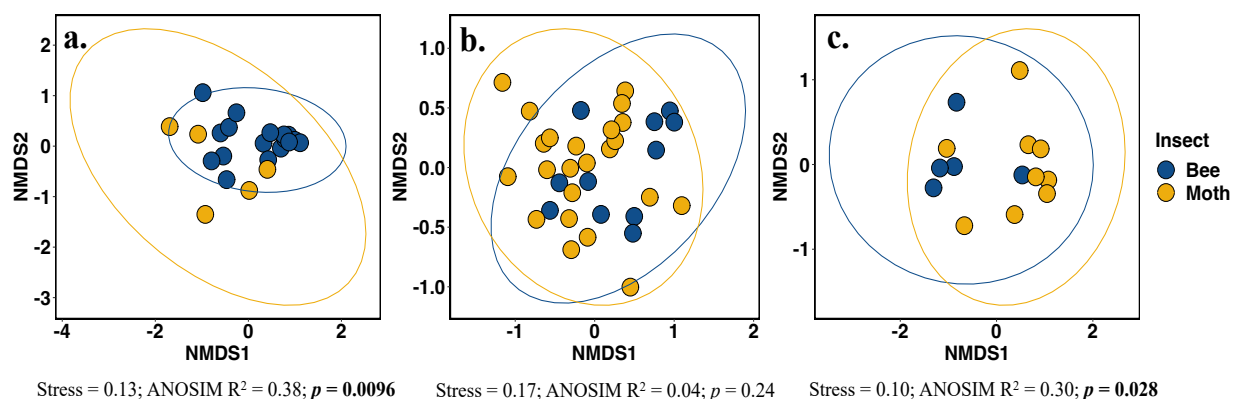


Figure 3.2: Non-metric multidimensional scaling (NMDS) plots showing divergence between bees (blue) and moths (gold) based on the plants visited in their pollen-transport networks in a) early summer (May), b) mid summer (July), c) late summer (September). Ellipses indicates 95% confidence intervals of the grouping in the spatial ordination.

The taxon-specific pollen assemblages (Figure 3.2) were accompanied by significant differences in overall pollen diversity between bees and moths, though the direction of these differences varied through the season. There was a significant taxon*time interaction for total plant species visited by bees and moths ($\chi^2 = 65.98$, $df = 2$, $p < 0.001$), and the average number of plant species visited by each insect species (generalisation of insect) ($\chi^2 = 18.24$, $df = 2$, $p < 0.001$) (Figure 3.3). Bees as a group visited more plant species than moths (Figure 3.3b), and individual bee species were significantly more generalist than moths (Figure 3.3c). However, post-hoc multiple comparison procedures show that this pattern is less pronounced in late summer (Table S3.9). There was also a significant taxon*time interaction for both insect species richness ($\chi^2 = 66.16$, $df = 2$, $p < 0.001$) and insect abundance ($\chi^2 = 188.76$, $df = 2$, $p < 0.001$), with richness and abundance peaking in spring for bees, and midsummer for moths (Figure 3.3a, b).

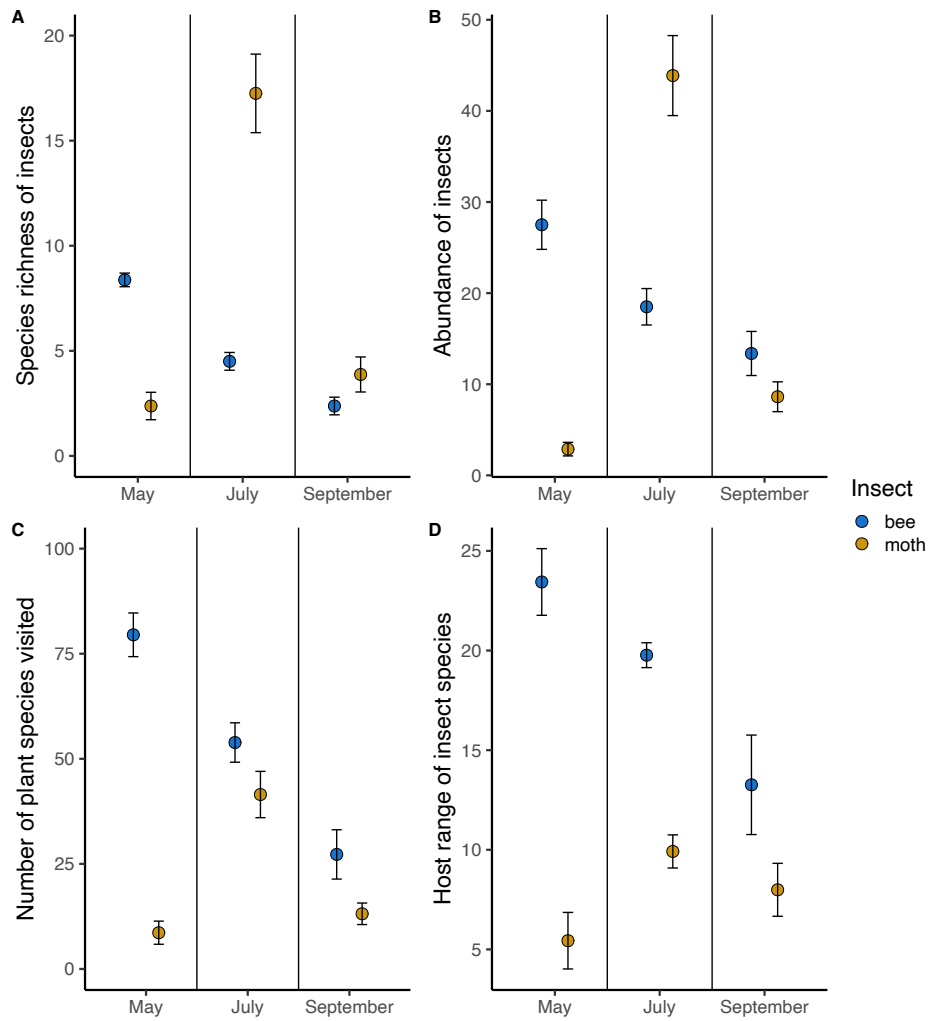


Figure 3.3: Insect community response and visiting patterns across time of bees (blue) and moths (yellow). a) number of insect species, b) abundance of insects, c) number of plant species visited by each insect group, d) host range of insect species (average number of plant species visited by each insect species). Data are means \pm SE of eight sites.

There were pronounced differences in network structure between taxa. Bee networks had higher linkage density ($\chi^2 = 153.81$, $df = 1$, $p < 0.001$), niche overlap (at insect species level) ($\chi^2 = 4.18$, $df = 1$, $p = 0.04$) and had higher robustness at plant level ($\chi^2 = 31.66$, $df = 1$, $p < 0.001$). However, these network structural differences were less pronounced in midsummer (Table 3.1).

Table 3.1: Network indices of bees and moths across time (pooled by site) and averaged across sites (pooled by time). P-values from generalised linear models (Type II comparisons of means Table S3.10).

Metric	Early summer		Mid summer		Late summer		Mean across sites				p - value
	Moth	Bee	Moth	Bee	Moth	Bee	Moth	SE	Bee	SE	
Nestedness	50.63	24.59	14.46	30.39	16.41	29.77	27.46	2.80	30.71	1.80	p > 0.05
Linkage density	7.69	31.51	15.97	24.29	12.34	21.88	7.91	0.32	19.96	0.92	p < 0.001
Niche overlap	0.23	0.50	0.42	0.41	0.33	0.49	0.27	0.03	0.33	0.02	p = 0.04
Robustness (Higher level)	0.58	0.72	0.67	0.66	0.57	0.62	0.62	0.01	0.64	0.01	p > 0.05
Robustness (Lower level)	0.93	0.98	0.93	0.97	0.87	0.97	0.89	0.01	0.96	0.00	p < 0.001

The nestedness of the networks changed across time, with moth pollen-transport networks being twice as nested than bees in early summer, but half as nested than bees in mid and late summer. Overall, the structure of moth pollen transport networks was considerably more dynamic and seasonally dependent relative to bee networks (Table 3.1, Figure 3.1).

Increasing urbanisation had a significant negative effect on pollen transport of both diurnal bees and nocturnal moths. Increasing percentage cover of impervious grey surface surrounding each allotment sites had a significant negative effect on the diversity of visited plant species, a pattern which held when considering grey space at a scale of 250 m (Figure 3.4; $\chi^2 = 6.36$, df = 1, p = 0.01) and 500 m ($\chi^2 = 4.53$, df = 1, p = 0.03), but not at 1 km ($\chi^2 = 1.05$, df = 1, p = 0.31). Site distance from the city centre also had a significant positive effect on the number of plant species visited ($\chi^2 = 5.99$, df = 1, p = 0.01). There were no effects of percent greyspace or distance from urban centre on insect species richness or abundance for either insect group at any scale (p > 0.05, Table S3.12-S13). Site size did not significantly affect number of plant species visited, insect species richness or insect abundance (p > 0.05, Table S3.11-13), but there was weak evidence that the proportion of site area that was uncultivated (i.e. percentage of disused plots) had a significant negative effect on the diversity of visited host plants for both insect groups ($\chi^2 = 4.13$, df = 1, p = 0.042, Figure S3.4).

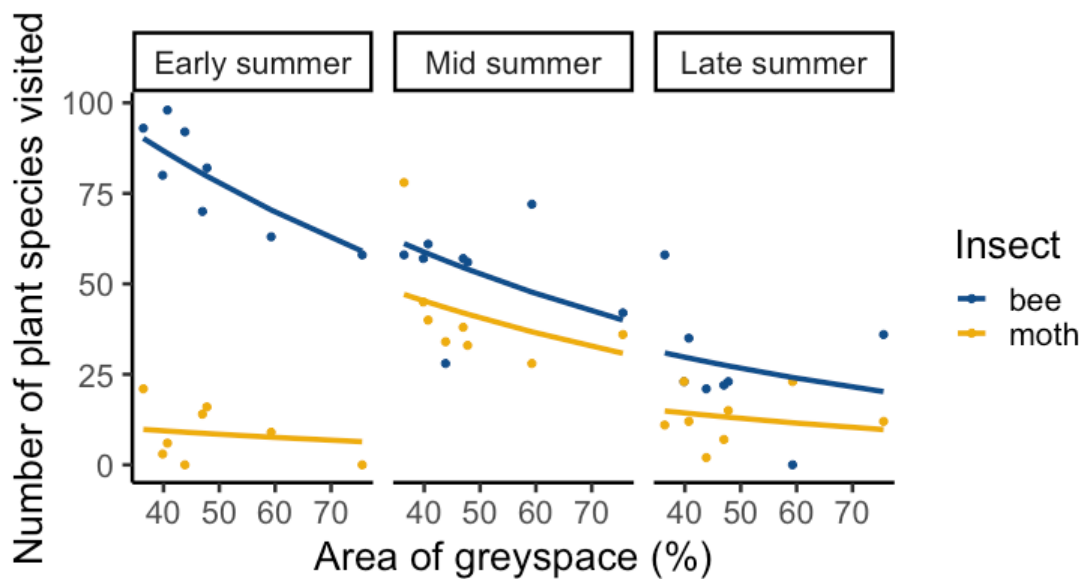


Figure 3.4: Negative effects of urbanisation on diurnal and nocturnal pollen-transport networks. The number of plants visited by bees and moths across the season decrease along an increasing urbanisation gradient (percent cover of grey space in 250m surrounding an allotment). Lines represent fitted generalized linear model with significant negative main effect of area of greyspace on number of plant species visited by bees and moths across the season ($\chi^2 = 6.36$, $df = 1$, $p = 0.01$), a significant interaction of insect taxon*time ($\chi^2 = 46.31$, $df = 2$, $p < 0.0001$), and common slopes as there was no significant interaction of predictor (area of greyspace) and insect taxon or time ($\chi^2 = 1.9$, $df = 2$, $p = 0.37$) (Table S3.11).

Discussion

Plant-pollinator networks are critical components of healthy urban ecosystems, but the resilience of these interacting communities to urbanisation remains poorly understood. Here, metabarcoding of insect pollen loads indicates that increasing urbanisation leads to a decrease in the diversity of pollen carried by both diurnal and nocturnal insects. The negative effect of urbanisation was similar in magnitude for both for bees and moths, and was observed throughout the growing season, despite significant temporal and spatial variation in the species composition of insect and plant communities. These results have important implications for urban pollinators, which

rely on the abundance and diversity of plants for adult and larval food sources; and for urban plant communities, which rely on insects for pollination.

The effect of urbanisation on pollen-transport suggests that reduced diversity or relative abundances of plant resources may be a primary factor contributing to observed declines of urban insect populations, including both bees and moths (Biesmeijer et al., 2006; Potts et al., 2010; Vanbergen et al., 2013; Wagner et al., 2021a). The significant negative effect of urbanisation on the number of plant species visited by both bees and moths showed an overall decrease of up to 42% of plant species richness when comparing our least (mean plant species richness = 53) and most urbanised sites (mean plant species richness = 31) (Figure 3.4). The reduced diversity of pollen suggests that even within relatively diverse allotments, urbanisation could be driving increased competition among pollinating insects for pollen or nectar resources and potentially reducing the resilience of urban insect communities. These effects may be best studied using multiple insect groups and considering multiple spatial scales. Here, the effect of urbanisation appeared to be partially scale-dependent and was not detected using the largest 1 km² buffer, suggesting that allotments may be ecological sinks for urban pollinators, particularly for species with limited foraging ranges, (i.e., nocturnal moths and solitary bees), which may exacerbate local competition. Overall, our results underscore the significance of protecting and enhancing existing urban greenspaces and understanding the detrimental effects of densification of impervious surface.

Our results highlight the importance of poorly understood taxa such as nocturnal moths, and the role of moths as urban pollinators. We found over half of individual moths carried pollen, significantly more than some prior studies (Devoto et al., 2011; Macgregor et al., 2019, but see Banza et al., 2015). This could be due to the greater sensitivity of metabarcoding compared to microscopic pollen identification (Macgregor et al., 2019) and/or the fact that allotments have higher plant (Borysiak et al., 2017) and pollinating insect (Baldock et al., 2019) diversity compared to prior study systems. Our analysis suggests that nocturnal moths in urban horticultural systems have highly complex, formerly unknown plant interactions (Devoto et al., 2011; Macgregor et al., 2015; Banza et al., 2019; Macgregor et al., 2019; Walton et al., 2020; Ribas-Marquès et al., 2022); for example, 8% of plant species (n = 25) were only found on moths and not on bees. Some of these fitted the moth-pollination 'syndrome' of pale and fragrant

flowers e.g.: *Sambucus nigra* (Adoxaceae). However, moths were also frequent visitors of common flowering trees (22% of their interactions), including lime (*Tilia platyphyllos*), sycamore (*Acer pseudoplatanus*) and ash (*Fraxinus spp.*). Moths may also play an important role as pollinators of crop species, including raspberry (*Rubus spp.*), apple (*Malus spp.*), and blueberry (*Vaccinium spp.*) (Walton et al., 2020; Macgregor et al., 2019; Culter et al., 2012). We identified pollen of several species not previously known to be moth-pollinated, including redcurrants (*Ribes rubrum*), strawberries (*Fragaria spp.*), and stone fruit (*Prunus spp.*), and pollen of non-fruit crops which may be visited for oviposition or adult feeding, including potato (*Solanum tuberosum*), and cole crops (*Brassica oleracea*). Macro-moth abundance has declined by ca. 33% in the last 50 years in the U.K. (Fox et al., 2021), and our results strongly suggest that these declines may represent a significant threat to pollination services for both wild and crop plants.

Our study allows us to directly compare the visitation networks of nocturnal moths with those of diurnal bees, and assess their relative importance in urban ecosystems. We found that bees were interacting with up to five times as many plant species as moths (Figure 3.4) consistent with the few previous studies (Devoto et al., 2011; Walton et al., 2020; Alison et al., 2022). Bee diversity was dominated by solitary, polylectic species in spring, and diversity and abundance declined linearly throughout the season. However, moth interactions were highly dynamic, with a pronounced peak in midsummer (Figure 3.3). Compared to the spring, midsummer moths were 7-fold more diverse, and carried pollen from 4.8-fold more plant species (Figure 3.3); however, average moth host breadth (generality) increased only modestly (1.8-fold). Somewhat surprisingly, this suggests that the midsummer peak was not driven by specialists or generalists. Overall, moths accounted for up to one third of the plant-pollinator interactions in this system, and in late summer visited as many plants as bees. (Figure 3.3). This suggests that in late summer moths may provide an equally important pollination service to bees in urban pollen-transport networks.

Bee pollen-transport networks are likely to be more resilient to urbanisation or other anthropogenic change compared to moths. Bee networks were consistently comprised of more interactions (approximately two-fold higher linkage density throughout the season), were more robust, and exhibited higher per-insect host range and niche overlap (Figure 3.3, Table 3.1) Notably, bee networks exhibited more stable

nestedness throughout the season, while moth nestedness was considerably lower in mid and late summer. Greater nestedness has been suggested as a metric for greater network resilience (Song et al., 2017), suggesting that compared to bees, moth pollination networks may be less robust to environmental perturbation.

Our results have direct implications for biodiversity conservation in urban greenspaces. Allotments represent <1% of the area of UK cities (Baldock et al., 2019), but provide numerous benefits (Edmondson et al., 2020), including supporting diurnal pollinator biodiversity (Baldock et al., 2019). Our study suggests that management of allotments should focus on conservation of both nocturnal and diurnal pollinators to maximise ecosystem service delivery and urban biodiversity. For instance, there may be benefits of targeted planting of species which benefit both insect groups. To date, only diurnal pollinators have been considered when testing the effectiveness of urban wildflower planting (Haaland et al., 2010; Albrecht et al., 2021; Van Druen et al., 2022). We show that several common garden plants frequently planted for diurnal insects (rhs.org.uk/plantsforpollinators) were also visited by moths, e.g., borage (*Borago officinalis*), nasturtium (*Tropaeolum spp.*) and comfrey (*Symphytum spp.*). Importantly, we find that both bees and moths were primarily visiting wild plants rather than crops, despite sampling in urban horticultural sites. Allowing natural regeneration of weedy wild species in urban greenspaces is known to be important for bees (Lerman et al., 2018; del Toro and Ribbons 2020), but our results show the importance of these plants for moths (Table S3.14). Conversely, the pronounced divergence in plant visitation patterns (Figure 3.2) suggests that taxon-specific interventions may also be needed. For example, bees were visiting non-woody flowering plants up to four times more often than woody trees and shrubs, whereas moths showed no preference, indicating a relatively greater role of woody perennial vegetation for nocturnal species. This is consistent with the limited research demonstrating a positive correlation between moth abundance and habitat structural complexity (i.e., tree density; Ellis and Wilkinson 2021; Bates et al., 2014).

Conclusion:

We compared the pollen-transport networks of urban bees and moths and show that these taxa differ significantly in the complexity and composition of their interaction

networks. Moreover, we show that the process of urbanisation (densification of grey space) is negatively affecting pollen-transport networks of both diurnal and nocturnal insects, reducing the diversity of plants visited by bees and moths. Our study underscores the importance of understanding the direct and indirect drivers of insect declines in increasingly urbanised landscapes, and highlights the role played by urban greenspaces for conserving the diversity and functioning of pollinator communities.

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Experimental floral additions increase pollination service delivery in urban agroecosystems.

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Abstract:

1. The addition of nectar-rich flower patches in modified systems is a common practice to mitigate the declines of pollinators and to boost pollination services. However, the associated benefits these additions have on pollinator communities and the pollination services they provide are rarely tested, especially in urban systems.
2. We used a city-scale experiment where we added floral resource provision to urban allotments to investigate the benefit to hoverflies and moths and how local and landscape features impacted the seed set of a model plant (*Solanum lycopersicum*).
3. We found that there were complex local and landscape-level drivers shaping pollinator communities and the pollination services they provided. Our results show that floral additions at small scales did not benefit insect communities but enhanced the provision of pollination services by a 20% increase in seed set in our model plant. There was also a significantly higher seed set in more urban sites.
4. We show that hoverflies, social bees, solitary bees, and moths have divergent foraging preferences and demonstrate that social bee abundance (*Bombus* and *Apis*) benefits from increasing area of floral resources whereas other insect taxa show no changes in abundance.
5. *Synthesis and application:* Current conservation practices for pollinators do not consider non-bee pollinator life histories that require non-floral resources. Consequently, the positive response to floral resource availability both through local additions and at a larger allotment site level was only present in bees.

Creating and sustaining flower-rich environments that a variety of adult pollinators can take advantage of requires additional efforts to support their various immature life stage needs. Finally, in modified urban systems there are important direct and indirect landscape drivers influencing these processes that need to be considered when making conservation decisions.

Introduction:

Pollination by insects is a crucial ecosystem service that underpins the functioning of terrestrial ecosystems (Ollerton et al., 2011). Humans are particularly dependent on pollination services by insects because they underpin 33% of global crop production (Potts et al., 2010). There are growing concerns for the resilience of these pollination services as evidence of global insect pollinator declines increases (Potts et al., 2010). In an effort to halt the declines in abundance and diversity of key pollinator groups such as bees, there has been a surge in pollinator conservation schemes, demonstrated in top-down approaches such as policy changes (Hall et al., 2017) and also in bottom-up approaches, encouraged and driven by NGOs to engage the general public (e.g. 'No-Mow May' (Plantlife, <https://www.plantlife.org.uk/>) and 'Gardening for Wildlife' (RSPB, <https://www.rspb.org.uk/>)).

Floral resources are vital for bee survival by providing both nectar and pollen (Frankie and Thorp, 2009), and there is strong evidence that floral resource availability affects the abundance and diversity of wild bee populations (Kennedy et al., 2013). Supplementing floral resources has therefore become a focus of pollinator conservation efforts, particularly in human-modified landscapes (Bommarco et al., 2013; Braman and Griffin, 2022). For example, the implementation of undisturbed field margins or restoration of hedgerows can offer abundant foraging resources and nesting sites for insect pollinators and in some cases, increase the yields of nearby insect-pollination-dependent crops (e.g. Morandin and Kremen, 2013). The impact of floral additions on pollinators has been well-studied in agricultural contexts where the impact is generally positive (Haaland et al., 2010; but see Delphia et al., 2022). However, despite the rapid expansion of urban areas, fewer studies have been conducted in cities, where the impact of floral additions at different scales remains unclear.

Although the expansion of cities through the process of urbanisation has been shown to be a key driver in the loss of pollinator biodiversity (Wagner et al., 2021a), there are important conservation opportunities for insects through the provision of floral resources within urban greenspaces. For example, urban home gardens and areas of urban horticulture can provide bees with diverse and nectar-rich floral resources (Baldock et al., 2019, Tew et al., 2022). Compared to agricultural land, cities can contain a high diversity of plants that are generally beneficial to pollinating insects (Clarke and Jenerette, 2015; Baldock et al., 2015). However, they are often interspersed in a matrix of impervious surfaces and other unsuitable habitats (McKinney, 2008), which limits the availability of these vital resources. Urbanisation can act as a filter on pollinator communities whereby it can promote some species and discriminate others (Wenzel et al., 2019). The probability of thriving in urban areas is highly trait-specific. Some traits can facilitate the survival and colonisation of pollinators in urban landscapes, specifically diet breadth and the sociality of insects (Wenzel et al., 2020). These traits have been shown to be beneficial in light of adaptation to these highly disturbed environments, and they are mostly seen in the generalist social bumble bees and honeybees (Ahrné et al., 2009; Banaszak-Cibicka et al., 2019; Wenzel et al., 2020). The conservation of urban pollinators is hindered by our lack of understanding of how non-bee pollinators respond to urbanisation. This is especially true for insects that rely on non-floral resources for the completion of their life cycles (Howlett et al., 2021). For example, hoverflies (Diptera, Syrphidae) and moths (Lepidoptera) have been shown to be less resilient to urbanisation largely due to their distinct life-history larval requirements that may not be abundant in highly urban areas such as host plant availability for moths and larval food prey for hoverflies (Bates et al., 2014; Theodorou et al., 2020; Ellis et al., *in prep*).

While bee and non-bee pollinators may respond differently to the complexity of the urban environment, each group may still contribute significantly to pollination (Hahn 2016; Rader et al., 2016; Rader et al., 2020; Buxton et al., 2022a). For example, moths complement diurnal pollination networks and comprise up to one-third of insect-plant interactions when included in bee-pollinator networks (Ellis et al., *in review(a)*) and have complex pollen-transport networks in agricultural ecosystems (Walton et al., 2020, MacGregor et al., 2018, Alison et al., 2022; Ellis et al., *in review(a)*). Hoverflies

are diurnal pollinators with divergent life-history traits from bees and have been shown to facilitate crop and wild plant pollination, while also contributing to the biocontrol of pest species (Jauker et al., 2012; Dunn et al., 2020; Rader et al., 2020). Despite their vulnerability to urbanisation these taxa are very rarely assessed when examining the benefits of habitat restoration or floral resource supplementation. Due to their non-floral resource requirements, it is likely that the addition of floral resources may not have the same benefits which have been shown in bee communities (Moquet et al., 2018). In light of the reported declines in all these insect groups (Potts et al., 2010; Ollerton et al., 2011; Fox et al., 2014; Lintott et al., 2014; Barendregt et al., 2022), it is timely to empirically test the response of these different groups to floral resource supplementation to optimise conservation practices that promote and support all pollinating insects.

Within urban areas, there are unique opportunities to test these processes. For example, urban horticultural spaces within cities (allotments) are composed of plots of land rented by an individual or household for growing fruits and vegetables. They directly benefit from the insect pollination of a diversity of these crops and they have been shown to be an excellent space for civic engagement with pollinator conservation (Siegener et al., 2020). The relatively high plant and insect diversity in allotments and their wide distribution across urban areas, provide an opportunity for simultaneously assessing the effects of floral resource additions on both pollinator diversity and the production of insect-pollinated crops in cities. Previously, we showed that the species richness and pollen-transport networks of nocturnal moths and diurnal bees within allotments are disrupted by the densification of impervious surface surrounding the greenspaces (Ellis et al., *in review(a)*; Ellis et al., *in prep*). However, little is known about the consequences for crop production, or whether resource supplementation could mitigate the negative effects of urbanisation for different insect groups.

We experimentally tested the benefits of supplemental floral and nesting additions to the pollinator community diversity and crop production in urban allotments. We had three specific objectives to test how enhancing habitat quality can (i) influence bee and non-bee pollinator diversity and abundance, (ii) improve pollination services (crop yields) and finally, (iii) assess the differences in feeding ecology of different groups of insect pollinators. These objectives were all assessed in relation to site level

management and landscape level urbanisation surrounding the sites. Overall, given that the supplementation of floral resources has been shown to benefit bees, and crop production in other contexts, we predict that in sites where floral additions were made, we will see an increase in insect abundance, and diversity. Subsequently, we expect to see enhanced pollination services, compared to sites where no additions were made but these responses may vary between bee and non-bee pollinators.

Methods:

Study system

This study was carried out in 24 allotment sites throughout the growing season in 2020 (March-October 2020) in Leeds, England (53°47'47.33"N, 1°32'52.26"W). The experimental allotment sites were chosen in eight independent groups of three sites (each of the eight groups are henceforth referred to as a block). The three sites in each block were clustered to avoid spatial confounding at a city scale and each block was located along an urbanisation gradient, radiating out from the city centre (Figure 4.1 A).

Experimental design

Each experimental block had one control allotment site where nothing was added. The second site in each block was assigned a floral and nesting addition treatment (Figure 4.1D), where flower patches (~100 m²) were sown with a nectar-rich seed mix (EuroFlor and Rigby Taylor Native pollinator and Banquet seed mix; Supplementary Table S4.1; Supplementary Text S4.1) in March and seven trap nests ('bee hotels') were placed around the site. The third site was set up to test a separate set of objectives looking at how cavity nesting bees can be influenced by increasing nesting resources. Cavity insect habitat was added by placing seven trap nests (One wooden block nest type and six PVC pipe design nests were added, Figure 4.1 B-C) around the site (trap nest design outline in Supplementary Figures S4.1 and S4.2).

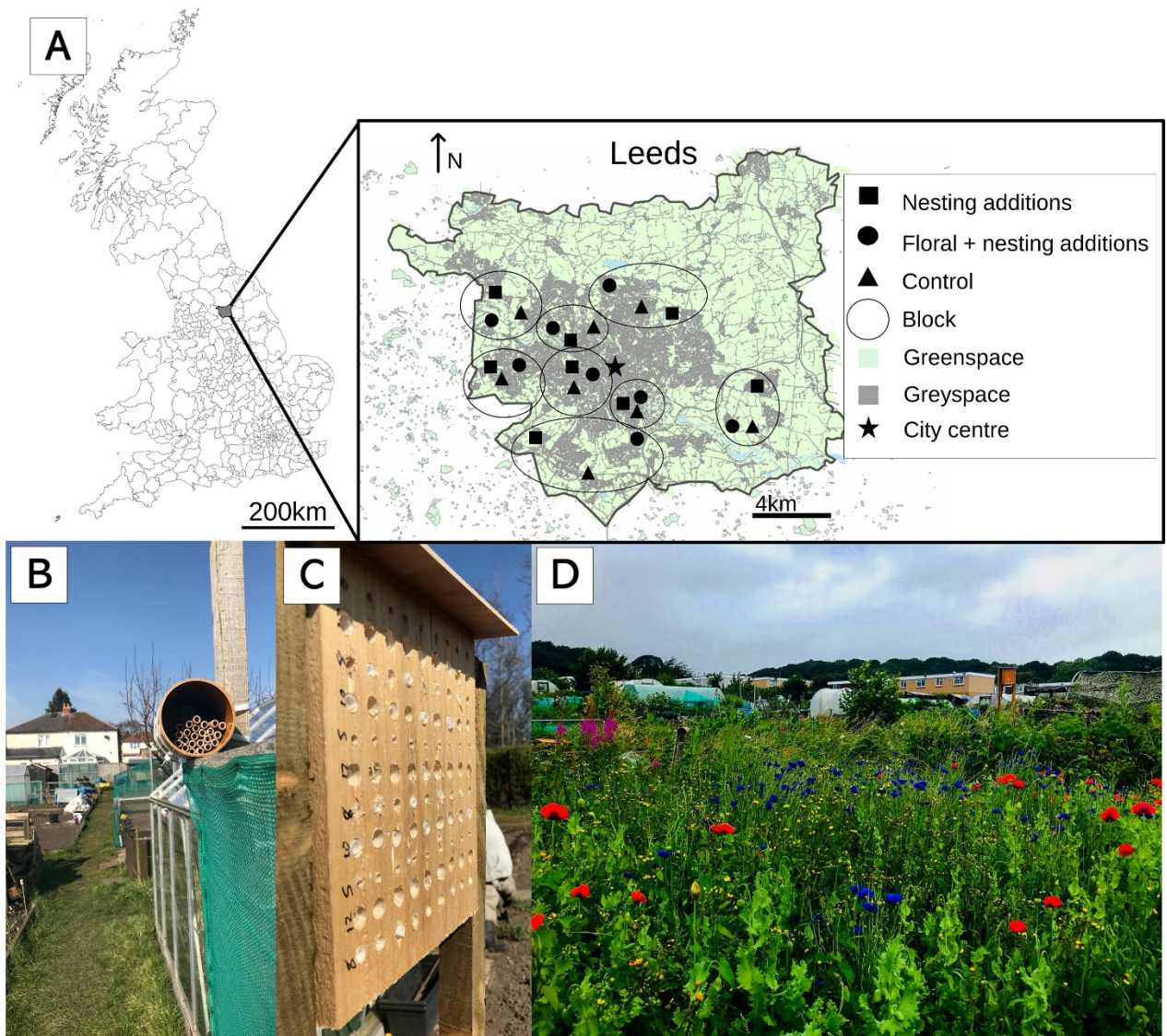


Figure 4.1 A) Left: City of Leeds location within the U.K., right the site locations, treatments and block set-up along an urbanisation gradient from the city centre. B-C) Nesting additions: B) Trap nests type 1, made of 8mm cardboard tubing, C) Trap nest type 2, made of 5mm,8mm,10mm, and 12mm drilled holes in wooden blocks. D) Floral additions: an example of one of the 100m² flower additions in allotment sites.

Sampling insects and flower-visitor interactions

At each site, we measured the species richness, abundance, and visitation networks of three insect groups: hoverflies (Diptera: Syrphidae), bees (Hymenoptera: Anthophila) and nocturnal moths (Lepidoptera). Insects were sampled on two occasions; the first was in early summer (May) before the mass flowering of flower patches and again in mid-summer (July) when the flowers were in full bloom. We

employed pan traps, light traps and sweep nets to sample insects which are common methods for collecting flying insects in studies of pollinator communities (Campbell et al., 2007; Truxa and Fiedler 2012; Pellet et al., 2012). As with any flying insect sampling method, each have their limitations, but by using this multi-sampling approach we ensure that our samples accurately represent the flying insect communities at these sites.

The three sites within each block were visited on the same day to minimise within-block variation and the three sampling methods were used during both sampling periods. Insects were sampled using six sets of blue, yellow and white pan traps (diameter: 7cm, height: 6cm) randomly placed around the sites. Each pan trap was 2/3 filled with unscented soapy water and emptied after five days at each sampling point.

To record site-level insect foraging networks, during each sampling point, twenty-minute transects with a sweep net were carried out through the central path of each allotment site and all insect-plant interactions were recorded (see Supplementary Methods S1). To test if the foraging patterns of insects were different in our manipulated nectar-rich floral patch addition compared to random flower patches, three, ten-minute focal surveys were carried out on 0.5 x 0.5 m flower patches (and on our added flower patches in the treatment sites). All insects and the plants they visited were recorded to the lowest taxonomic rank. Moths were sampled on calm, warm nights using a 12-volt portable Heath Trap (NHBS product code SK22) equipped with a 15W actinic bulb at each sampling point.

Quantifying pollination services

To quantify differences in pollination services across our floral and nesting addition treatments and controls, we used greenhouse-raised tomato plants (*Solanum lycopersicum*) as 'pollinometers' (Theodorou et al., 2020) at each site and evaluated their pollination success. Though *Solanum lycopersicum* is predominantly visited by bumblebees (*Bombus spp.*), there is evidence that they also benefit from supplemental pollination by non-buzz visitors (Cooley and Vallejo-Marin 2021). Tomatoes are commercially grown as annual plants with a global annual value of USD 10.8B (Cooley and Vallejo-Marin 2021) and they are also one of the most frequently

grown fruits on allotments (Edmondson et al 2020). These attributes make them an appropriate model system to quantify the ecosystem service of pollination in our study region.

Seeds of tomatoes (Montello-F1 bush variety) were germinated and grown for one month (April-May) in an insect-free greenhouse before placement at our study sites. Six tomato plants, each in individual compost growbags (Tomorite Grow Bag), and with two trusses of open inflorescences (flowers), were placed in our 24 allotment sites during the mass flowering of the experimental flower patches additions (early June). Each growbag was randomly placed around the site with the aim to have them spread around the site. In the floral addition sites, there were two plants next to flower patches in treatment sites. In each plant, one truss was bagged throughout the experiment in the field with fine net (2mm gauze) to prevent visitation by pollinators. Once the fruit had set, three tomatoes on each of the open and bagged trusses were harvested. All seeds were counted and the average number of seeds per plant was used as a measure of the ecosystem service of pollination.

Local and landscape variables:

At each allotment site, a series of site (local) and landscape-scale variables potentially related to insect pollinators and pollination were determined. The area of 'wild flowering plants' (e.g., disused plots and areas of 'weeds'), and the area of 'cultivated flowers' (e.g., managed flower beds, flowering fruit and crops on each plot) were surveyed at each site in July 2020. Here, areas of wild flowering plants and cultivated flowers were mapped onto aerial imagery on-site. These maps were then digitised in ImageJ (Schneider et al., 2012) and the area (m²) of these two variables was extracted. In addition, a proxy measure for urbanisation measured at a landscape scale was collected for each site. Here, we quantified the area of impervious space in a 250 m buffer surrounding each allotment using 'manmade' land cover data from OS Mastermap in a geographic information system (see Supplementary Methods S2, ArcGIS version 10.7.1).

To assess if insects were visiting flowers with higher nectar sugar content, we used measures of sugar per floral unit (ug) derived from Tew et al., (2021). We extracted

data for 65 of the plant species that were recorded during our transects (38% of the total species observed; Supplementary Table S4.2) which equated to 2121 of our recorded insect-plant interactions (48% of our total observations).

Data analysis:

Unless otherwise stated all analysis was done in R version 4.12 (R Core Team 2022).

Network construction:

We constructed diurnal networks based on field observations to compare the network structure metrics of hoverflies, solitary, and social bees and to assess how their visitation patterns are influenced by our floral and nesting addition treatments, site-level floral resources and the surrounding urbanisation. Using the data from sweep net insect-plant observations (both line-transect and focal surveys), we constructed networks for 24 sites and calculated the following network metrics: total number of plants foraged on (bipartite::networklevel; Dormann et al., 2017), linkage density and host range of insect species.

Due to the practical difficulty of observing moth-flower interactions (MacGregor et al., 2019), we estimated moth visitation using metabarcoding of pollen from their proboscis following Ellis et al., (*in review* (a)) to assess if the floral addition treatment increased the number of plants visited by nocturnal moths. The moth samples were pooled by sites and did not include sites that only receive trap nest addition (samples $n = 16$). This was due to limitations in the number of samples that were available to us to run on the MiSeq. Therefore, the only metrics we were able to derive were the estimated number of plant species visited and most used plants (across sites). The sampling mismatches of these nocturnal (pollen load analysis) and diurnal network (direct observations) constructions limited our ability to compare diurnal and nocturnal networks directly.

Statistical testing:

Given our block experimental design, the rationale in our statistical analyses was to use block ($n = 8$) as a random factor because sites within each block were arranged to be clustered together to prevent spatial confounding. First, to test how the addition

of floral and nesting resources influences insect communities and pollination, we modelled the effect of treatment on three response variables, including insect abundance, insect species richness and mean tomato seed number. Covariates including site size, time (early summer, mid summer) and insect group (hoverfly, bee and moth) were also included in the models. Next, the area of cultivated flowers within the sites and the area of greyspace were included in the models as covariates to assess how the local and landscape factors were influencing the insect communities and pollination. *A priori* testing showed that the area of greyspace was positively correlated with site-level area of cultivated flowers ($F_{(1,23)} = 6.15$, $df = 1$, $p = 0.02$, Figure S4.3) thus, these continuous variables were analysed in separate models.

We used generalised linear mixed effect models (`glmer::lme4`, Bates et al. 2015) with either Gaussian or Poisson distributions, depending on the visual assessment of the residuals. Gaussian models were tested with Type II Analysis of Variance Table with Satterthwaite's method (`lmerTest`, Kuznetsova et al., 2017). Poisson models were constructed using `MCMCglmm::MCMCglmm` (Hadfield, 2010) as the data were over-dispersed, zero-inflated, and Poisson distribution assumptions were the best match. P-values were derived from the posteriors with standard parameter-expanded priors. In all analyses with multiple terms and interactions, any non-significant terms or interactions were removed from the final model.

Results:

Fly, bee, and moth communities in allotments across the city

In total, 7616 insects, belonging to 311 species were recorded during the sampling period (Table 4.1). The honeybee (*Apis mellifera*) accounted for 22% of the observations ($n = 1680$) and bumblebees (*Bombus spp.*) made up 27% of the observations ($n = 2091$). Moths were the most species rich, with 203 species recorded (2617 individuals) (Table 4.1; Supplementary Tables S4.3-S4.5 for full species list). During the transects and focal collections, we recorded a total of 4611 insect-plant interactions (i.e. observed plant visits). In total, 169 plant species were visited (Supplementary Table S4.6) and the most visited plants were *Rubus sp.*, ($n = 472$ visits), *Origanum vulgare* ($n = 368$ visits), *Centaurea cyanus* ($n = 302$), *Jacobaea*

vulgaris (n = 253), *Borago officinale* (n = 249). Moths visited *Rubus* sp., *Ligustrum vulgare* and *Buddleja* spp. at all the seventeen sites (Supplementary Table S4.7)

Table 4. 1 Summary of the insect species richness and abundance of bees, hoverflies and moths collected in urban agricultural sites in Leeds during the growing season 2020.

	Abundance	Species richness
Bees	4303	49
Solitary	532	38
Social	3771	11
Hoverflies	554	41
Moths	2617	203
Total	7616	311

Insect community responses to floral and nesting additions:

Within our experimentally added flower patches, 47 species of plants were recorded (this was less than hoped due to drought in spring). The most visited flowers in the patches were *Centaurea cyanus* (n = 203), *Borago officinalis* (n = 100), *Limnathes douglasii* (n = 56), *Symphytum officinale* (n = 51), *Cirsium vulgare* (n = 48), *Jacobaea vulgaris* (n = 30) and *Sonchus oleraceus* (n = 28). We found that the addition of floral resources (~100 m) did not significantly increase the site-level area of flowers in our treated sites compared to our control sites ($F = 2.43$, $df = 1$, $p = 0.13$, Figure 4.2)

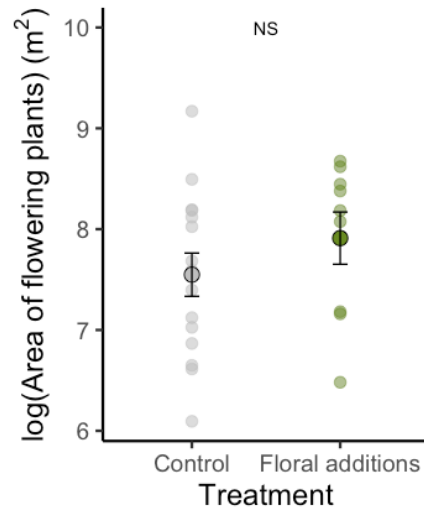


Figure 4. 2 The total area of flowering plants in allotment sites across two treatments, control, where no floral resources were added and treatment of floral additions where ~100m of nectar rich flower mixes were added to the sites. NS = Type II Analysis of Variance with Satterthwaite's method showed no significant difference between the treatments ($F = 2.43$, $df = 1$, $p = 0.13$).

When mean insect abundance and species richness were compared across treatments, there was no evidence that the supplemental floral or nesting resources had any effect on insect communities in the allotment sites (Figure 4.3). However, the site scale covariates had important effects on insect abundance, but not species richness (Figure 4.4). Sites with higher areas of cultivated flowers had higher abundances of insects ($F = 3.06$, $df = 3$, $p = 0.03$). This response was taxon-specific and posthoc tests found that this pattern was driven by social bees only ($F = 14.69$, $df = 1$, $p < 0.001$).

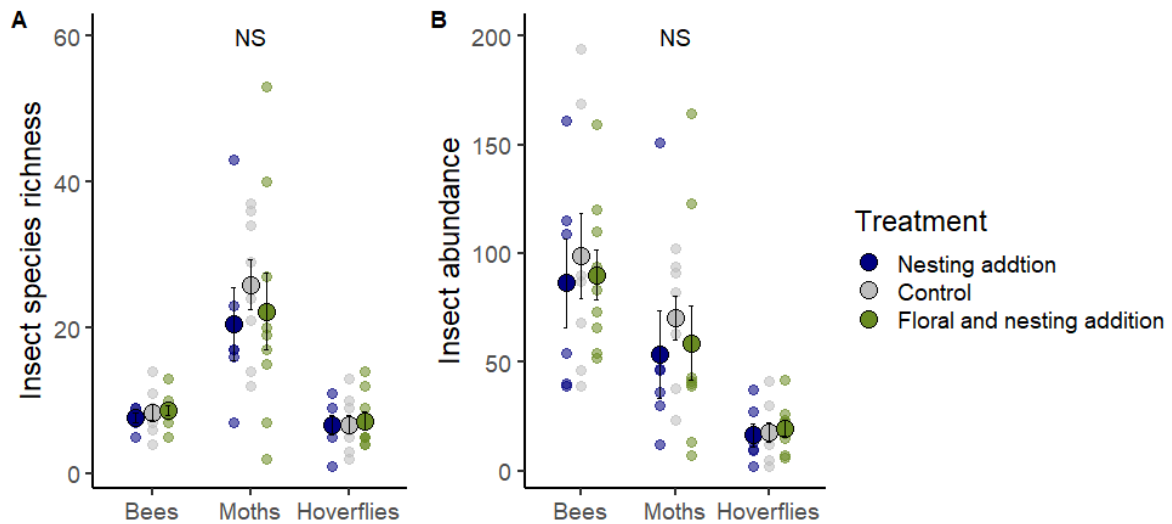


Figure 4. 3 The addition of nesting and floral resources has no significant effect on the A) abundance ($F = 1.53$, $df = 1$, $p = 0.22$) or B) species richness ($F = 1.8$, $df = 1$, $p = 0.17$) of bees, moth and hoverflies.

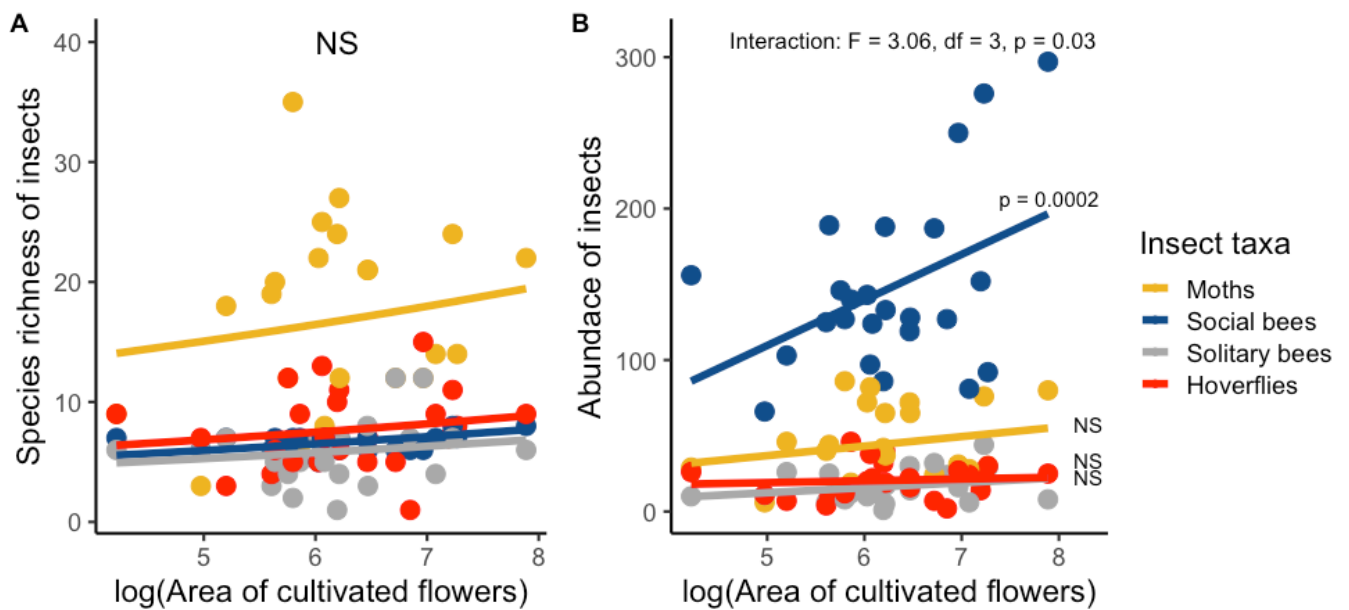


Figure 4. 4 Insect community responses to an increasing area of cultivated flowers in allotment sites. A) Species richness of moths, bees or hoverflies had no significant response to cultivated flowers, lines show non-significant model fit- with no interaction terms. B) Abundance of insects was positively associated with increasing areas of cultivated flowers, but this was taxon-specific, lines show a significant effect of cultivated flowers: insect taxa interaction ($F = 3.06$,

df = 3, p = 0.03) and this was driven by social bees (F = 14.69, df = 1, p = 0.0002).

Pollination services:

Pollination services were affected by a combination of local level (floral resource addition and site level cultivated flower areas) and landscape level (area of greyspace surrounding site) variables (Figure 4.5). Tomato seed set was 20% higher in the sites with floral additions compared to control and nesting addition sites (F = 6.02, df = 1, p = 0.014) (Figure 4.5A). We also found that sites with a greater proportion of surrounding greyspace had higher seed set (F = 8.98, df = 1, p = 0.007) (Figure 4.5B). In addition, as the area of cultivated flowers at a site level increases, so does the number of tomato seeds (F = 4.78, df = 1, p = 0.018) (Figure 4.5C). Species richness (F = 15.86, df = 1, p = 0.0006; Figure 4.5D) and abundance (F = 11.6, df = 1, p = 0.003) of bees also had a significant positive effect on the mean number of tomato seeds.

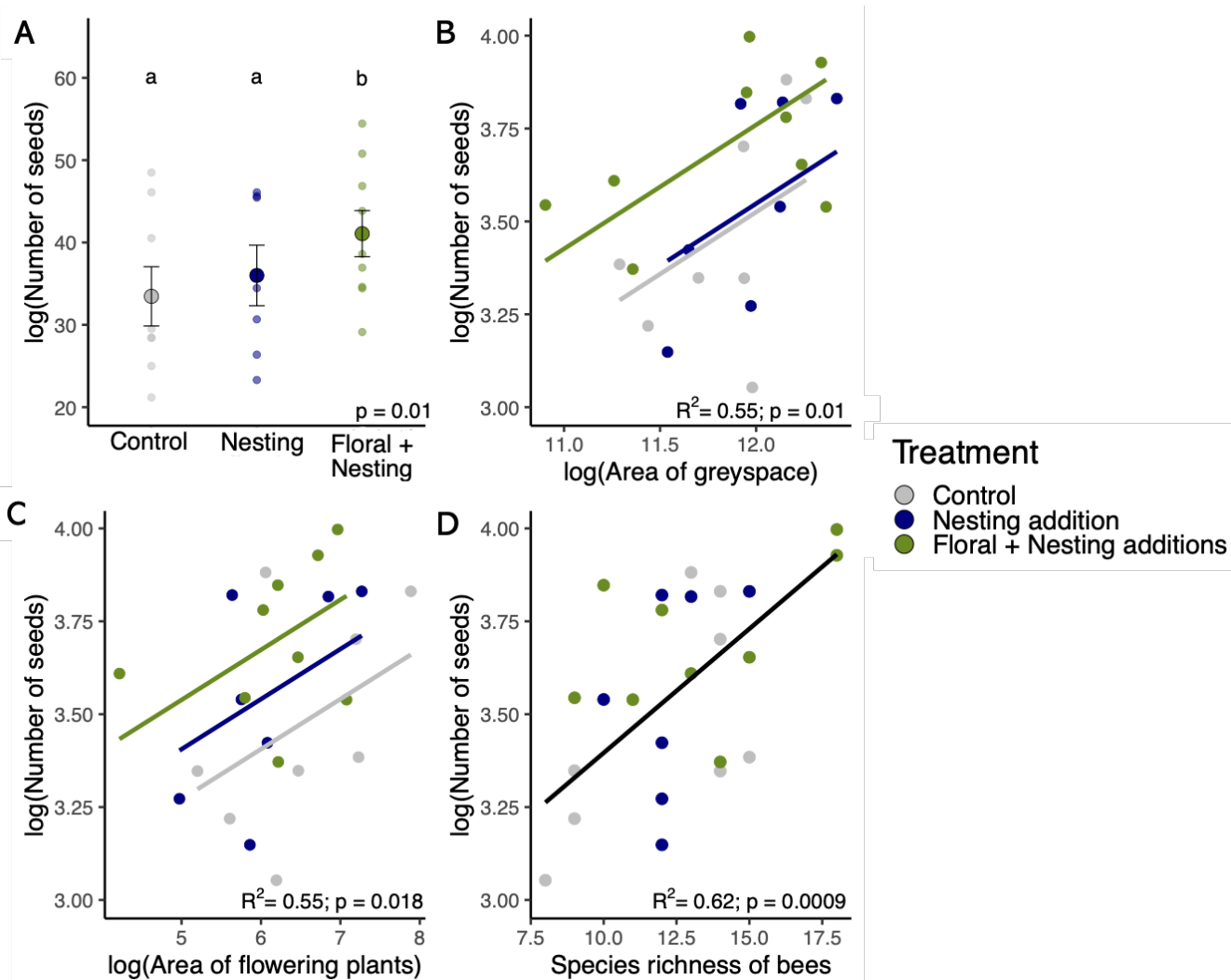


Figure 4. 5 Assessing the drivers of pollination efficiency using tomato seeds (mean per allotment site, $n = 24$) as a model crop. Panel A) shows that sites where we added floral resources (100m² areas of nectar rich flower patches) had a significantly higher seed set compared to the control and nesting addition sites. Panels B-D) show the highly related continuous variables of B) urbanisation (area of greyspace (m²) surrounding the sites (250m buffer), C) area of cultivated flowers (m²) in each site and D) species richness of bees was positively correlated with seed set of tomatoes ($p < 0.05$). (B-C) Solid lines represent model fit showing significantly higher seed set in the floral addition treatment compared to nesting additions and control with no significant interaction of treatment and the continuous variable. (D) Solid black line denotes a significant overall positive effect (non-interactive effects) of bee species richness on the mean number of tomato seeds across all treatments.

Feeding ecology of different groups of insect pollinators

Solitary and social bees and hoverflies visited distinct floral communities. Only 25% of the 171 plant species recorded were visited by all functional groups. The addition of hoverfly-plant interactions increased the number of plant species by 14%, with 23 plant species exclusively visited by hoverflies. When bees were separated based on sociality, we also found distinct plant communities visited by social (Apidae) and solitary (non-Apidae) species with only 33% overlap. Social bees dominated the plant visitation observations, visiting more plant species, and having higher individual host ranges and linkage density compared to solitary bees and hoverflies (Supplementary Figure S4.4). These foraging patterns and subsequent visitation networks of bees and hoverflies also varied across the season in different ways. There were significant interactions between time point and insect taxa (solitary bees, social bees, and hoverflies) for the network metrics, including the total number of plants visited ($X^2 = 33.30$, $df = 2$, $p < 0.00001$), number of plant species per insect species ($F = 5.92$, $df = 2$, $p = 0.003$) and linkage density ($F = 12.7$, $df = 2$, $p < 0.00001$). Despite the differences in the foraging patterns of hoverflies, social and solitary bees, we found that bees and hoverflies (and moths) visited flowers with higher sugar per floral unit more frequently ($F = 8.63$, $df = 1$, $p = 0.004$; Figure 4.6).

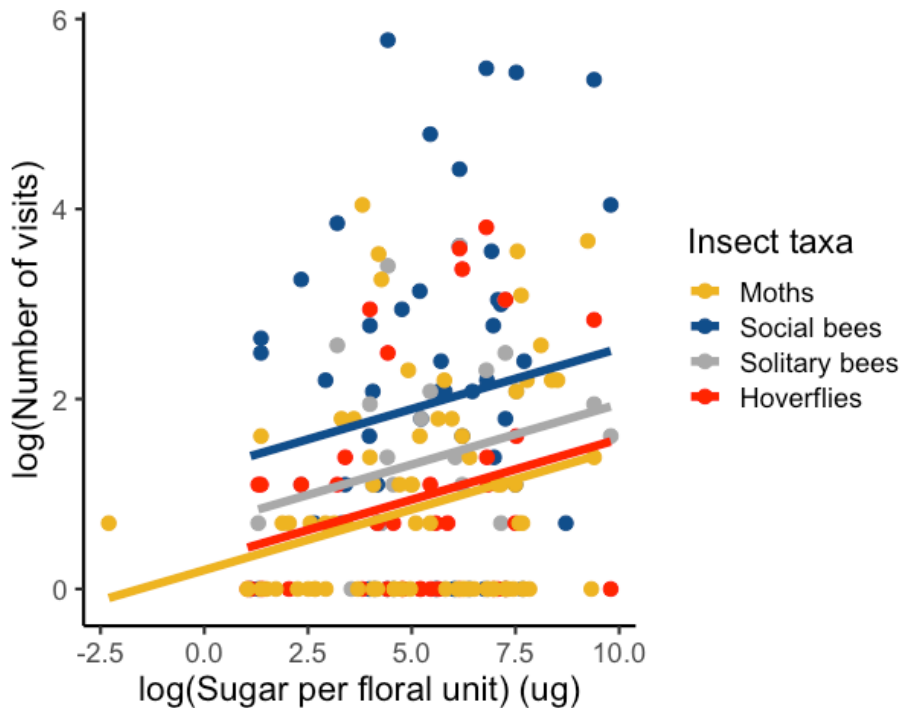


Figure 4. 6 Number of visits by bees, moths and hoverflies to plant species with different sugar per floral unit (ug). Trendlines show a significant effect of sugar per floral unit on the number of visits across all insect taxa (no significant taxon x sugar per floral unit interaction).

There was no change in pollinator-plant networks across our three treatments, but all network metrics were positively affected by increasing area of cultivated flowers at a site level, and this pattern was seen across all diurnal insect taxa (Figure 4.7). Significant positive effects of the area cultivated flowers were seen on all diurnal network metrics tested, number of plants visited ($F = 12.27$, $df = 1$, $p = 0.0005$, Figure 4.7A), the host range of insect species ($F = 5.67$, $df = 1$, $p = 0.02$, Figure 4.7B) and linkage density ($F = 7.34$, $df = 1$, $p = 0.008$ Figure 4.7C).

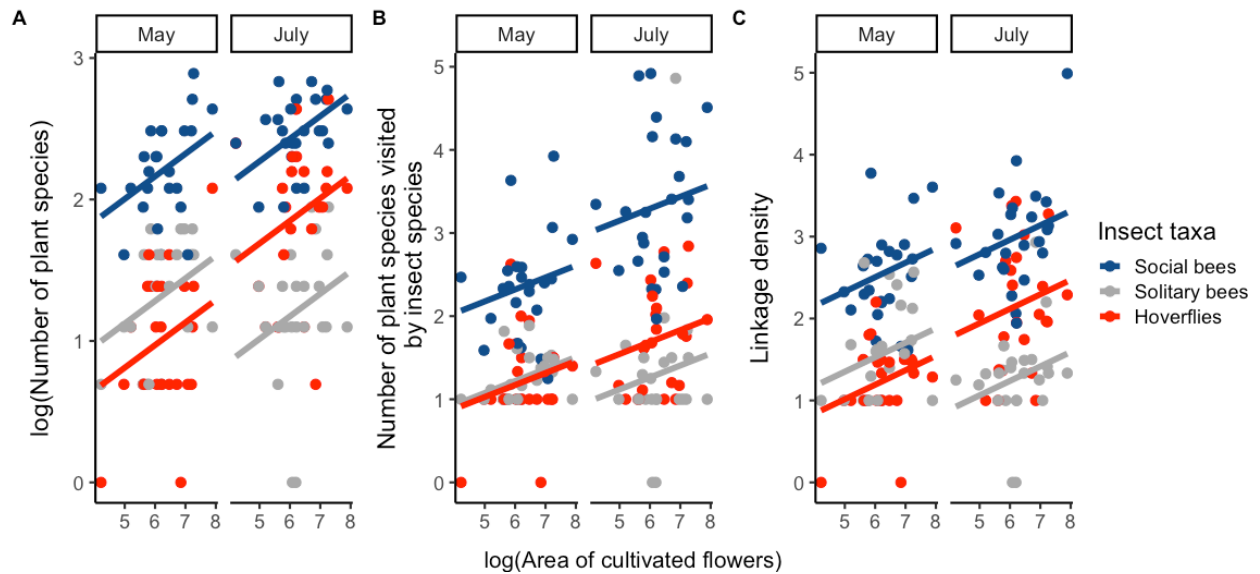


Figure 4. 7 Positive effects on insect-flower visitation network metric of diurnal pollinators (hoverflies, social bees, solitary bees) as area of cultivated flowers increases in allotment sites in both early summer (May) and mid-summer (July). Lines show fitted models, with significant main effect of area of cultivated flowers ($p < 0.05$), significant insect group*time interactions ($p < 0.001$) and non-significant interaction (i.e. same slope) between insect group* area cultivated flowers ($p > 0.05$).

Nesting resources:

The addition of cavity nesting trap resources was not the focus of this study due to very low uptake. Only 3% of the cavities were filled across the sites. The first year of trap nest instalments is usually low (MacIvor et al., 2017), and therefore any conclusions about nesting limitations are most likely a simple artefact of slow community establishments. Statistically, this is highlighted in the lack of differences in all analyses when nesting addition treatment sites were compared to control sites. We subsequently continued the trap-nest experiment for an additional year (2021) and found an 8-fold increase in the uptake of these nest, though we found no influence on the addition of floral resources nor site-level cultivation (see Chapter 5 for more details).

Discussion:

The addition of nectar rich flower patches in intensively modified ecosystems is a common practice to mitigate the declines of pollinators and to boost pollination services. However, the benefits to insect communities and their pollination services have rarely been tested in urban areas, especially for non-bee pollinators. Using a well-replicated large-scale, manipulation experiment, we found that there were complex local and landscape level drivers shaping pollinator communities as well as the pollination services they provide. Our experiment revealed that the addition of nectar rich floral resources increased the pollination of our model crop and that pollination services were higher in more urban sites compared to less urban sites. This pattern was likely driven by interrelated direct and indirect local and landscape factors. For example, the total floral resources (floral addition plus area of cultivated and wild flowering plants) in our sites was positively correlated with increasing area of grey space surrounding the site. This increase in floral resources, within more urban landscapes, was associated with higher abundance and diversity of bees, which enhanced the pollination services of our model crop. Interestingly, we found that the supplementation of nectar and habitat resources had no direct effect on the insect communities, their foraging patterns, or their pollination-networks in these urban greenspaces. This indicates that there are larger site-level and landscape-level drivers that are important in influencing plant-pollinator processes. Therefore, to effectively conserve insect pollinators (especially non-bees) these drivers must be considered for urban pollinator habitat conservation when using resource supplementation approaches.

The role of habitat amendments for pollination:

Scale-dependent factors such as the local area of floral resources and landscape-level modification can have a profound impact on both nocturnal and diurnal pollinator abundance and diversity, including moths (Bates et al., 2014; Ellis et al., *in prep*), hoverflies (Bates et al., 2011; Ellis et al., *in prep*) and wild bees (Ahrné et al., 2008; Banaszak-Cibicka et al., 2012; Ellis et al., *in prep*) and consequently on their pollination services (Griffiths-Lee et al., 2020; Theodorou et al., 2020; McDougall et al., 2022; Theodorou 2022). To date, the supplementation of floral resources has been

predominantly tested in an agricultural setting and shown to benefit the pollination services of crops (Albrecht et al., 2021). More recently, this has also been shown in urban gardens, where planting strawberry plants (*Fragaria × ananassa*) next to nectar-rich borage (*Borago officinalis*) increased the market value and size of the fruit by as much as 32% (Griffiths-Lee et al., 2020). McDougall et al., (2022) however, highlighted the complexity of pollination service delivery in urban garden crops and showed that crop yield in gardens was best explained by both local and landscape features, such as local canopy cover and garden-scale plant species richness.

Our experimental results similarly show that there are complex local and landscape-level drivers influencing pollination service delivery. In our experiment, floral additions increased the tomato seed set by up to 20% compared to sites where no flowers were added. Despite a lack of insect community response to our supplemental floral additions, we also found that bee species richness, site-level area of flowering plants, and landscape-level of urban intensity all had important positive effects on the pollination of tomatoes. Our work supports the importance of understanding larger drivers when assessing pollinator-plant interactions and pollination services as highlighted by Theodorou et al., (2020) and McDougall et al., (2022).

Disentangling the drivers of plant-pollinator interactions as well as their pollination services is a difficult task, especially in urban areas where both the local patch and landscape are intensely modified (Figure 4.8). We propose that the increase in pollination services observed in areas of greater urban intensity and the correlation with site-level cultivation are being driven by an ecological process known as the 'honeypot' effect (Theodorou et al., 2020). Specifically, flower-rich sites (i.e. allotments) located within an inhospitable landscape (highly urban) may attract insects from further afield than sites nested within a floristically-rich landscape (less urban). The associated reduction in greenspace as greyspace increases results in a concentration of foraging in greenspaces in highly urban areas, which then enhances the pollination services provided.

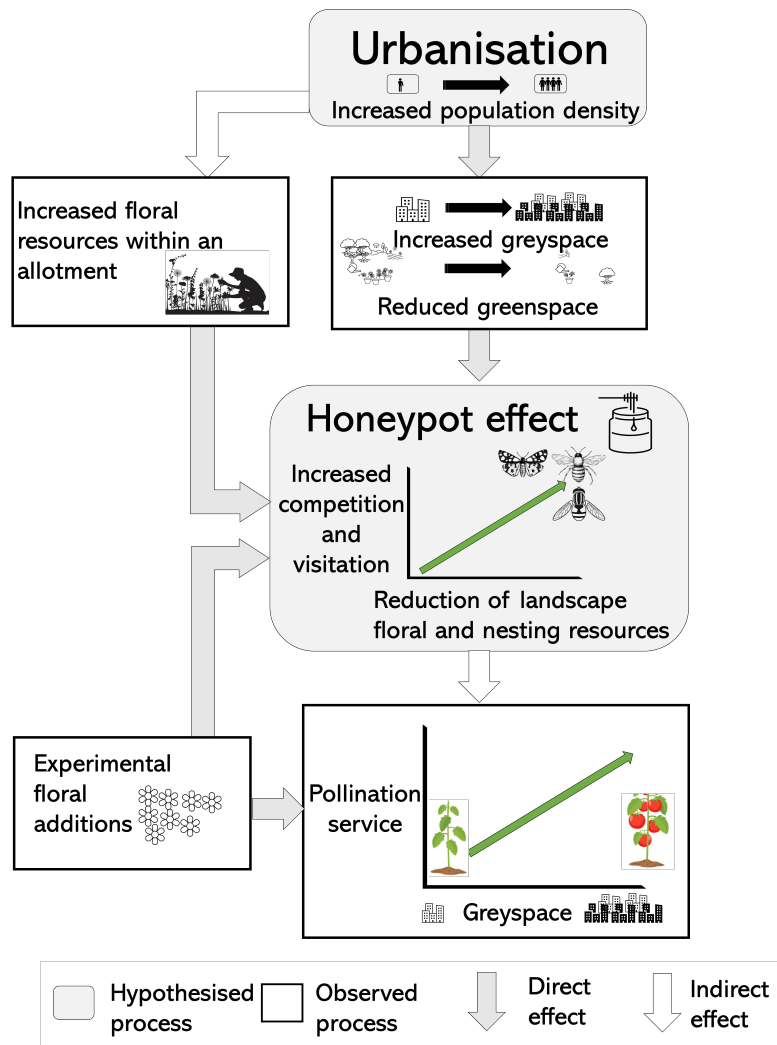


Figure 4. 8 Proposed mechanism for pollination services increasing in urban areas: as urbanisation increases so does the population density. This directly influences the increased area of greyspace (and the associated reduction of greenspace). As greenspaces become fewer in highly urban areas, this can cause increased competition and plant visitation in limited areas of floral resources. This, therefore, increases the pollination services within highly urban areas (honeypot effect).

Furthermore, the positive correlation between the site-level area of cultivated flowers and urban intensity (Supplementary Figure S4.3) increased the suitability of highly urban sites acting as a refuge for these insects (Figure 4.8). The circumstances that led to allotment sites in more urban areas having larger areas of cultivated flowers was not specifically measured in this study. However, this pattern could be driven by an

increased public demand for allotments and greenspaces in urban centres resulting in greater land-use efficiency at a site level with greater levels of floral cultivation (Figure 4.8). Although the increase of seed set could be seen as a benefit of increasing urbanisation, the robustness of these services may be fragile due to the increased anthropogenic pressures that also arise from urban intensity, such as pollution, habitat degradation and subsequent biodiversity losses that can decrease the stability of ecosystem functions such as pollination. This raises important questions about the resilience of pollination services in areas of higher urban intensity.

The role of habitat amendments for insects:

In urban ecosystems, there is some evidence that floral additions are beneficial for bees (e.g. Griffiths-Lee et al., 2022; Simao et al., 2018), but the effects on non-bee pollinators remain largely unknown and our results show that they may not benefit all insect taxa. Here we show that our additions of ~100 m² nectar-rich floral resources had no detectable direct effect on insect pollinator communities or their pollination networks. We believe there are two reasons for this observation; firstly, we found no difference in the overall flower area at a site level in our floral additions compared to the control sites (Figure 4.2) which implies that our patch area of 100 m² was not a big enough intervention to change site-level floral resources (as seen in Griffiths-Lee et al., 2022). Secondly, allotments have been shown to be floral and pollinator insect hotspots (Borysiak et al., 2017; Baldock et al., 2019). The lack of floral resource treatment effect could be diluted by the high floral density making it hard to detect any associated benefits in insect community or pollinator-network structure (Simao et al., 2018). Alternatively, if a system in which adding flower patches greatly enhanced overall nectar and pollen production were used, there may be a more significant effect on insect visitation (Potts et al., 2016; Lerman et al., 2018; Turo and Gardiner, 2019; del Toro et al. 2020).

Our results show that there were distinct floral communities visited by social bees, solitary bees, hoverflies and moths, with only a quarter of the plant species visited by all insects. This implies that the addition of floral resources may be less effective for whole insect communities unless specifically tailored to taxon-specific floral preferences. Despite differing visitation patterns, we found that all insect taxa

preferentially visited plants with higher sugar per floral unit (Figure 4.6). Our results support Tew et al., (2021), who highlights the importance of management for nectar supply rather than total area of flowering plants when conserving insect pollinators. However, the nectar sugar measurements only covered half our recorded plant species, so this requires further investigation to truly understand these patterns. Additionally, we show that increased area of cultivated plants in an allotment site increases the network complexity of bees and hoverflies. This result supports Matteson and Langellotto (2011) by showing that commonly planted (mostly exotic) garden plants, high in nectar and pollen rewards such as Cornflowers (*Centaurea cyanus*) and *Borago officinale* are being utilised by pollinating insect communities.

There was a positive effect of site-level cultivated flowers on insect abundance, but this was driven by social bees only (Figure 4.4B). This adds important evidence to previous observations that social bees are more resilient to urbanisation compared to other diurnal and nocturnal taxa (Theodorou et al., 2020; Ellis et al., *in prep*). The sociality behaviour displayed by the bees in our experiment suggests behavioural and ecological flexibility which might also facilitate their survival in urbanised environments Banaszak-Cibicka and Żmihorski, 2012; Wenzel et al., 2020). In contrast, moths, hoverflies, and solitary bees have distinct and divergent life-history traits. Although we show that all adult insect taxa preferred nectar with higher sugar (Figure 4.6), the lack of abundance or species richness responses to overall floral resources suggests that there are important larval, nesting and host plant requirements to consider when improving habitat quality for non-social bee pollinators.

Conclusion

To improve the effectiveness of flower patch plantings in promoting pollinator insect diversity and pollination services, we need to better understand what determines their success or failure. Disentangling the drivers shaping insect pollinator communities, plant-pollinator interaction, as well as their pollination services, is a difficult task, especially in urban areas where both the local patch and landscape are intensely modified. Our results show that floral additions at small scales did not benefit insect communities but increased the provision of pollination services. There were also important landscape and site-level effects influencing these processes, highlighting

the need to consider the complex scale-dependent direct and indirect factors when conserving pollinating insects. Finally, we show that not all insect pollinators benefited from floral resource availability. Therefore, it is essential to create or preserve flower-rich habitat that will be used by a variety of adult stage pollinators. Additionally, separate strategies must be employed in order to support the different requirements of their immature life stages.

Supplementing floral resources does not mitigate the negative effects of urbanisation on cavity nesting bees and wasps.

Formatted for Biological Conservation

Abstract

Concern over pollinator declines has directly influenced the management of urban greenspaces in an effort to conserve pollinating insects. One such management tactic is improving floral resources available for bees and conserving and enhancing floral communities. However, there have been few studies testing the complementary and critical need for nesting site provisioning, or the relative importance of nest site and food constraints on pollinator populations. We manipulated floral and nesting resources by adding nectar-rich flower patches and artificial 'bee hotels' (trap nests) in horticultural sites along an urbanisation gradient and assessed nest colonisation by solitary bees and wasps. Cavity-nesting insect abundance was negatively affected by increasing urbanisation and appears to be driven by nesting resource limitation. The addition of floral resources did not mitigate the negative effects of urbanisation on nest uptake or increase the abundance of solitary bees or wasps. Our results suggest that conservation strategies for urban pollinators should consider the need for multiple types of management intervention to better support diverse insect communities.

Introduction

The process of urbanisation is one of the main drivers of global declines in insect diversity and is largely driven by the conversion of non-urban agricultural, natural or semi-natural habitats into areas of impervious surfaces (Wagner et al., 2021a). The remaining mosaic of greenspaces within urban areas act as refuges for numerous pollinating insect taxa, such as bees (Hall et al., 2012), especially when compared to agricultural areas (Baldock et al., 2015; Theodorou et al., 2020). These greenspaces are usually individually managed, creating heterogeneity in the resources provided by greenspaces. This heterogeneity can be influenced by efforts to conserve pollinators, both through bottom-up approaches (e.g. 'No-Mow May' (Plantlife, <https://www.plantlife.org.uk/>) and 'Gardening for Wildlife' (RSPB, <https://www.rspb.org.uk/>)) and top-down policy approaches e.g. the U.K. National Pollinator Strategy 2021-2024 (DEFRA, 2022). However, while certain greenspace types (e.g., allotments and gardens, Baldock et al., 2019) and management interventions can offer suitable habitat for insect pollinators, the role of such interventions in heterogeneous urban landscapes remains poorly understood.

Floral resources (pollen and nectar) are vital for bee survival (Frankie and Thorp, 2009), and variation in floral resource availability strongly affects the abundance and diversity of wild bee populations (Roulston and Goodell, 2011). Supplementing floral resources has therefore become a focus of urban pollinator conservation. Wild bees are also limited by nesting habitat and nest site locations (Kammerer et al., 2021). Consequently, a common intervention is addition of 'bee hotels', i.e., artificial trap nests for cavity nesting bees and wasps (Maclvor and Packer, 2015; Maclvor, 2017). Solitary cavity nesting bees are short-distance, central-place foragers once they have established their nests (Simanonok and Burkle, 2019) and are likely to benefit from the local addition of floral resources. Although less frequently tested, flower patch additions have been shown to benefit predatory wasps, though with unknown effects on parasitic wasps (Haaland et al., 2010). However, despite the clear interlinked dependence of bees and wasps on both food and nesting resources, the relative effectiveness of these different interventions is rarely tested.

The conservation of solitary wild bees is a key step in conserving pollination services as their morphological and behavioural diversity increases the stability of successful pollination (Winfree et al., 2008; Brittain et al., 2013; Garibaldi et al., 2013). This is particularly significant in pollination-limited environments such as cities where ecosystem functioning, underpinned by pollination, is vulnerable due to increased disturbance. Wild bees are globally important pollinators and have been shown to enhance crop production (Garibaldi et al., 2013). They are also key pollinators of both cultivated and wild plants in urban areas of the UK (Ollerton et al., 2011; Lowenstein et al., 2015; Baldock et al., 2019), however, the response of cavity nesting bees to increasing urbanisation is unclear. Areas of high urbanisation have been shown to reduce plant availability and foraging range of bees, resulting in population declines for solitary bees (Hernandez et al., 2006). However, increased urban density, with a complex mix of green and grey infrastructure may also provide increased nesting opportunities in built structures (Cane, 2005; Banaszak-Cibicka and Zmihorski, 2012; Hinners et al., 2012; Cardoso and Gonçalves, 2018); potentially buffering them against urbanisation (Xie et al., 2022).

Nesting cavities are also an important resource for a wide range of non-anthophilous insects, many of which may be sensitive to the effects of urbanisation. For example, predatory and parasitoid wasps are frequent occupants of artificial traps nests (Tscharntke et al., 2005). Predatory, parasitoid and cleptoparasitic species are known to be vulnerable to habitat fragmentation and isolation (Zabel and Tscharntke, 1998; Gibb and Hochuli, 2002; Sheffield et al., 2013), and by extension could suffer more than bees from the negative effects of urbanisation. Solitary wasp communities provide ecosystem services such as the regulation of insect pest populations (Tscharntke et al., 2005; Bianchi et al., 2006; Careless et al., 2014), yet their communities are poorly understood, particularly in urban areas, due in part to negative public perception of wasps (Sumner et al., 2018). Parasitoids are more impacted by land cover than their hosts (Nelson and Forbes, 2014) and predators respond negatively to increasing impervious surface area (Rocha and Fellowes 2018); however, there are relatively few studies assessing the factors shaping their communities.

We tested the hypothesis that increasing floral resources benefit cavity nesting insects by mitigating the negative effects of urban landscapes. We experimentally manipulated floral resources by adding patches of nectar-rich flower patches and compared the colonisation of trap nests in these sites compared to sites where no additions were made. We monitored insect diversity and abundance in the nests over two years to address two main research questions: 1) how does urbanisation affect trap-nest colonisation; and 2) are the effects of urbanisation influenced by the addition of flower resources?

Methods

Study system:

This study was carried out in areas of urban horticulture: allotments. Allotments are urban green spaces composed of plots of land rented by an individual or household for growing vegetables. They have been identified as pollinator and plant hotspots in urban areas (Baldock et al., 2019), containing high diversity due to their high floral resources and habitat heterogeneity (Tew et al., 2021). These greenspaces also offer important opportunities for urban conservation through habitat manipulation due to the high plasticity of the individual plots which is driven by the seasonal and annual dynamics of individual plot holder managements. For example, they have the flexibility to engage in various activities such as crop rotation, intercropping, mulching, composting, and wildlife-friendly gardening.

Experimental design:

This study was carried out in 24 allotment sites throughout the 2020 and 2021 growing seasons (March-October) in Leeds, England (53°47'47.33"N, 1°32'52.26"W). The sites were chosen in eight blocks of three, where the blocks of sites were clustered together to avoid spatial confounding and each block was located along an urbanisation gradient, radiating out from the city centre (Figure 5.1A). Within each block there was one site assigned nesting provisioning treatment where trap nests were added to supplement cavity insect nesting resources. The second site was assigned a nesting and a floral provisioning treatment where flower patches (~100 m²) were sown with a nectar-rich (annual and perennial) seed mix (species list

Supplementary Table S4.1; detailed methods Supplementary Text S4.1) in March of each year as well as the addition of trap nest (Figure 5.1). The third site was a control where no additions were added. Here, we report a comparison of the treatment sites only, henceforth referred to as pairs (+nesting and +nesting and floral resources). The control site was used as part of another experiment that tested the effects local floral addition had on the bees, moths and hoverflies and the subsequent pollination services provided (see Chapter 4).

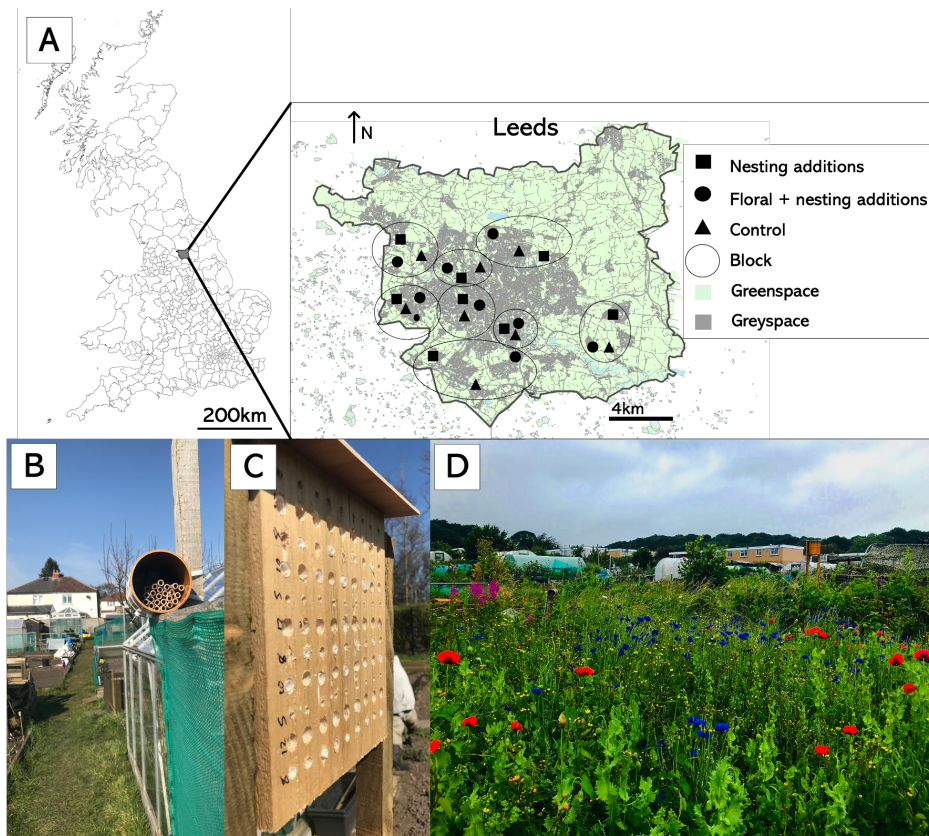


Figure 5. 1 A) Left: city of Leeds location within the U.K., right the site locations, treatments and block set-up along an urbanisation gradient. B-C) Nesting additions: B) Trap nests type 1, made of 8mm cardboard tubing, C) Trap nest type 2, made of 5mm,8mm,10mm,12mm drilled holes in wooden blocks. D) Floral additions: Example of one of the 100m² flower additions in allotment sites (see Chapter 4)

Trap nests:

We constructed 96 trap nests from PVC pipe filled with cardboard tubes (diameter 8 mm; length 13cm; n= 25 per PVC pipe; Supplementary Material Figure S4.1),

henceforth referred to as cardboard nests (www.masonbees.co.uk) (Figure 5.1B). Twenty-four blocks of unprocessed pine wood (25 x 20 x 20cm) were drilled with 90 holes of different diameters (5mm (n holes = 36), 8mm (n holes = 27), 10mm (n holes = 27), 12mm (n holes = 27)) and 13cm in length (henceforth referred to as wooden nests; Figure 5.1C). Each hole was lined with parchment paper before being put in the field so that the larvae could be extracted in winter (Supplementary Material Figure S4.2).

We placed 112 trap nests out for two years (2020 and 2021): all 1.2 m-1.5 m off the ground, in full sun, in a south-facing position. They were put out in early March of 2020 and collected in October 2020 (to prevent mould and bacterial colonisation), all empty tubes were cleaned, and all colonised tubes were overwintered at 4°C and then incubated at 21°C starting early March until all insects had emerged (following adapted methods from MacIvor (2017)). Bees were identified to species level and wasps they were identified to morphospecies (due to their complex taxonomy). The cleaned nests were replaced in the field in early March in 2021 and then collected, overwintered, and incubated as described above. In 2020 six cardboard nests and one wooden nest were placed randomly around each site. In 2021 two more wooden nests were also added (wooden nests n = 3 per site). We quantified four related measures of nest uptake: (1) the total number of bees and wasps that emerged (abundance), (2) the total number of species of bees and wasps (species richness), (3) the number of tubes filled per site (number of nests), (4) the number of insects per occupied tube (fecundity).

Habitat maps and urbanisation:

For each allotment site, a series of variables related to insect pollinators were determined at the local (site) and landscape level. The area of 'wild flowering plants' (e.g. flowering areas of disused plots and areas of 'weeds'), and the area of 'cultivated flowers' (e.g. managed flower beds, flowering fruit and crops on each plot) were surveyed at each site in July 2020. The area of wild and cultivated flowering plants were mapped onto aerial imagery on-site. These maps were then digitised in Image J (Schneider et al., 2012) and the area (m²) of these two variables was extracted. Using ArcGIS (version 10.1.7), we quantified urbanisation as the area of impervious surface

surrounding the allotment sites, which was extracted from UK Ordnance Survey MasterMap© (See Supplementary Methods S1; <https://digimap.edina.ac.uk/>). Impervious surface included all land-types described as 'manmade', including buildings and roads were selected. Circular buffers surrounding the allotment site, with the centre of the circle being the centre of the site, were drawn with a radius of 250m which has been previously shown to be an important landscape scale when investigating pollinator responses to urbanisation (Ellis et al. in prep; Ellis et al., in review). The area of impervious surfaces was then exported and used for subsequent analysis.

Data analysis:

All analysis was done in R version 4.12 (R Core Team 2022).

We analysed how insect abundance, species richness, nest occupancy and fecundity were affected by: 1) local floral cover and landscape urbanisation, 2) the treatment (nest additions vs nest+floral additions), and 3) the interaction of habitat covariates and treatment.

Generalised linear mixed models were constructed using MCMCglmm::MCMCglmm (Hadfield, 2010) as the data were over-dispersed, zero-inflated, and Poisson distribution assumptions were the best match. P-values were derived from the posteriors with standard parameter-expanded priors. We included the season (year 2020 and 2021), nest-type (cardboard nest and wooden nest) and insect taxa (bees and wasps) as model terms, outlined below. In all analyses with multiple terms and interactions, any non-significant interactions were removed from the final model.

trap nest uptake measure ~ *Insect taxa* + *Treatment* + ***Habitat variable***
+ (*Treatment* * ***Habitat variable***) + (*Insect taxa* * *Treatment*)
+ (*Insect taxa* * ***Habitat variable***) + *Year* (2020,2021) + *Nest type*
+ (1| *Pair*)

Due to the skewed species distributions, we also separately analysed the four most abundant species (*Monodontomerus* spp., *Megachile ligniseca*, *Osmia leaiana*, *Hylaeus* spp.), pooled across site, and tested their abundance against urbanisation and our treatment:

$$\begin{aligned} \text{total insect abundance} \sim & \text{Treatment} + \text{Habitat variable} + \\ & (\text{Treatment} * \text{Habitat variable}) + \\ & (\text{Insect taxa} * \text{Treatment}) + \\ & (\text{Insect taxa} * \text{Habitat variable}) + (1|\text{Pair}) \end{aligned}$$

Results

Dataset description:

Across the two years, a total of 2527 insects emerged from the trap nests (Figure 5.2 for most abundant). Twenty-five species of insect were found to colonise the trap nests, including eight species of bees. Bees accounted for 39% (n = 979) of the total community, and wasps 59% (n = 1491). The remaining 2% (n = 57) were flies (Insecta: Diptera) and were excluded in all analyses as they only occurred in two trap nests. In total 17 wasp morphotypes were recorded (Supplementary Table S5.1-S5.2). The wasp community comprised bee parasites and predators of other arthropods, such as aphids, spiders (*Passaloecus/Pemphredon* spp.), and caterpillars (*Ancistrocerus* spp.). Small parasitic chalcid wasps (*Monodontomerus* spp.) were the most abundant with 1164 individuals (46% of all insects). The leaf cutter bee (*Megachile ligniseca*) was the second most abundant insect (n=296) followed by mason bee *Osmia leaiana* (n= 211) and yellow faced bees *Hylaeus hyalinatus* (n = 199) and *Hylaeus communis* (n = 130). The most used cavity size was 8mm (n = 1191 insects), followed by 5mm (n = 376), 10mm (n = 140) and 12mm (n = 13).

Uptake was low in the first year (2020) with only 15 of the 112 trap nests (13%) being used but increased to 41 of the 126 trap nests (32%) in 2021. Both bees and wasps showed a preference for wooden trap nests compared to cardboard nests with higher species richness (95% CI: 1.91- 0.81, p < 0.0001) and abundance (95% CI = 1.82- 5.56, p = 0.02) in wooden blocks. The average number of larvae hatched per tube was different among species ($\chi^2 = 338.72$, df = 7, p < 0.0001) and higher in cardboard nesting tubes compared to wooden boxes ($\chi^2 = 14.2$, df = 1, p = 0.04).

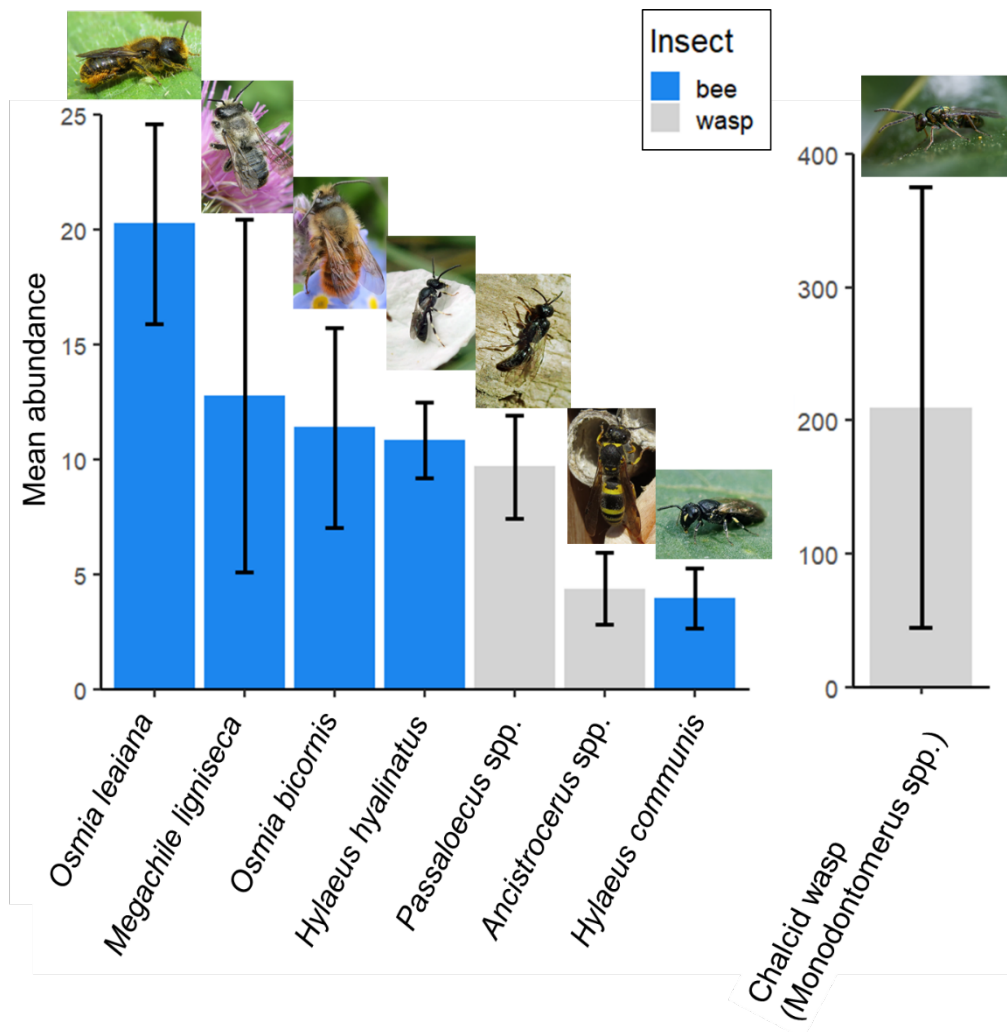


Figure 5. 2 Mean \pm SE abundance of eight most abundant cavity nesting insect species across allotment sites. *Photo credit: Steven Falk and Chalcid wasp by Brian Valentine.*

The influences of floral additions:

There was no difference in nest uptake, abundance (Figure 5.3A), species richness (Figure 5.3B), the number of tubes occupied in each site ($\chi^2 = 0.59$, $df = 1$, $p = 0.44$), and the number of larvae in tube, across time and nest type ($\chi^2 = 0.18$, $df = 1$, $p = 0.67$) between sites with nests and added floral resources and sites with nests only. At a site level, the total area of flowering plants, the area of cultivated flowers and the area of wildflowers also had no effect on the uptake of trap nests ($p > 0.05$, Supplementary Material Tables S5.3-S5.6).

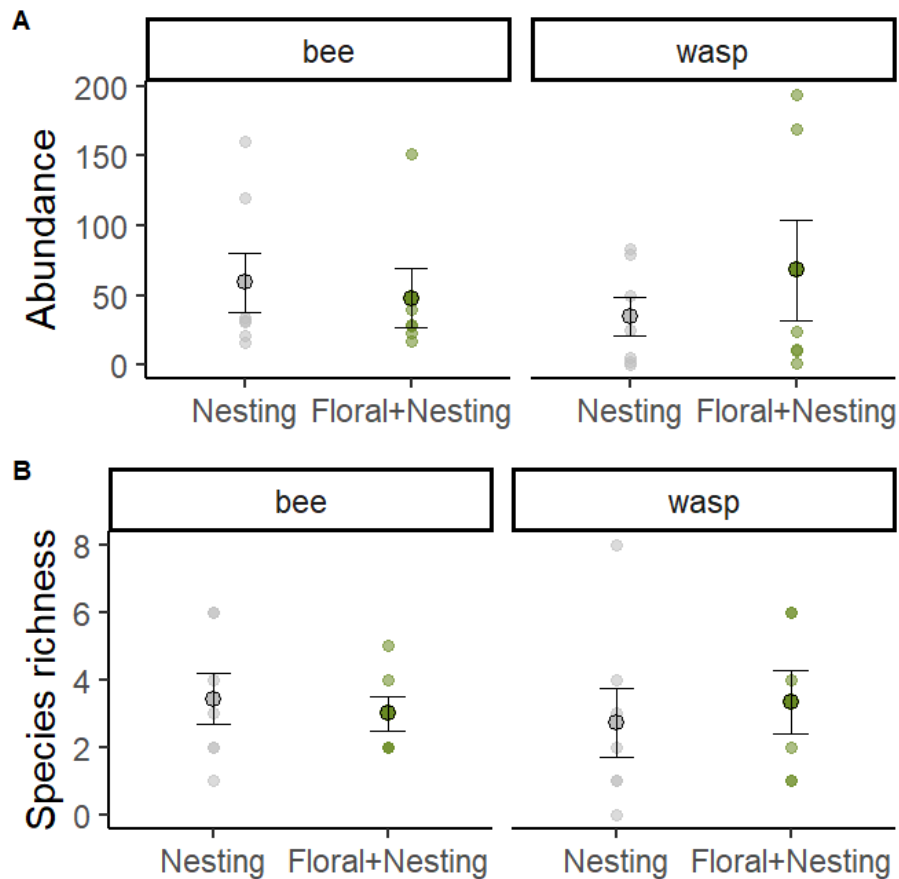


Figure 5. 3 Effect of floral additions on the uptake of trap nests both for A) abundance and B) species richness of bees and wasps in allotments.

The influence of urbanisation:

Sites with higher area of greyspace surrounding them had lower uptake of bee nests compared to sites with lower greyspace and the addition of floral resources did not mitigate these declines (Figure 5.4). Increasing urbanisation had negative effects (with no significant interaction) on the overall abundance of bees and wasps (95% CI = -2.68- -0.13, $p = 0.036$; Supplementary Material Table S5.7). There was no significant effect of urbanisation on species richness of bees or wasps (95% CI = -1.38- 0.15, $p = 0.11$; Supplementary Material Table S5.8).

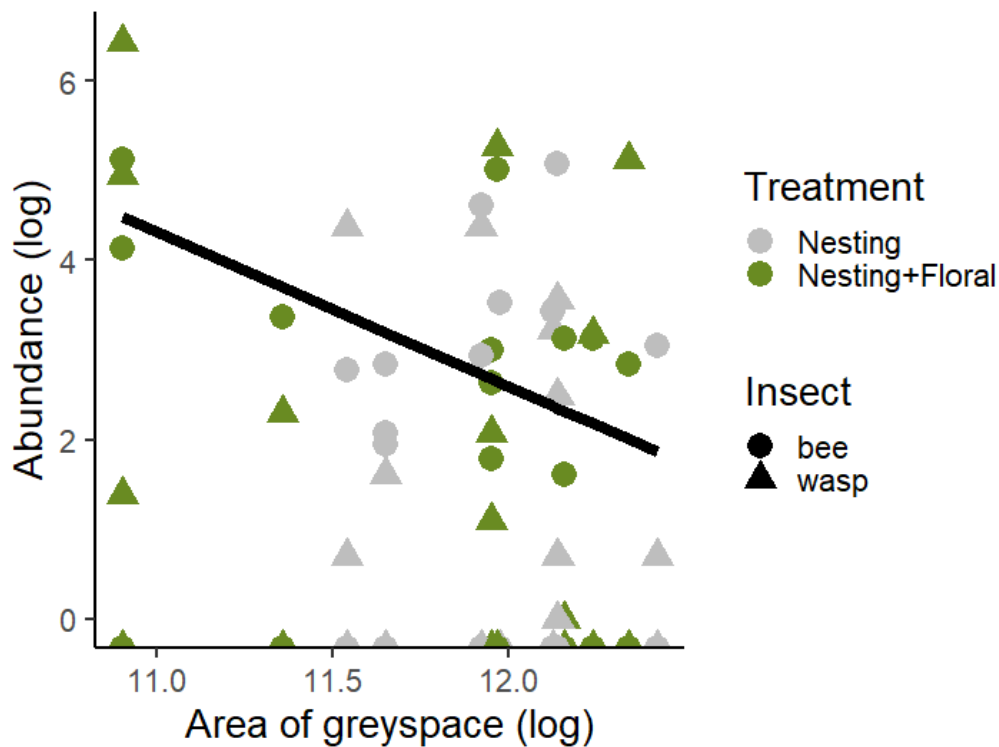


Figure 5. 4 Relationship between bees and wasp abundance and area of greyspace surrounding an allotment, for each treatment. Solid black line denotes a significant overall negative effect of urbanisation on both bee and wasp abundance (95% CI = -2.68- -0.13, $p = 0.036$), across all treatment and taxon combinations.

Species-specific responses:

There was evidence of species-specific variation in the response to urbanisation. Specifically, the abundance of mason bees (*Osmia leaniana*) and chalcid wasps (*Monodontomerus spp.*) declined with increasing urbanisation, floral additions did not affect this response (Figure 5.5; Supplementary Material Table S5.9). There was also weaker (non-significant) evidence that the leaf cutter bee (*Megachile ligniseca*) had higher abundance in sites with floral addition ($p = 0.089$; Supplementary Material Table S5.9) and the abundance was negatively influenced by urbanisation but only in the allotment sites where floral resources were added (urbanisation x treatment interaction: $p = 0.088$; Figure 5.5 B). Yellow-faced bees (*Hylaeus spp.*) showed no response to increasing area of urbanisation (95% CI = -1.76- 3.28, $p = 0.68$; Figure 5 C).

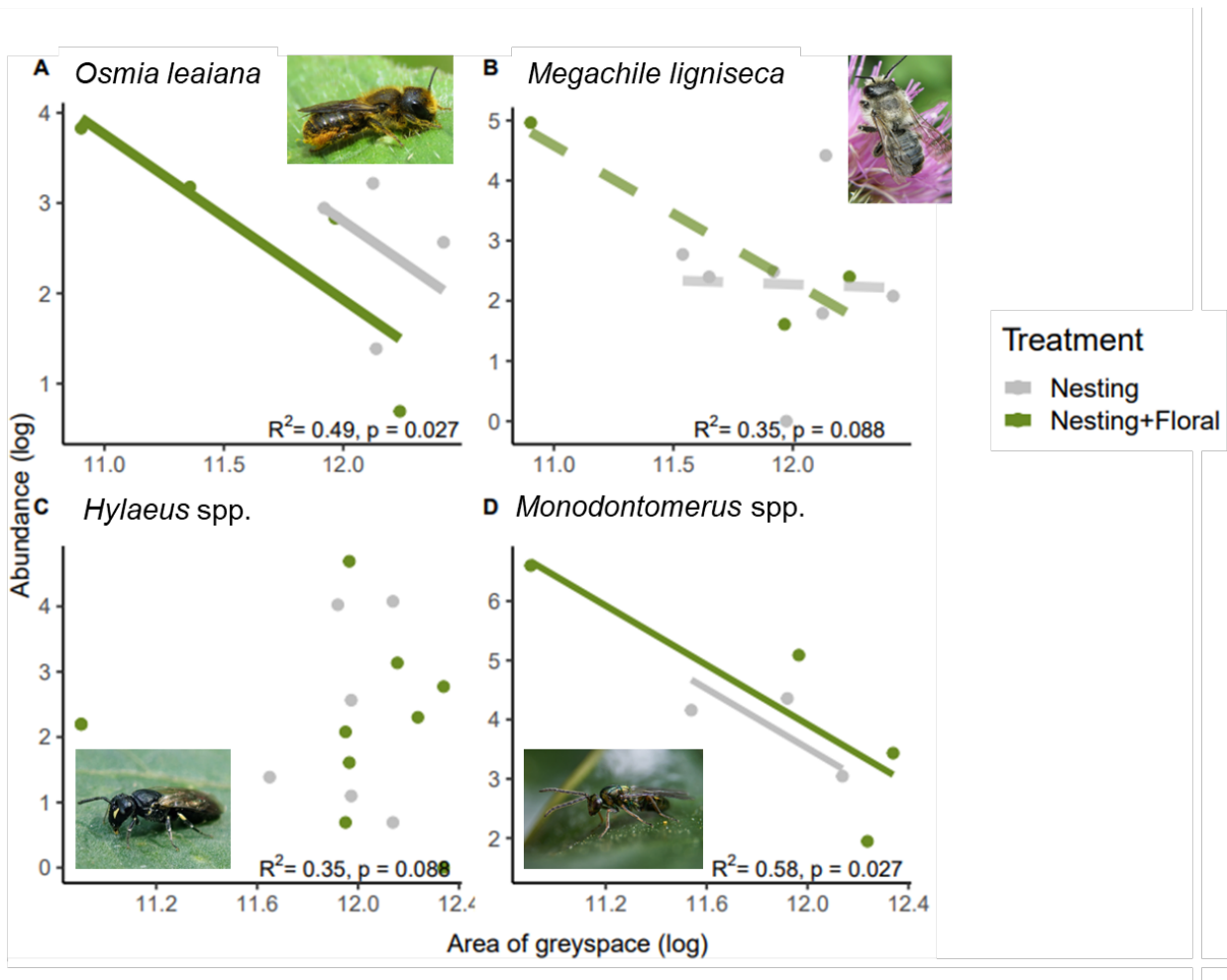


Figure 5. 5 Effect of increasing urbanisation on the abundance of A) *Osmia leaiana*, B) *Megachile ligniseca*, C) *Hylaeus* spp. and D) *Monodontomerus* spp. found in trap nests. Solid lines illustrate the significant overall effect of urbanisation (no interaction); B) dashed lines show some evidence of an urbanisation*treatment interaction ($p = 0.088$; Supplementary Material Table S5.9).

Discussion

A key bee conservation management strategy is the improvement of floral resources through habitat preservation and enhancement (Potts et al., 2005; Spivak et al., 2011; Kirk and Howes 2012). Many solitary bee species are also limited by nest sites, particularly in urban environments, and trap nest provisioning, therefore, represents an additional important intervention to support bee populations. However, the joint effects of these management tactics are rarely assessed while accounting for the

complex landscape impacts of urbanisation. Our experimental manipulation of floral resources and nesting sites along an urbanisation gradient revealed few overall benefits of additional flower patches. However, we found that with increasing area of impervious surface there was a negative effect on both wasp and bee colonisation of trap nests.

Considering the reported ecological value of the pollination services provided by cavity nesting bees in urban systems (Fernandes et al., 2022), the reported declines in abundance as urbanisation increases poses potential threats to pollination in cities. This is especially important for urban horticulture as these areas are highly dependent on insect pollinators for crop production. There are also broader implications for understanding the resource requirements and conservation of cavity nesting bees. For example, in agricultural systems, it has been shown that mason and leaf-cutter bees (*Osmia* and *Megachile*) can be more efficient pollinators than honeybees for rosaceous crops (e.g. apple, cherry, pear, and almonds; Matsumoto and Maejima, 2010; Sheffield et al., 2008). As a result, solitary bee species are now being established as commercial pollinators (e.g. Bosch and Kemp, 2001; Biddinger et al., 2008; Sampson et al., 2009; Pitts-Singer et al., 2018). Our results suggest that in agricultural systems, the common practice of adding floral resources may not offer the resources requirements to mitigate the landscape pressures they are facing (Gresty et al., 2018; Bihaly et al., 2020). Therefore, it is likely that conservation interventions need to be specifically tailored to support these important pollinators and subsequently optimise the ecosystem services they provide.

Our results contrast with reports of increased abundance of cavity-nesting bees in response to increasing urbanisation (Banaszak-Cibicka and Zmihorski 2012; Cane, 2005; Hinnens et al., 2012). Some studies have suggested that cavity nesting bees may be equipped with an 'essential' trait for urban survival (Wenzel et al., 2020), but, our results suggest that their communities are still declining, e.g. by 6-fold in our most urban site compared to our least urban site (Figure 5.4). Diet breadth has also been shown to facilitate urban pollinator survival (Wenzel et al., 2020), with polylectic (host generalist) species having increased resilience to urbanisation compared to oligolectic species. However, all insect species in this study are considered generalist foragers

(Falk, 2015) and their declines indicate that even generalists are at risk in urban areas. Our specific species analysis revealed that highly generalist species are declining, including mason bees (*O. leaiana*) (Figure 5.5A), however many species in our study were not influenced by urbanisation. For example, yellow faced bees (*Hylaeus* spp.) showed no response to urbanisation, consistent with the response reported by Banaszak-Cibicka and Zmihorski (2012). Their resilience may be based on their particular suite of functional traits: generalist feeders, smaller body size (allowing access to a wider range of cavity sizes) and late spring/summer activity peak. These species-specific responses add to the growing recognition that not all bees respond uniformly to ecosystem changes (Banaszak-Cibicka and Zmihorski 2012; De Palma et al., 2015; Rader et al., 2020). Future work should take an explicit trait-based approach to understanding urbanisation impacts on wild bees.

Contrary to our predictions, at a community level, wasps were not more sensitive to urbanisation. (Figure 5.5). The life history of the wasp community in this study is most likely to be the reason for this. The majority of non-chalcid wasp species sampled consisted of spider- and aphid-hunters (*Passaloecus*/*Pemphredon* spp. 65%), which have been shown to thrive in urban areas (Alaruiikka et al., 2002; Shochat et al., 2004; Soga et al., 2014; Guenat et al., 2019). However, our species-specific analysis provided anecdotal evidence that some parasitic chalcid wasps may be more sensitive than their hosts: e.g., the response of the leafcutter bee, *Megachile ligniseca* was not significantly affected by urbanisation, while the *Megachile* parasitoid *Monodontomerus* spp. was strongly affected.

Our experiment aimed to identify whether nesting sites or floral resources were more important constraints on wild solitary bees. Although the addition of floral resources is one of the most common conservation practices used to support pollinators, especially in urban greenspaces, nectar-rich flowers did not increase cavity nesting bee and wasp abundance, and there was little indication that site-level variation in overall flower abundance affected bees and wasps (supporting Campbell et al., 2017). This suggests that there may be limitations on the utility of this management intervention such as the limitation of pollen resources offered by nectar rich mixes. Similarly, our

overall uptake rates (max 32% in year 2), suggest there was minimal competition for trap nest cavities, indicating that the availability of nest sites was also not a primary constraint on the species using these trap nests.

A likely explanation for the lack of overall treatment effect is that these interventions were insufficient in the face of the strong negative impact of urbanisation. These results suggest that the mechanisms by which urbanisation impacts wild bees may be more complex than we currently appreciate. For example, studies rarely consider source-sink dynamics when assessing urbanisation impacts on bees. Despite the short range foraging behaviours of cavity nesting bees, the highly modified patch-level floral resources may be inadequate for the construction of broods and therefore they rely on the extended landscape surrounding their nest. Pollen from trees has been shown to be an important resource for cavity nesting bees (Maclvor et al., 2014; Splitt et al., 2021; Fernandes et al., 2022) and as urbanisation increases, the availability of trees decreases (Nock et al., 2013; Lüttge and Buckeridge, 2020) which could be driving the declines in abundance in highly urban areas. Analysis of the pollen collected by cavity nesting bees is an important future step to understanding the dependency on local and landscape resources. Furthermore, dispersal and patch-level modelling could help elucidate the roles of patch size and connectivity in urban solitary bee declines, and integrating these findings could then help guide management strategies on the locations, types of intervention and the size of insect-beneficial management strategies.

General Discussion

Overview:

In this study I have conducted a wide-ranging investigation into pollinating insects in U.K. cities. Using a multidisciplinary approach, I have assessed the influence local and landscape factors have on nocturnal and diurnal insect communities, their pollen-transport networks and the subsequent pollination services they provide. Chapter 2 evaluates divergent insect communities across multiple cities using rigorous sampling methods, identifying trends in biodiversity associated with landscape properties at multiple scales. It highlights the importance of semi-natural urban habitat and urban trees whilst demonstrating the overall negative effect the increasing area of impervious land cover has on bees, moths and hoverflies. Chapter 3 characterises the pollen-transport networks of nocturnal and diurnal insects using molecular approaches, and demonstrates that visitation patterns vary across bees and moths and throughout the season, and that insect-plant interactions change along an urban density gradient. In Chapter 4, a large-scale manipulation experiment was implemented and the associated benefits of supplementing floral resources were quantified, at an insect community level, a pollination-network level and finally at a crop pollination level. This experiment demonstrated that pollination services are influenced by local interventions and change with urban density. Finally, Chapter 5 demonstrates that the addition of floral resources, although a common conservation practice, did not mitigate the negative effects urbanisation had on cavity nesting bees and wasps.

Despite a surge in urban-pollinator research, the mechanisms shaping the pollinator communities, especially non-bee pollinators remain unclear and partly because the majority of research does not utilise the multitude of methods available to address these knowledge gaps. Throughout this thesis I have demonstrated that a novel combination of traditional insect collection, molecular approaches and applied experimental approaches can be used to gather the ecological data that are essential to understand the multifaceted responses, interactions and processes insects

communities are undergoing in complex urban landscapes (Figure 6.1). Overall, the work described in this thesis contributes to our understanding of the ecology and functioning of insect pollinators in cities and has important relevance to the wider body of research into overall pollinator responses to human-mediated environmental changes that are occurring across the globe.

Here, I synthesise some of the key finds across chapters, demonstrating the complexity of insect community responses to urban landscapes and the knock-on effects these have on ecosystem functioning. Specifically, I focus on the overarching and consistently reported negative effects of urbanisation on pollinating insects and how the work herein provides key insight into the mechanisms driving the changes observed along urbanisation gradients. I also highlight the novel insights into nocturnal pollination and then discuss the implications this thesis has for informing urban conservation management practices and set the findings with the context of current research, and suggest avenues for further research.

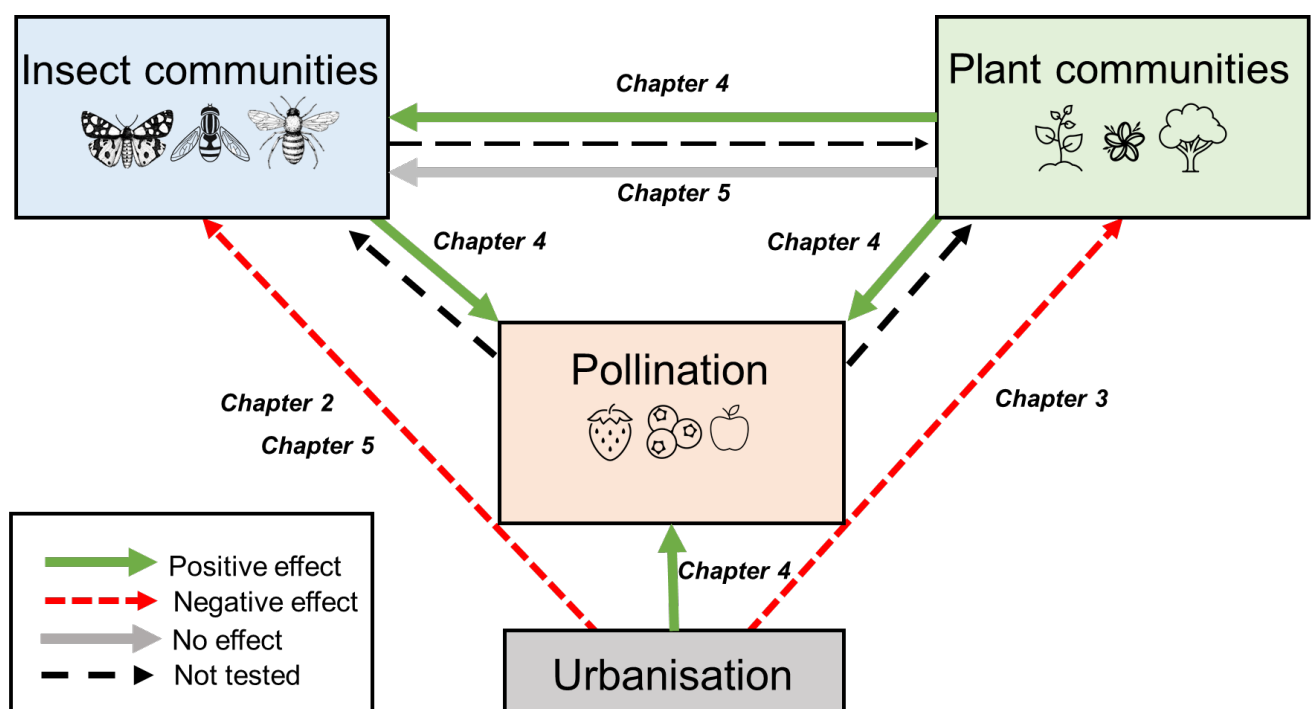


Figure 6. 1 The contribution this thesis has made to the understanding of complex pollinator-plant interactions and their pollination service delivery in response to urbanisation

6.1 Urbanisation:

As greyspace extent increases it reduces the availability of floral and nesting resources within greenspaces for insect pollinators (Wenzel et al., 2020). Therefore, identifying the habitats important to pollinating insects is a vital step in understanding urban pollination processes and informing conservation plans. The data I present in this thesis underscores the value of urban greenspaces for pollinators. I show that the reduction of semi-natural habitat and area of urban trees is driving changes in urban pollinator communities and their functioning, and this is a common theme throughout my thesis: In Chapter 2, across multiple cities we show that increasing urbanisation reduces the availability of semi-natural greenspaces and trees which drives the declines in insect communities (as also seen in Chapter 5). This is one of only a handful of studies to use a multi-taxon and multi-city approach in an effort to disentangle the underlying mechanisms of insect declines in urban areas and is the first to include both diurnal and nocturnal insects when assessing these processes. I highlight that moths and hoverflies may be more sensitive to urbanisation than bees which could have serious knock-on effects to the pollination services they provide.

Then in Chapter 3, this is further evidenced when the investigation of insect pollen loads revealed that increasing urbanisation reduces the pollen diversity found on insects. This suggests that reduced diversity or relative abundances of plant resources may be a primary factor contributing to observed declines of urban insect populations, including both bees and moths, observed in Chapter 2. In the discussion of Chapter 3 I suggest that consequences of reduced landscape-scale floral resources with increased urban intensity could be driving increased competition among pollinating insects for pollen or nectar resources. This is subsequently shown in Chapter 4 where I show the increased pollination of tomatoes in highly urban areas compared to less urban areas. This suggests that the associated reduction in floral resources at a landscape level increases the foraging and visitation patterns within allotments, which increases the pollination services provided. In other words, using the term coined from Theodorou et al. (2020), the 'honeypot' effect, which suggests that flower-rich sites located within an inhospitable landscape (highly urban) may attract insects from further afield than sites nested within a floristically rich (less urban) landscape.

There are however knowledge gaps that still exist. Chapter 1 highlights the complexity of the responses depending on the scale and insect taxa that is examined. We propose the mechanism of declines in moths and hoverflies is through the reduction of trees and semi-natural cover and the associated reduction of non-floral resources, but I suggest that future studies should endeavour to quantify these resources at a landscape level and examine if their availability influences these communities. Furthermore, the 'honeypot' effect shown in Chapter 4 suggests that pollination services increase with increased urbanisation. Although the increase of seed set could be seen as a benefit of increasing urbanisation, the robustness of these services may be fragile due to the increased anthropogenic pressures that also arise from urban intensity, such as pollution, habitat degradation and subsequent biodiversity losses that can decrease the stability of ecosystem functions such as pollination. This raises important questions about the resilience of pollination services in areas of higher urban intensity and should be tested empirically.

6.2 Nocturnal pollination and non-bee pollinators:

Throughout this thesis, an emphasis has been placed on the importance of including multiple taxa when assessing their responses to environmental change. However, there are still insect groups, largely overlooked in the literature that are not examined in this thesis. As we show that three of the 'big four' orders of pollinating insects are declining in response to increasing urbanisation, further study is needed for Coleoptera, non-syrphid flies and of course butterflies – all of which have been shown to be declining due to land-use change (Wagner, 2020a).

Macro-moth abundance has declined by ca. 33% in the last 50 years in the U.K (Potts et al., 2021) and there is a growing awareness of the significance of these declines. During the course of this study for example, from late 2018 to 2022, the recognition of moths as pollen vectors and pollinators in human modified landscapes has increased. In the last 2 years there have been a 6-fold increase in moth publications which demonstrate their complex contributions of pollen transport in agroecosystems (Cutler et al. 2012; MacGregor et al. 2019, Walton et al. 2020; Alison et al. 2022; Buxton et al., 2022), natural systems (Devoto et al., 2011) and their sensitivity to light pollution (MacGregor et al., 2017; Boyes et al., 2021) and wildfires (Banza et al., 2019).

However large knowledge gaps still remain and the inclusion of nocturnal moths in this research has provided novel insights into their previously unknown role as pollen vectors in urban areas. Chapter 3 for example, is the first attempt to simultaneously compare moths and bees by metabarcoding pollen carried on the bodies, Chapter 2 is the first to include moths in a study looking at them along an urbanisation gradient, and Chapter 4 is the first to test if moths benefit from the addition of floral supplementation, both at a community level and at plant interaction level. This thesis, in other words, has provided important knowledge into the roles moths play as pollinators and the drivers influencing their communities and their pollen-transport networks.

Although insect-plant visitation is a commonly used proxy for a pollination event, there is a need to accurately quantify whether moth-visitation can be confirmed as important for pollination (Buxton et al., 2022). A diverse range of pollen, from both wild plants and crops, such as oilseed rape, avocados, raspberries, and blueberries, has been found on the mouth parts and body of the moths (Hahn and Bruhl 2016; Cutler et al. 2012; MacGregor et al. 2019; Buxton et al. 2022; Walton et al. 2020). My work supports calls for future research to be conducted that rigorously quantifies the effectiveness of moth pollinators, especially in the context of global crop production.

6.3 Implications for greenspace management and knowledge exchange:

There is a growing movement to conserve pollinators and this is an exciting opportunity to exploit the new-found public and political concern over the conservation of insect pollinators. However, current methods of floral supplementation in modified systems are still limited by lack of empirical testing, especially in urban areas. The results of my work make a strong cases for moving from a current trend of 'save the bees' needs to move to 'save all insects'. Firstly, in Chapter 3 and 4 I show that moths, bees and hoverflies have distinct foraging preferences and they visit different plant communities. This result indicates that floral additions, as a way to conserve insect pollinators need to be designed to facilitate all adult pollinators, taking into account their foraging preferences (as shown in agroecosystems; Howlett et al. 2021). Secondly, the lack of community response to the addition of floral resources in Chapter 4 and 5 highlights there are important, broader and more complex processes to

consider when simply adding floral resources. Specifically, I want to highlight the importance of understanding the non-floral resource requirements needed for pollinators to complete their lifecycles and carefully design seed mixes to provide floral resources for all adult insects.

To date, conservation for pollinators neglects to consider the non-floral resource requirements needed to facilitate diverse pollinator life-histories. This limits the benefits of common conservation practices such as supplementing floral resource (as seen in Chapter 4), especially if other non-floral resources are not available (as seen in Chapter 5). Creating and sustaining flower-rich environments that a variety of adult pollinators can take advantage of requires additional efforts to support their various immature life stage needs. Additionally, it is probable that both tactics will be successful, because in contrast to adult bees that must return to their nests to provide pollen for their larvae (Greenleaf et al., 2007), adult flies, moths, butterflies and beetles can travel long distances to colonise new areas within a season. Non-bee pollinators also boast high reproductive rates, with multiple generations per year. This facilitates their adaptation to changes in resource availability (Rader et al., 2020). As a result, supplying resources for different non-bee pollinators at various life stages could lead to a sudden population growth in these species. This, in turn, would increase the rate of pollination and improve seed or fruit set (Garibaldi et al., 2013).

Next, choosing the seed mixes and plant communities that are going to be added is an important consideration to optimise the effect of the floral resources. Although I show distinct preferences of bees, hoverflies and moths in Chapter 3, the overlap of the plant communities' visited by both bees and moths has the potential to aid design of seed mixes composed of plants visited by multiple insect taxa. I show that several common garden plants frequently planted for diurnal insects (rhs.org.uk/plantsforpollinators) were also visited by moths, e.g., borage (*Borago officinalis*), nasturtium (*Tropaeolum spp.*) and comfrey (*Symphytum spp.*). Additionally, in Chapter 4, I found that all insect taxa preferentially visited plants with higher sugar be floral unit. Which supports the point raised by Tew et al. (2022), who

highlight and emphasise the importance of management for nectar supply when designing floral supplementation regimes.

Finally, the effective management of greenspace needs to assess more complex local and landscape components when deciding where to plant, at what scale and in what configuration. The scale of floral resources has been shown to be an important step to consider (Dauber et al. 2010; Blaaw and Isaacs, 2014), and although not explicitly answered in this thesis, I believe there needs to be more research explicitly testing the scales at which these additions need to be made in developing effective conservation interventions. Coupled with this, the floral limitation of the greenspace in question will likely be an important factor to consider when choosing locations for floral additions. For example, in Chapter 4 I suggest that allotments are perhaps not the best place to carry out a floral addition experiment as they are already saturated with floral resources (Griffiths-Lee et al., 2022), which is highlighted by no difference in the overall flower area at a site level in our floral additions compared to the control sites which implies that our patch area of 100 m² was not a big enough intervention to change site-level floral resources. Whereas, if adding flower patches greatly enhanced overall floral availability, we would see an effect as seen in amenity grassland additions (Hofmann and Renner, 2020) and road verges (reviewed by Phillips et al., 2020). Therefore, choosing floral limited habitat will most likely yield more obvious benefits for floral additions.

In summary, the most effective plans for urban insect conservation will strive to conserve important greenspaces for pollinating insects at a landscape level such as urban trees and semi-natural habitat whilst designing habitat modifications to provide floral and non-floral resources of a diverse range of insect pollinators, both bees and non-bees.

Conclusion:

The human mediated process of urbanisation is one of the most drastic changes to natural environments. There are many negative effects associated with the conversion of natural habitats to human-made impervious surfaces. However, there is increasing evidence that the insect pollinators within cities can be resilient to these changes and utilise the resources available in the matrix of urban greenspace. There is a growing momentum behind pollinator conservation and a large number of individual gardeners,

local authorities and private land owners interested in adopting pollinator friendly garden management. If we can harness the interest in insect conservation among the general public and policymakers, we can stop the decline in insect populations before it is too late. We must continue to disentangle the complex interactions occurring within cities if we are to provide evidenced based management advice that could see effective conservation actions.

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Supplementary Material

Supplementary Methods

Supplementary Methods S1: Landscape analysis:

S1.1 GIS landscape data extraction: All GIS data was extracted from OS MasterMap Topography Layer®, we used Landuse classifications to group our greyspace, greenspace and gardens: greyspaces were all 'Manmade' classified polygons which included buildings, roads and other impervious surfaces, semi-natural greenspaces used were classified as 'Natural' which include areas of many habitats such as grassland, shrubs, semi-natural greenspaces and all gardens data was classified as 'Multi' which are specifically garden polygons. For tree canopy data we used was from BlueSky® data which provides detailed GIS data on urban trees.

S1.2: Site selection: In each city, all the allotments were filtered from the data of OS Greenspaces layer in Mastermap (using ArcGIS version 10.3). Only sites that were $>5,000\text{m}^2$ and $<30,000\text{m}^2$ were chosen as these included the majority (80%) of all sites in each city. The lower filter was chosen as a site of $5,000\text{m}^2$ roughly has 20 plots (average plot size is 250m^2 (Edmondson unpublished)) and anything less than 20 plots would make it difficult to recruit plot holders and find space to set up the sampling regime. For site selection purposes, we used distance from the city centre as a proxy for urbanisation because it was an efficient way to ensure the sites were spread evenly across the cities.

The centre point of the city was defined by the middle-most point of the area with the highest urban fabric density area (using OS Mastermap built-land layer). The cities were divided into four bands, radiating from the city centre to the administrative boundary. In Sheffield the bands increased by a radius of 2km for every band, Leeds, 4km and Leicester 1km.

Chapter 2: Two sites in each band were randomly chosen (total sites per city = eight). If a site was chosen that was less than two km next to the previously chosen site then another site was chosen, this was to make an effort to ensure sites were as independent as possible, and also to ensure the sites were spread evenly throughout the city.

Chapter 3: The same sites in Leeds were used for chapter 3 as were used in chapter 2.

Chapter 4 & 5: Sites were filtered by size as described above. The sites were then chosen (where possible) in blocks of three within each band that radiated out of the city center (2 blocks per band).

Supplementary Methods S2: Insect collections:

S2.1 Site sampling order: In all chapters sites were sampled using a stratified random approach. Where the order of site visits was randomly chosen within their cities (Chapter 2,3) or blocks Chapter 4,5). We ensured that sites, cities or blocks were not visited at the same time during each sampling event (e.g. morning, early afternoon, late afternoon).

S2.2 Transects:

Chapter 2: Time transects (30 minutes) were used instead of fixed distance transects due to the fact that each allotment site was a different size (i.e. the distances varied). For timed transects all insects were collected following the main, central path in each allotment site. The insects (both flower visitors and insects flying by) were sampled at 1m from either side (and above) of the transect line. If the site path was walked faster than 30 minutes, the time was stopped and 10 minutes to allow insects to return to the path and the timer was started again and the transect was re-walked (until the time ran out). Plot-level timed transects were carried out as described above but for 10 minutes and the main path of the plot was walked. Transects were carried out on clear, calm days during the first two weeks of the three sampling periods (weather permitting). Most bumblebees (non-cryptic common species) and honeybees were identified in the field when they were too abundant to catch (i.e. >5 individuals).

Chapter 3: Timed transects were carried out as in chapter 2 but for 20 minutes along the central path of the allotment sites only.

Chapter 4 & 5: Timed transects were carried out as described in chapter 2 but only insects visiting flowers, and the flowers they were visiting were identified. These transects were carried out for 20 minutes along the central path of the allotment sites only.

Supplementary Methods S3: Insect identification

All insects were identified by EEE using material by Falk (2015) for bees, Stubbs and Falk (1983) for hoverflies, Sterling and Parsons (2018) for micromoths and Waring and Townsend (2017) for macromoths. Any difficult identifications were double checked by expert taxonomists Roger Morris (hoverflies), Steven Falk (bees and hoverflies) and Sean Foote (moths). In the field and for subsequent lab identifications and analysis *Bombus terrestris* *agg.* was used rather than *Bombus lucorum* *agg.* as it is not possible to confidently separate *B. lucorum* in the field from *B. terrestris*

Supplementary Material Chapter 2:

Supplementary Figures S2:

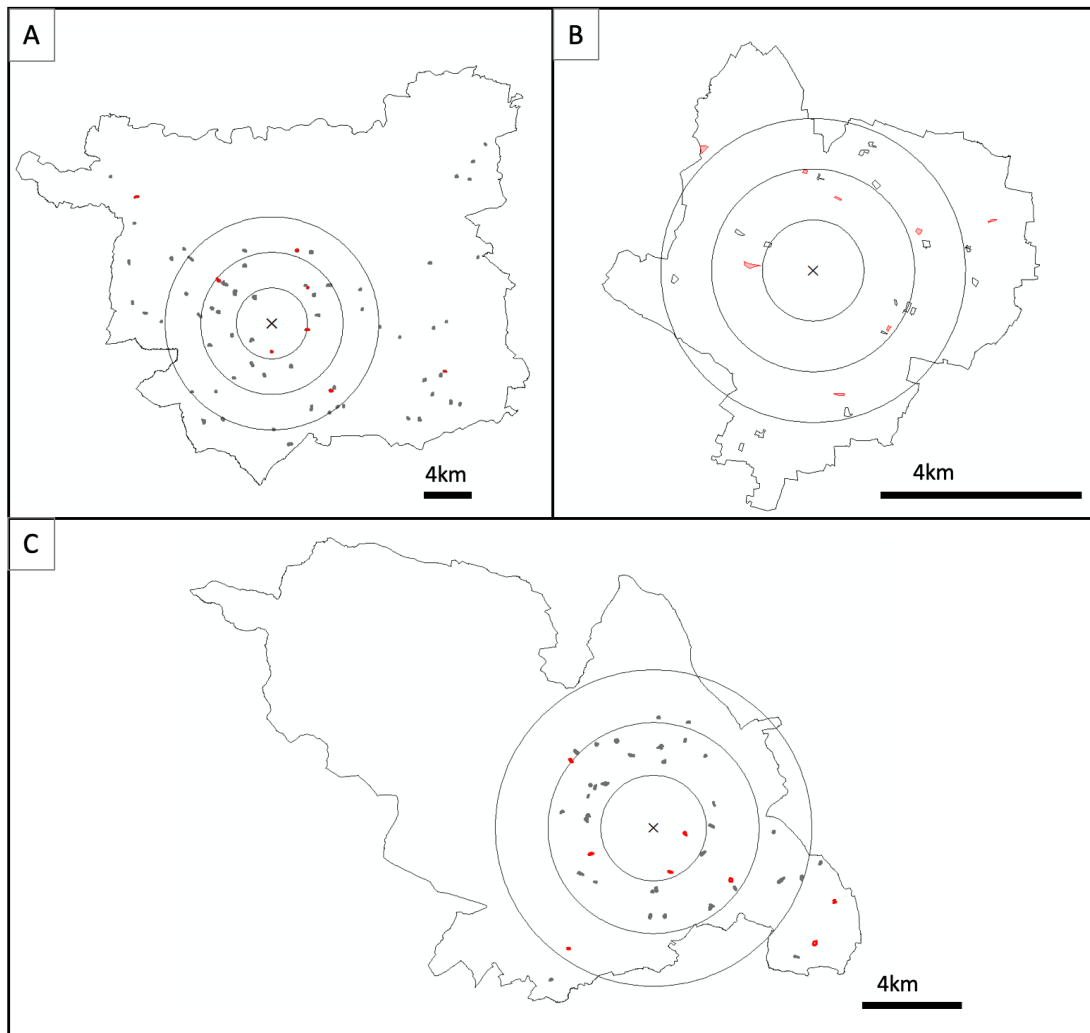


Figure S2. 1 A) Leeds, (B) Leicester and (C) Sheffield city administrative boundaries with the bands radiating out equally from the city centre. Grey dots are allotment sites present between 5,000m² and 30,000m³; red dots indicate the allotment sites chosen for this study.

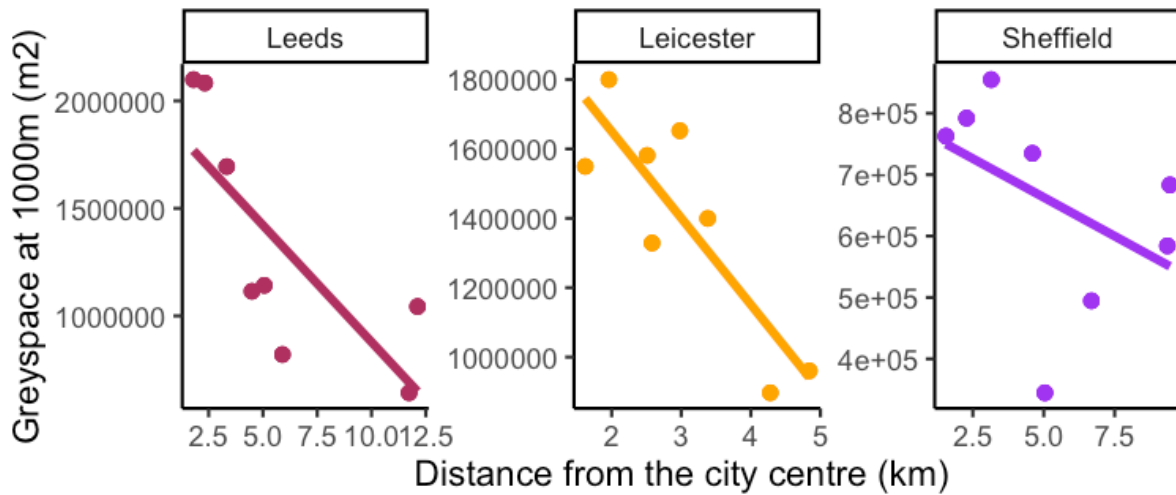


Figure S2. 2 Distance from the city centre explains 77% (R^2 value) of the variation in the areas of greyspace surrounding allotment sites. The area of greyspace decreases significantly as distance from the city centre increases. Lines show fitted model that had significant negative main effect of increasing distance from the city centre on the area of greyspace and a significant city interaction.

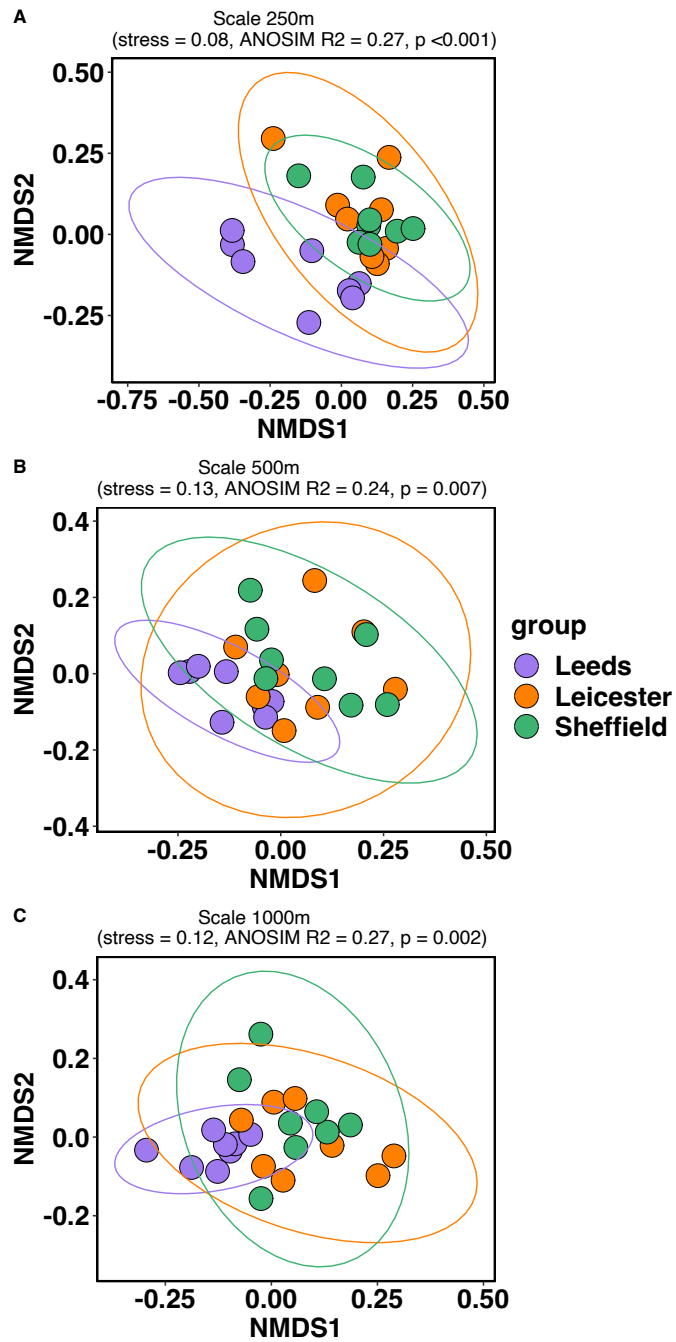


Figure S2. 3 NMDS plots showing the differences of landscape composition surrounding allotments in Leeds, Leicester and Sheffield at multiple scales a) 250m, b) 500m, c) 1000m surrounding the sites. Based on area of greyspace, semi-natural green, trees and gardens).

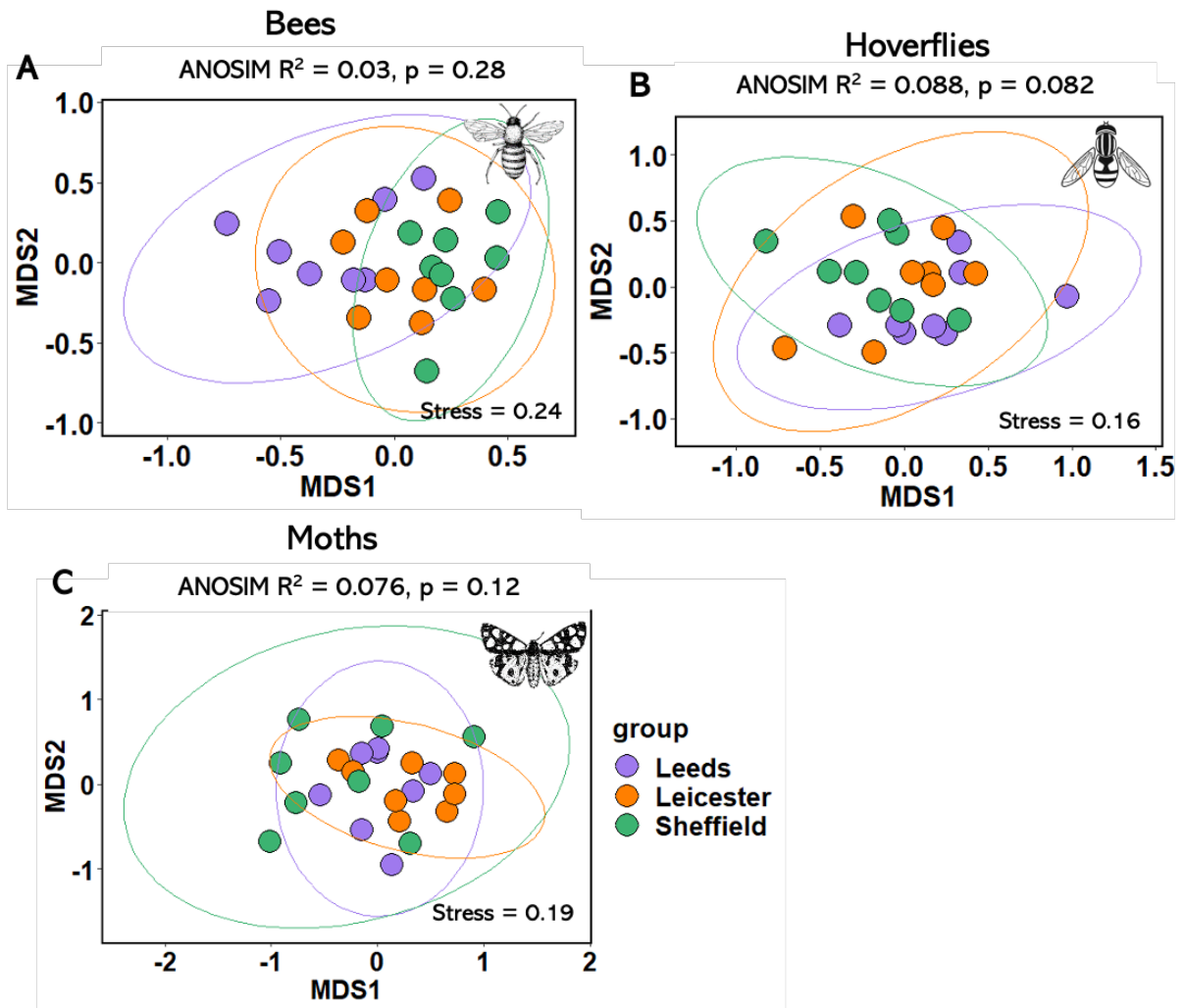


Figure S2. 4 NMDs plots showing the differences of A) bees B) hoverflies and C) moths in Leeds Leicester and Sheffield. P-values from analysis of similarity(ANOSIM).

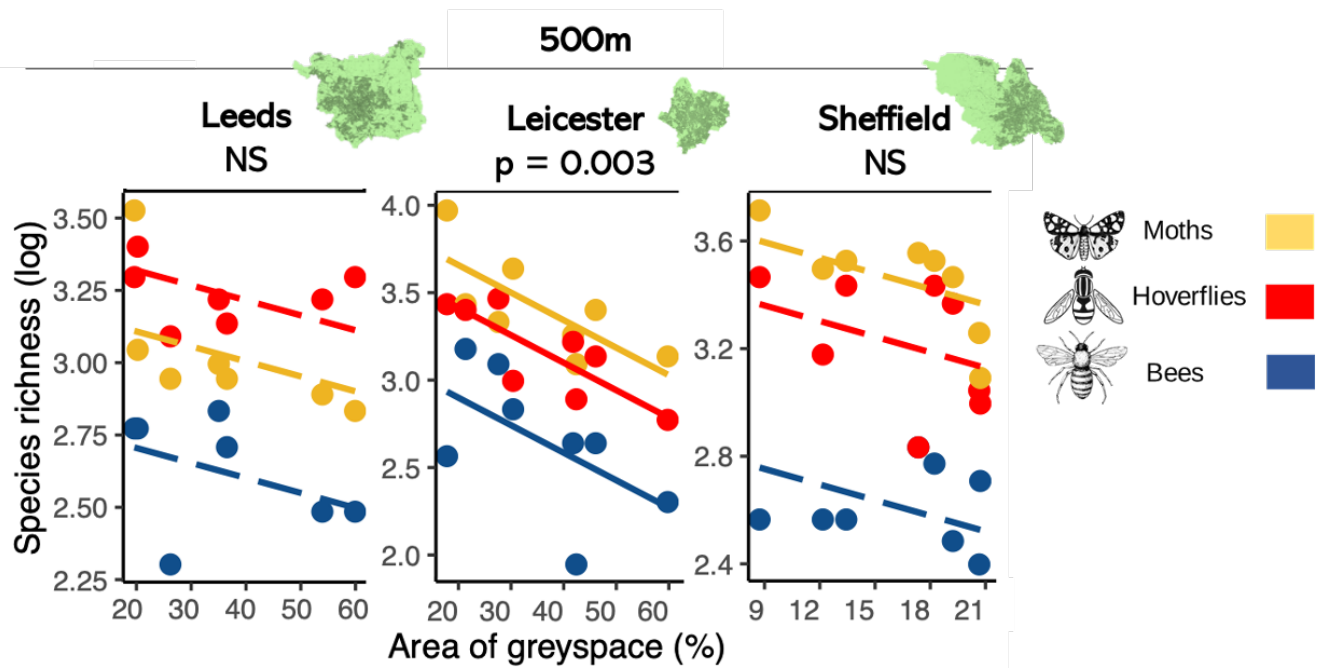



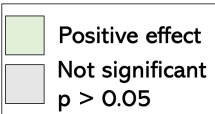


Figure S2. 5 Insect species richness of moths hoverflies and bees decreases as area of greyspace surrounding allotment sites (250m) increases (no insect taxa x urbanisation interaction). There was a significant city x are of greyspace interaction. Lines show model predictions, post hoc tests showed that Leeds and Sheffield were not significant (dashed lines), Leicester was significant (solid line).













Land use type	Total abundance		
	Buffer scale		
	250m	500m	1000m
Tree canopy 	NS $F_{(1,21)} = 1.18; p = 0.29$	NS $F_{(1,21)} = 1.94; p = 0.18$	NS $F_{(1,21)} = 1.67; p = 0.21$
Semi-natural habitat 	NS $F_{(1,21)} = 0.04; p = 0.85$	NS $F_{(1,21)} = 3.6; p = 0.07$	* $F_{(1,21)} = 7.33; p = 0.01$
Gardens 	NS $F_{(1,21)} = 0.03; p = 0.86$	NS $F_{(1,21)} = 0.05; p = 0.82$	NS $F_{(1,21)} = 0.4; p = 0.52$



Positive effect
Not significant $p > 0.05$

Figure S2. 6 The effect of increasing area of tree canopy, area of semi-natural greenspaces and area of gardens on the total species abundance of bees, moths and hoverflies across the three cities. Landscape composition was measured at three buffer scales surrounding sites of urban horticulture (250m, 500m, 1000m). Colours of cells indicate positive response (or non-significant) effects tested using Anova type II of generalized linear models.

Species richness (with abundance in model)

Land use type	Buffer scale		
	250m	500m	1000m
 Greyspace	 *  $F_{(1,18)} = 7.6; p = 0.012$	 *  $F_{(1,17)} = 7.8; p = 0.016$	 **  $F_{(1,17)} = 8.9; p = 0.009$
 Tree canopy	NS $F_{(1,16)} = 1.39; p = 0.25$	NS $F_{(1,14)} = 1.8; p = 0.19$	NS $F_{(1,14)} = 0.2; p = 0.66$
 Semi-natural habitat	NS $F_{(1,15)} = 3.11; p = 0.097$	 *  $F_{(1,16)} = 6.74; p = 0.019$	NS $F_{(1,16)} = 3.8; p = 0.067$
 Gardens	NS $F_{(1,17)} = 0.17; p = 0.71$	NS $F_{(1,17)} = 1.1; p = 0.31$	NS $F_{(1,17)} = 0.22; p = 0.22$










Insect taxa Moths Hoverflies Bees   	City Leeds Sheffield Leicester   	 Negative effect  Positive effect  Not significant $p > 0.05$
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Figure S2.7: Disentangling the landscape drivers of insect communities in urban agroecosystems across multiple scales. The effect of area of greyspace, area of tree canopy, area of semi-natural greenspaces and area of gardens on the species richness of bees, moths and hoverflies (with abundance included in the model) across the three cities. Landscape composition was measured at three scales surrounding sites of urban horticulture (250m, 500m, 1000m). Colours of cells indicate positive or negative response (or non-significant) effects tested using anova type II of generalized linear mixed effect models. Icons of insect taxa and city indicate if there were significant interactions between the environmental variable and insect taxa/ city (Table S2.6).

Supplementary Tables S2:

Table S2. 0 Site locations, distance from the city centre and size of 24 allotments in three UK cities used for the assessment of the effects urban landuse cover has on insect biodiversity in 2019. .

City	Site code	Size (m ²)	Distance from the city centre (km)	Grid reference (UK grid)
Leicester	LC1	27210	1.62	SK 57002 04890
Leicester	LC2	6428	1.96	SK 59328 06658
Leicester	LC3	6639	2.51	SK 60696 03229
Leicester	LC4	8951	2.58	SK 58461 07371
Leicester	LC5	16043	2.98	SK 61442 05816
Leicester	LC6	10203	3.38	SK 59378 01479
Leicester	LC7	7686	4.84	SK 63482 06070
Leicester	LC8	23201	4.28	SK 55825 08013
Leeds	LD1	11500	1.8	SE 29939 31394
Leeds	LD2	11775	2.32	SE 32329 32835
Leeds	LD3	5192	3.33	SE 32184 35723
Leeds	LD4	22640	4.49	SE 26452 36117
Leeds	LD5	14038	5.9	SE 33867 28846
Leeds	LD6	14857	5.06	SE 31633 38032
Leeds	LD7	11127	12.12	SE 21170 41561
Leeds	LD8	8289	11.73	SE 41340 30084
Sheffield	SH1	12402	1.55	SK 36796 86719
Sheffield	SH2	8720	2.28	SK 35939 84932
Sheffield	SH3	17239	4.6	SK 38950 84508
Sheffield	SH4	13499	3.15	SK 32267 85808
Sheffield	SH5	6071	6.68	SK 31184 81295

Sheffield	SH6	14877	5.04	SK 31301 90255
Sheffield	SH7	24689	9.45	SK 42916 81504
Sheffield	SH8	8059	9.36	SK 43886 83447

Table S2. 1 Species list and abundance of bees collected across three UK cities.

Insect	Family	Species	Leeds	Leicester	Sheffield
Bee	Andrenidae	<i>Andrena fulva</i>	0	0	2
Bee	Andrenidae	<i>Andrena barbilabris</i>	0	0	1
Bee	Andrenidae	<i>Andrena bicolor</i>	1	26	2
Bee	Andrenidae	<i>Andrena chrysoseles</i>	0	1	2
Bee	Andrenidae	<i>Andrena cineraria</i>	0	0	1
Bee	Andrenidae	<i>Andrena flavipes</i>	0	2	1
Bee	Andrenidae	<i>Andrena fulva</i>	1	0	0
Bee	Andrenidae	<i>Andrena haemorrhoea</i>	1	0	2
Bee	Andrenidae	<i>Andrena minutula</i>	5	14	2
Bee	Andrenidae	<i>Andrena nigroaenea</i>	1	3	4
Bee	Andrenidae	<i>Andrena nitida</i>	0	1	0
Bee	Andrenidae	<i>Andrena scotica</i>	1	0	11
Bee	Andrenidae	<i>Andrena scotica shylopized</i>	0	0	1
Bee	Apidae	<i>Anthophora furcata</i>	7	4	0
Bee	Apidae	<i>Anthophora plumipes</i>	1	1	2
Bee	Apidae	<i>Apis mellifera</i>	285	283	278
Bee	Apidae	<i>Bombus hortorum</i>	14	23	16
Bee	Apidae	<i>Bombus hypnorum</i>	89	42	24
Bee	Apidae	<i>Bombus lapidarius</i>	29	68	48
Bee	Apidae	<i>Bombus pascuorum</i>	242	221	189
Bee	Apidae	<i>Bombus pratorum</i>	94	39	39
Bee	Apidae	<i>Bombus terrestris agg.</i>	188	445	290
Bee	Apidae	<i>Bombus vestalis</i>	0	1	0
Bee	Apidae	<i>Nomada fabriciana</i>	0	4	0
Bee	Apidae	<i>Nomada flava</i>	5	0	5
Bee	Apidae	<i>Nomada flavoguttata</i>	0	2	1
Bee	Apidae	<i>Nomada rufipes</i>	0	0	1
Bee	Colletidae	<i>Colletes daviesanus</i>	1	6	3
Bee	Colletidae	<i>Hylaeus communis</i>	2	14	3
Bee	Colletidae	<i>Hylaeus confusus</i>	0	1	0
Bee	Colletidae	<i>Hylaeus hyalinatus</i>	3	0	1
Bee	Halictidae	<i>Halictus rubicundus</i>	3	0	0
Bee	Halictidae	<i>Halictus tumulorum</i>	2	10	0

Bee	Halictidae	<i>Lasioglossum cupromicans</i>	1	0	0
Bee	Halictidae	<i>Lasioglossum albipes</i>	6	3	0
Bee	Halictidae	<i>Lasioglossum calceatum</i>	2	1	6
Bee	Halictidae	<i>Lasioglossum calceatum</i>	0	2	0
Bee	Halictidae	<i>Lasioglossum cupromicans</i>	2	0	3
Bee	Halictidae	<i>Lasioglossum lativentre</i>	1	0	0
Bee	Halictidae	<i>Lasioglossum leucopus</i>	5	8	0
Bee	Halictidae	<i>Lasioglossum leucopus</i>	0	8	0
Bee	Halictidae	<i>Lasioglossum leucozonium</i>	0	7	0
Bee	Halictidae	<i>Lasioglossum morio</i>	0	1	1
Bee	Halictidae	<i>Lasioglossum smeathmanellum</i>	0	1	2
Bee	Halictidae	<i>Lasioglossum villosulum</i>	18	39	5
Bee	Halictidae	<i>Sphecodes crassus</i>	0	1	0
Bee	Halictidae	<i>Sphecodes ephippius</i>	1	0	0
Bee	Halictidae	<i>Sphecodes geoffrellus</i>	2	5	0
Bee	Halictidae	<i>Sphecodes monilicornis</i>	0	0	1
Bee	Halictidae	<i>Sphecodes puncticeps</i>	0	1	0
Bee	Megachilidae	<i>Chelostoma campanularum</i>	0	2	0
Bee	Megachilidae	<i>Megachile centuncularis</i>	7	9	2
Bee	Megachilidae	<i>Megachile ligniseca</i>	1	2	1
Bee	Megachilidae	<i>Megachile willughbiella</i>	0	0	2
Bee	Megachilidae	<i>Osmia bicornis</i>	8	2	15
Bee	Megachilidae	<i>Osmia Bicornis</i>	7	0	0
Bee	Megachilidae	<i>Osmia bicornis</i>	6	0	0
Bee	Megachilidae	<i>Osmia caeruleascens</i>	2	5	0
Bee	Megachilidae	<i>Osmia leaiana</i>	6	2	3
Bee	Megachilidae	<i>Osmia spinulosa</i>	0	1	0
Bee	Melittidae	<i>Melitta haemorrhoidalis</i>	1	0	0

Table S2. 2 Species list and abundance of hoverflies collected across three UK cities.

Insect	Family	Species	Leeds	Leicester	Sheffield
Syrphid	Asilidae	<i>Dioctria baumhaueri</i>	0	0	2
Syrphid	Asilidae	<i>Leptogaster cylindrica</i>	0	1	0
Syrphid	Bibionidae	<i>Bibionidae (Dilophus)</i>	1	0	0
Syrphid	Caliphoridae	<i>Caliphoridae</i>	1	0	0
Syrphid	Calypterate	<i>Calypterate</i>	10	5	5
Syrphid	Chloropidae	<i>Chloropidae</i>	0	0	7
Syrphid	Conopidae	<i>Conops quadrifasciatus</i>	2	0	1
Syrphid	Conopidae	<i>Physocephala rufipes</i>	0	0	1
Syrphid	Conopidae	<i>Sicus ferrugineus</i>	2	0	0
Syrphid	Dolichopodidae	<i>Dolichopodidae</i>	0	0	1
Syrphid	Drosophilidae	<i>Drosophila suzukii</i>	2	0	0

Syrphid	Empididae	<i>Empididae</i>	0	0	1
Syrphid	Pipunculidae	<i>Pipunculidae</i>	1	1	8
Syrphid	Rhagionidae	<i>Chrysopilus asiliformis</i>	2	1	0
Syrphid	Stratiomyidae	<i>Chloromyia formosa</i>	2	0	0
Syrphid	Stratiomyidae	<i>Chorisops nagatomii</i>	0	0	1
Syrphid	Stratiomyidae	<i>Chorisops tibialis</i>	9	5	13
Syrphid	Stratiomyidae	<i>Microchrysa polita</i>	17	2	19
Syrphid	Stratiomyidae	<i>Sargus bipunctatus</i>	1	0	4
Syrphid	Syrphidae	<i>Baccha elongata</i>	1	3	1
Syrphid	Syrphidae	<i>Cephalops sp. Pipunculidae</i>	0	0	1
Syrphid	Syrphidae	<i>Cheilosia bergenstammi</i>	0	1	0
Syrphid	Syrphidae	<i>Cheilosia caerulescens</i>	0	1	0
Syrphid	Syrphidae	<i>Cheilosia proxima</i>	1	0	0
Syrphid	Syrphidae	<i>Chrysotoxum bicinctum</i>	23	9	7
Syrphid	Syrphidae	<i>Chrysotoxum festivum</i>	14	4	16
Syrphid	Syrphidae	<i>Chrysotoxum verralli</i>	0	16	3
Syrphid	Syrphidae	<i>Dasysyrphus albostrigatus</i>	17	1	9
Syrphid	Syrphidae	<i>Dasysyrphus tricinctus</i>	1	0	1
Syrphid	Syrphidae	<i>Dasysyrphus venustus</i>	1	0	0
Syrphid	Syrphidae	<i>Epistrophe eligans</i>	3	2	2
Syrphid	Syrphidae	<i>Epistrophe grossulariae</i>	2	0	0
Syrphid	Syrphidae	<i>Epistrophe nitidicollis</i>	0	0	1
Syrphid	Syrphidae	<i>Episyrphus balteatus</i>	77	133	113
Syrphid	Syrphidae	<i>Eristalis arbustorum</i>	1	1	0
Syrphid	Syrphidae	<i>Eristalis arbustorum</i>	1	20	0
Syrphid	Syrphidae	<i>Eristalis intricaria</i>	1	0	0
Syrphid	Syrphidae	<i>Eristalis nemorum</i>	0	1	3
Syrphid	Syrphidae	<i>Eristalis pertinax</i>	3	0	6
Syrphid	Syrphidae	<i>Eristalis tenax</i>	34	33	15
Syrphid	Syrphidae	<i>Eumerus funeralis</i>	11	15	14
Syrphid	Syrphidae	<i>Eumerus strigatus</i>	2	1	0
Syrphid	Syrphidae	<i>Eumerus strigatus s.s.</i>	0	2	0
Syrphid	Syrphidae	<i>Eupeodes bucculatus</i>	7	0	2
Syrphid	Syrphidae	<i>Eupeodes corollae</i>	100	125	53
Syrphid	Syrphidae	<i>Eupeodes latifasciatus</i>	5	1	3
Syrphid	Syrphidae	<i>Eupeodes luniger</i>	224	236	310
Syrphid	Syrphidae	<i>Eupeodes nielseni</i>	1	0	0
Syrphid	Syrphidae	<i>Eupeodes sp.</i>	0	0	1
Syrphid	Syrphidae	<i>Eupeodes sp. (?bucculatus)</i>	1	0	0
Syrphid	Syrphidae	<i>Ferdinandia ruficornis</i>	1	0	0
Syrphid	Syrphidae	<i>Helophilus hybridus</i>	0	1	0
Syrphid	Syrphidae	<i>Helophilus pendulus</i>	12	4	9
Syrphid	Syrphidae	<i>Leucozona lucorum</i>	0	0	1

Syrphid	Syrphidae	<i>Melangyna cincta</i>	2	0	1
Syrphid	Syrphidae	<i>Melangyna triangulifera</i>	3	0	1
Syrphid	Syrphidae	<i>Melanostoma mellinum</i>	144	102	65
Syrphid	Syrphidae	<i>Melanostoma scalare</i>	11	13	34
Syrphid	Syrphidae	<i>Melanostoma sp.</i>	2	0	2
Syrphid	Syrphidae	<i>Meligramma trianguliferum</i>	0	2	0
Syrphid	Syrphidae	<i>Meliscaeva auricollis</i>	5	3	9
Syrphid	Syrphidae	<i>Merodon equestris</i>	12	9	6
Syrphid	Syrphidae	<i>Musca sp.</i>	0	1	0
Syrphid	Syrphidae	<i>Myathropa florea</i>	3	5	5
Syrphid	Syrphidae	<i>Neoascia podagrica</i>	5	1	2
Syrphid	Syrphidae	<i>Paragus haemorrhous</i>	6	0	2
Syrphid	Syrphidae	<i>Pipizella viduata</i>	1	3	2
Syrphid	Syrphidae	<i>Pipizella virens</i>	0	3	1
Syrphid	Syrphidae	<i>Platycheirus albimanus</i>	45	22	25
Syrphid	Syrphidae	<i>Platycheirus ambiguus</i>	1	0	0
Syrphid	Syrphidae	<i>Platycheirus angustatus</i>	31	48	22
Syrphid	Syrphidae	<i>Platycheirus clypeatus</i>	0	0	3
Syrphid	Syrphidae	<i>Platycheirus clypeatus s.s.</i>	33	1	0
Syrphid	Syrphidae	<i>Platycheirus granditarsus</i>	1	0	0
Syrphid	Syrphidae	<i>Platycheirus manicatus</i>	1	0	0
Syrphid	Syrphidae	<i>Platycheirus peltatus s.s.</i>	7	7	1
Syrphid	Syrphidae	<i>Platycheirus rosarum</i>	0	0	1
Syrphid	Syrphidae	<i>Platycheirus scutatus</i>	1	6	4
Syrphid	Syrphidae	<i>Platycheirus scutatus agg.</i>	0	0	1
Syrphid	Syrphidae	<i>Platycheirus scutatus s.s.</i>	2	14	3
Syrphid	Syrphidae	<i>Platycheirus scutatus sl.</i>	35	43	17
Syrphid	Syrphidae	<i>Sargus irridatus</i>	2	0	2
Syrphid	Syrphidae	<i>Scaeva pyrastris</i>	3	3	0
Syrphid	Syrphidae	<i>Scaeva selenitica</i>	1	1	0
Syrphid	Syrphidae	<i>Sciapus sp.</i>	0	0	3
Syrphid	Syrphidae	<i>Sericomyia silentis</i>	1	0	0
Syrphid	Syrphidae	<i>Sphaerophoria rueppellii</i>	4	12	0
Syrphid	Syrphidae	<i>Sphaerophoria scripta</i>	425	483	106
Syrphid	Syrphidae	<i>Sphaerophoria sp.</i>	0	1	0
Syrphid	Syrphidae	<i>Syritta pipiens</i>	13	25	4
Syrphid	Syrphidae	<i>Syrphus ribesii</i>	370	83	273
Syrphid	Syrphidae	<i>Syrphus torvus</i>	3	2	3
Syrphid	Syrphidae	<i>Syrphus vitripennis</i>	12	0	10
Syrphid	Syrphidae	<i>Volucella bombylans</i>	3	0	1
Syrphid	Syrphidae	<i>Volucella inanis</i>	5	1	3
Syrphid	Syrphidae	<i>Volucella pellucens</i>	2	2	3
Syrphid	Syrphidae	<i>Volucella zonaria</i>	0	1	0

Syrphid	Syrphidae	<i>Xanthogramma pedisequum</i>	0	1	0
		<i>Xanthogramma</i>			
Syrphid	Syrphidae	<i>pedisequum</i>	0	2	0
		<i>Xanthogramma</i>			
Syrphid	Syrphidae	<i>pedisequum</i> s.s.	0	6	0
Syrphid	Syrphidae	<i>Xylota segnis</i>	1	2	3
Syrphid	Tabanidae	<i>Haematopota pluvialis</i>	0	2	0
Syrphid	Tachinidae	<i>Eriothrix rufomaculata</i>	3	0	0
Syrphid	Tachinidae	<i>Phania funesta</i>	0	0	1
Syrphid	Tachinidae	<i>Tachina fera</i>	4	0	1
Syrphid	Tachinidae	<i>Tachinidae</i>	1	0	1

Table S2. 3 Species list and abundance of moths collected across three UK cities.

Insect	Family	Species	Leeds	Leicester	Sheffield
Moth	Autostichidae	<i>Oegoconia</i> spp.	1	0	0
Moth	Blastobasidae	<i>Blastobasis adustella</i>	4	1	1
Moth	Crambidae	<i>Agriphila inquinatella</i>	0	1	6
Moth	Crambidae	<i>Agriphila latistria</i>	0	0	4
Moth	Crambidae	<i>Agriphila selasella</i>	0	0	1
Moth	Crambidae	<i>Agriphila straminella</i>	3	1	12
Moth	Crambidae	<i>Agriphila tristella</i>	0	7	3
Moth	Crambidae	<i>Anania coronata</i>	4	1	1
Moth	Crambidae	<i>Anania hortulata</i>	0	11	10
Moth	Crambidae	<i>Catoptria pinella</i>	1	0	0
Moth	Crambidae	<i>Chrysoteuchia culmella</i>	22	72	5
Moth	Crambidae	<i>Crambus ericella</i>	1	4	4
Moth	Crambidae	<i>Cydalima perspectalis</i>	1	0	0
Moth	Crambidae	<i>Eudonia delunella</i>	3	0	0
Moth	Crambidae	<i>Eudonia lacustrata</i>	14	14	5
Moth	Crambidae	<i>Eudonia</i> spp.	0	1	2
Moth	Crambidae	<i>Pleuroptya ruralis</i>	0	1	23
Moth	Crambidae	<i>Pyrausta aurata</i>	0	0	2
Moth	Crambidae	<i>Udea lutealis</i>	0	6	0
Moth	Crambidae	<i>Udea uliginosalis</i>	0	1	0
Moth	Erebidae	<i>Calliteara pudibunda</i>	1	0	1
Moth	Erebidae	<i>Eilema complana</i>	1	1	2
Moth	Erebidae	<i>Eilema depressa</i>	0	1	0
Moth	Erebidae	<i>Eilema griseola</i>	0	2	4
Moth	Erebidae	<i>Hypena proboscidalis</i>	1	0	2
Moth	Erebidae	<i>Manulea lurideola</i>	16	3	6
Moth	Erebidae	<i>Phragmatobia fuliginosa</i>	0	29	0
Moth	Erebidae	<i>Rivula sericealis</i>	0	1	1
Moth	Erebidae	<i>Scoliopteryx libatrix</i>	0	0	1

Moth	Erebidae	<i>Spilosoma lubricipeda</i>	0	0	3
Moth	Erebidae	<i>Tyria jacobaeae</i>	0	5	1
Moth	Gelechiidae	<i>Bryotropha spp.</i>	0	2	0
Moth	Gelechiidae	<i>Helcystogramma rufescens</i>	0	1	0
Moth	Gelechiidae	<i>Helcystogramma rufescens</i>	0	0	1
Moth	Geometridae	<i>Abraxas grossulariata</i>	0	1	0
Moth	Geometridae	<i>Aplocera plagiata plagiata</i>	0	0	1
Moth	Geometridae	<i>Biston betularia</i>	1	2	0
Moth	Geometridae	<i>Campaea margaritaria</i>	1	0	0
Moth	Geometridae	<i>Chiasmia clathrata clathrata</i>	0	0	1
Moth	Geometridae	<i>Colostygia pectinataria</i>	0	0	1
Moth	Geometridae	<i>Crocallis elinguaris</i>	3	4	3
Moth	Geometridae	<i>Dysstroma truncata truncata</i>	2	2	4
Moth	Geometridae	<i>Ecliptopera silaceata</i>	0	0	1
Moth	Geometridae	<i>Ennomos fuscantaria</i>	0	0	4
Moth	Geometridae	<i>Epirrhoe alternata</i>	0	1	1
Moth	Geometridae	<i>Eulithis prunata</i>	1	0	0
Moth	Geometridae	<i>Eupithecia centaureata</i>	1	0	0
Moth	Geometridae	<i>Eupithecia linariata</i>	0	0	1
Moth	Geometridae	<i>Eupithecia spp.</i>	2	10	22
Moth	Geometridae	<i>Geometrid spp.</i>	0	2	0
Moth	Geometridae	<i>Hemithea aestivaria</i>	1	0	0
Moth	Geometridae	<i>Hydriomena furcata</i>	0	0	2
Moth	Geometridae	<i>Idaea aversata</i>	11	34	23
Moth	Geometridae	<i>Idaea biselata</i>	1	1	0
Moth	Geometridae	<i>Idaea dimidiata</i>	0	8	0
Moth	Geometridae	<i>Lomaspilis marginata</i>	0	0	2
Moth	Geometridae	<i>Odontopera bidentata</i>	2	0	0
Moth	Geometridae	<i>Opisthograptis luteolat</i>	0	1	1
Moth	Geometridae	<i>Ourapteryx sambucaria</i>	5	0	3
Moth	Geometridae	<i>Peribatodes rhomboidaria</i>	0	1	11
Moth	Geometridae	<i>Selenia dentaria</i>	1	0	0
Moth	Geometridae	<i>Xanthorhoe fluctuata</i>	0	1	4
Moth	Geometridae	<i>Xanthorhoe montanata</i>	0	0	3
Moth	Hepialidae	<i>Korscheltellus lupulina</i>	1	15	8
Moth	Hepialidae	<i>Triodia sylvina</i>	0	1	7
Moth	NA	<i>Unknown</i>	11	14	25
Moth	NA	<i>Unkown</i>	1	33	5
Moth	Noctuidae	<i>Abrostola tripartita</i>	0	0	1
Moth	Noctuidae	<i>Agrotis exclamationis</i>	41	94	27
Moth	Noctuidae	<i>Agrotis puta puta</i>	7	9	18
Moth	Noctuidae	<i>Agrotis putaputa</i>	0	2	1
Moth	Noctuidae	<i>Agrotis segetum</i>	0	13	0

Moth	Noctuidae	<i>Amphipyra berbera</i>	0	0	2
Moth	Noctuidae	<i>Amphipyra pyramidea</i>	5	2	21
Moth	Noctuidae	<i>Amphipyra tragopoginis</i>	0	0	5
Moth	Noctuidae	<i>Anarta trifolii</i>	0	0	1
Moth	Noctuidae	<i>Apamea lithoxylaea</i>	1	0	6
Moth	Noctuidae	<i>Apamea monoglypha</i>	68	84	52
Moth	Noctuidae	<i>Apamea remissa</i>	0	2	3
Moth	Noctuidae	<i>Apamea sordens</i>	0	2	0
Moth	Noctuidae	<i>Aporophyla nigra</i>	2	1	0
Moth	Noctuidae	<i>Autographa gamma</i>	0	4	3
Moth	Noctuidae	<i>Axylia putris</i>	3	1	0
Moth	Noctuidae	<i>Bryophila domestica</i>	0	8	10
Moth	Noctuidae	<i>Caradrina clavipalpis</i>	0	0	1
Moth	Noctuidae	<i>Caradrina morpheus</i>	3	6	0
Moth	Noctuidae	<i>Cerapteryx graminis</i>	0	0	1
Moth	Noctuidae	<i>Cosmia trapezina</i>	4	6	2
Moth	Noctuidae	<i>Craniophora ligustri</i>	0	1	0
Moth	Noctuidae	<i>Diachrysia chrysitis</i>	1	0	2
Moth	Noctuidae	<i>Diarsia mendica mendica</i>	1	1	6
Moth	Noctuidae	<i>Diarsia rubi</i>	0	6	0
Moth	Noctuidae	<i>Hoplodrina alsines/blanda</i>	44	36	8
Moth	Noctuidae	<i>Hoplodrina ambigua</i>	0	2	0
Moth	Noctuidae	<i>Hydraecia micacea</i>	0	0	4
Moth	Noctuidae	<i>Lacanobia oleracea</i>	5	2	1
Moth	Noctuidae	<i>Lenisa geminipuncta</i>	0	0	1
Moth	Noctuidae	<i>Litoligia literosa</i>	0	0	3
Moth	Noctuidae	<i>Luperina testacea</i>	0	2	2
Moth	Noctuidae	<i>Mesapamea agg.</i>	19	36	79
Moth	Noctuidae	<i>Mormo maura</i>	1	2	1
Moth	Noctuidae	<i>Mythimna albipuncta</i>	0	1	0
Moth	Noctuidae	<i>Mythimna conigera</i>	6	0	1
Moth	Noctuidae	<i>Mythimna ferrago</i>	3	6	0
Moth	Noctuidae	<i>Mythimna impura</i>	36	25	5
Moth	Noctuidae	<i>Mythimna pallens</i>	0	10	6
Moth	Noctuidae	<i>Naenia typica</i>	2	1	0
Moth	Noctuidae	<i>Noctua comes</i>	12	24	18
Moth	Noctuidae	<i>Noctua fimbriata</i>	0	8	24
Moth	Noctuidae	<i>Noctua interjecta</i>	0	0	4
Moth	Noctuidae	<i>Noctua janthe</i>	1	2	47
Moth	Noctuidae	<i>Noctua janthina</i>	0	0	1
Moth	Noctuidae	<i>Noctua orbona</i>	0	4	0
Moth	Noctuidae	<i>Noctua pronuba</i>	80	202	652
Moth	Noctuidae	<i>Noctuid spp.</i>	0	3	10

Moth	Noctuidae	<i>Ochropleura plecta</i>	0	1	0
Moth	Noctuidae	<i>Oegoconia spp.</i>	5	22	54
Moth	Noctuidae	<i>Omphaloscelis lunosa</i>	0	1	0
Moth	Noctuidae	<i>Phlogophora meticulosa</i>	0	0	1
Moth	Noctuidae	<i>Thalpophila matura</i>	0	1	0
Moth	Noctuidae	<i>Xestia c-nigrum</i>	8	25	1
Moth	Noctuidae	<i>Xestia ditrapezium</i>	1	0	0
Moth	Noctuidae	<i>Xestia sexstrigata</i>	0	0	5
Moth	Noctuidae	<i>Xestia triangulum</i>	1	10	0
Moth	Noctuidae	<i>Xestia xanthographa</i>	4	3	1
Moth	Notodontidae	<i>Phalera bucephala</i>	0	1	0
Moth	Notodontidae	<i>Pheosia tremula</i>	1	0	0
Moth	Oecophoridae	<i>Crasa unitella</i>	1	8	1
Moth	Oecophoridae	<i>Crassa unitella</i>	0	5	0
Moth	Oecophoridae	<i>Endrosis sarcitrella</i>	0	1	1
		<i>Hofmannophila</i>			
Moth	Oecophoridae	<i>pseudospretella</i>	3	0	0
Moth	Oecophoridae	<i>Tachystola acroxantha</i>	0	0	2
Moth	Plutellidae	<i>Plutella xylostella</i>	0	1	7
Moth	Pterophoridae	<i>Emmelina monodactyla</i>	1	0	1
Moth	Pyalidae	<i>Aphomia sociella</i>	1	0	0
Moth	Pyalidae	<i>Endotricha flammealis</i>	2	0	0
Moth	Pyalidae	<i>Euzophera pinguis</i>	0	0	1
Moth	Pyalidae	<i>Homoeosoma sinuella</i>	0	1	0
Moth	Pyalidae	<i>Phycita rolorella</i>	0	1	0
Moth	Pyalidae	<i>Phycitodes saxicola</i>	0	0	1
Moth	Sphingidae	<i>Laothoe populi</i>	1	2	0
Moth	Tortricidae	<i>Agapeta hamana</i>	0	2	1
Moth	Tortricidae	<i>Celypha striana</i>	1	1	0
Moth	Tortricidae	<i>Clepsis consimilana</i>	0	1	0
Moth	Tortricidae	<i>Cydia pomonella</i>	5	1	3
Moth	Tortricidae	<i>Ephiphyas postvittana</i>	0	3	6
Moth	Tortricidae	<i>Hedya nubiferana</i>	0	2	6
Moth	Tortricidae	<i>Lobesia abscisana</i>	0	1	0
		<i>Notocelia rosaecolana/</i>			
Moth	Tortricidae	<i>trimaculana</i>	0	0	1
Moth	Tortricidae	<i>Pandemis cerasana</i>	2	0	0
Moth	Tortricidae	<i>Pseudagyrotota conwagana</i>	0	1	4
Moth	Tortricidae	<i>Rhopobota stagnana</i>	0	0	2
Moth	Tortricidae	<i>Syndemis musculana</i>	0	0	1
Moth	Tortricidae	<i>Thera agg.</i>	0	0	1
Moth	Tortricidae	<i>Tortricid</i>	0	1	2
Moth	Yponomeutidae	<i>Yponomeuta sp.</i>	2	2	1
Moth	Yponomeutidae	<i>Yponomeuta spp.</i>	0	2	3

Table S2. 3 Generalised linear model outputs for total species richness and abundance along urbanisation gradients.

Response variable	Buffer scale	Explanatory variables	Sum sq	Df	F	p value
Abundance						
	250m	Greyspace area	0.31	1.00	2.19	0.16
		Size	0.14	1.00	1.03	0.32
		CultivationScore	0.03	1.00	0.20	0.66
		Residuals	2.65	19.00		
	500m	Greyspace area	0.33	1.00	2.39	0.14
		Size	0.19	1.00	1.35	0.26
		CultivationScore	0.06	1.00	0.40	0.53
		Residuals	2.62	19.00		
	1000m	Greyspace area	0.26	1.00	1.85	0.19
		Size	0.23	1.00	1.60	0.22
		CultivationScore	0.03	1.00	0.21	0.65
		Residuals	2.69	19.00		
Species richness						
	250m	Greyspace area	0.24	1.00	8.23	0.01
		Size	0.02	1.00	0.76	0.40
		CultivationScore	0.00	1.00	0.00	0.97
	500m	Greyspace area	0.17	1.00	5.10	0.04
		Size	0.04	1.00	1.22	0.28
		CultivationScore	0.00	1.00	0.08	0.78
		Residuals	0.63	19.00		
	1000m	Greyspace area	0.19	1.00	6.03	0.02
		Size	0.05	1.00	1.65	0.22
		CultivationScore	0.00	1.00	0.01	0.93

Table S2. 4 Model outputs from generalised linear mixed effect model testing the influence of urbanisation (250m) on the abundance of bees, moths and hoverflies. Showing post-hoc test of significant insect x urbanisation interaction.

Type II Analysis of Variance Table with Satterthwaite's method						
Terms	Sum Sq	Mean Sq	NumDF	DenDF	Fvalue	p value
City	0.61	0.30	2	20	2.21	0.14
Insect	2.61	1.30	2	40	9.53	0.00
log(Urbanisation(250m))	0.72	0.72	1	20	5.24	0.03
City:Insect	1.96	0.49	4	40	3.58	0.01
Insect:log(Urbanisation(250m)) (Post-hoc test)	1.13054	0.56527	2	40	4.13	0.02
Insect = Bee:						
model term					F.ratio	p value
City			2	52	0.20	0.82
log(Urbanisation(250m))			1	52	0.07	0.79
Insect = Moth:						
model term					F.ratio	p value
City			2	52	5.26	0.01
log(Urbanisation(250m))			1	52	9.55	0.00
Insect = Syrphid:						
model term					F.ratio	p value
City			2	52	3.16	0.04
log(Urbanisation(250m))			1	52	4.51	0.04

Table S2.6: Type II Analysis of variance tables with Satterthwaite's method testing linear mixed effect models examining the influence of landcover (urban, tree canopy, semi-natural and gardens) at the three spatial surrounding allotment sites (250m, 500m, 1000m) in three cities (Sheffield, Leicester and Leeds) has on insect species richness with insect abundance included in the analysis.

Type II Analysis of Variance Tables with Satterthwaite's method

Urbanisation (250m)							
	Sum sq	Mean sq	NumDF	DenDF	F value	p value	
log(Abundance)	0.73	0.73	1.00	47.83	23.05	<0.001	
City	0.12	0.06	2.00	17.56	1.89	0.18	
Insect	0.02	0.01	2.00	39.31	0.31	0.74	
log(Urbanisation_250m)	0.24	0.24	1.00	18.55	7.61	0.01	
scale(Size)	0.00	0.00	1.00	16.86	0.03	0.87	
City:Insect	0.14	0.03	4.00	37.95	1.10	0.37	
Insect:log(Urbanisation_250m)	0.02	0.01	2.00	38.28	0.32	0.73	
Urbanisation (500m)							
	Sum sq	Mean sq	NumDF	DenDF	F value	p value	
log(Abundance)	0.53	0.53	1.00	49.06	17.24	<0.001	
City	0.12	0.06	2.00	16.67	2.03	0.16	

Insect	0.01	0.01	2.00	38.72	0.22	0.80
log(Urbanisation_500m)	0.22	0.22	1.00	17.03	7.08	0.02
scale(Size)	0.00	0.00	1.00	15.73	0.00	0.96
City:log(Urbanisation_500m)	0.15	0.07	2.00	16.72	2.39	0.12
City:Insect	0.19	0.05	4.00	38.91	1.53	0.21
Insect:log(Urbanisation_500m)	0.04	0.02	2.00	38.40	0.71	0.50

Urbanisation (1000m)

	Sum sq	Mean sq	NumDF	DenDF	F value	p value
log(Abundance)	0.88	0.88	1.00	37.51	28.48	<0.001
City	0.15	0.08	2.00	14.71	2.44	0.12
Insect	0.02	0.01	2.00	39.09	0.30	0.74
log(Urbanisation_1000m)	0.27	0.27	1.00	15.42	8.92	0.01
scale(Size)	0.01	0.01	1.00	15.10	0.21	0.65
City:log(Urbanisation_1000m)	0.15	0.08	2.00	14.71	2.44	0.12
City:Insect	0.17	0.04	4.00	38.66	1.41	0.25
Insect:log(Urbanisation_1000m)	0.07	0.03	2.00	39.15	1.13	0.33

Tree canopy (250m)

	Sum sq	Mean sq	NumDF	DenDF	F value	p value
log(Abundance)	0.89	0.89	1.00	51.14	28.20	<0.001
City	0.01	0.00	2.00	16.53	0.10	0.91
Insect	0.03	0.02	2.00	37.35	0.52	0.60
log(Tree Canopy_250m)	0.04	0.04	1.00	16.49	1.39	0.25
City:Insect	0.12	0.03	4.00	36.08	0.94	0.45
Insect:log(Tree Canopy_250m)	0.05	0.03	2.00	35.59	0.82	0.45

Tree canopy (500m)

	Sum sq	Mean sq	NumDF	DenDF	F value	p value
log(Abundance)	1.19	1.19	1.00	53.32	37.33	<0.001
City	0.07	0.03	2.00	14.34	1.09	0.36
Insect	0.05	0.03	2.00	41.96	0.80	0.45
log(Tree Canopy_500m)	0.06	0.06	1.00	14.42	1.84	0.20
scale(Size)	0.00	0.00	1.00	14.52	0.04	0.84
City:log(Tree Canopy_500m)	0.07	0.04	2.00	14.33	1.12	0.35
Insect:log(Tree Canopy_500m)	0.05	0.02	2.00	41.84	0.75	0.48

Tree canopy (1000m)

	Sum sq	Mean sq	NumDF	DenDF	F value	p value
log(Abundance)	0.67	0.67	1.00	51.41	21.86	<0.001
City	0.06	0.03	2.00	14.47	0.91	0.42

Insect	0.03	0.01	2.00	37.30	0.44	0.65
log(Tree Canopy_1000m)	0.01	0.01	1.00	14.64	0.20	0.66
scale(Size)	0.00	0.00	1.00	14.45	0.04	0.85
City:log(Tree Canopy_1000m)	0.06	0.03	2.00	14.51	1.01	0.39
City:Insect	0.15	0.04	4.00	36.98	1.26	0.30
Insect:log(Tree Canopy_1000m)	0.06	0.03	2.00	36.07	1.05	0.36

Semi-natural habitat (250m)

	Sum sq	Mean sq	NumDF	DenDF	F value	p value
log(Abundance)	1.24	1.24	1.00	46.19	38.60	<0.001
City	0.01	0.00	2.00	16.02	0.14	0.87
Insect	0.09	0.04	2.00	37.18	1.35	0.27
log(Natural_250m)	0.10	0.10	1.00	15.75	3.12	0.10
scale(Size)	0.00	0.00	1.00	16.32	0.00	1.00
City:Insect	0.13	0.03	4.00	36.97	0.99	0.43
Insect:log(Natural_250m)	0.09	0.04	2.00	36.58	1.33	0.28

Semi-natural habitat (500m)

	Sum sq	Mean sq	NumDF	DenDF	F value	p value
log(Abundance)	1.30	1.30	1.00	53.87	41.40	<0.001
City	0.04	0.02	2.00	15.61	0.64	0.54
Insect	0.10	0.05	2.00	41.83	1.55	0.22
log(Natural_500m)	0.21	0.21	1.00	16.25	6.74	0.02
scale(Size)	0.03	0.03	1.00	16.07	1.09	0.31
City:log(Natural_500m)	0.04	0.02	2.00	15.62	0.63	0.55
Insect:log(Natural_500m)	0.06	0.03	2.00	41.77	1.01	0.37

Semi-natural habitat (1000m)

	Sum sq	Mean sq	NumDF	DenDF	F value	p value
log(Abundance)	1.38	1.38	1.00	45.05	42.61	<0.001
City	0.01	0.00	2.00	16.99	0.15	0.86
Insect	0.09	0.04	2.00	37.31	1.36	0.27
log(Natural_250m)	0.12	0.12	1.00	16.59	3.83	0.07
City:Insect	0.13	0.03	4.00	37.08	0.98	0.43
Insect:log(Natural_250m)	0.09	0.04	2.00	36.69	1.36	0.27

Supplementary Material Chapter 3:

Supplementary Figures S3:

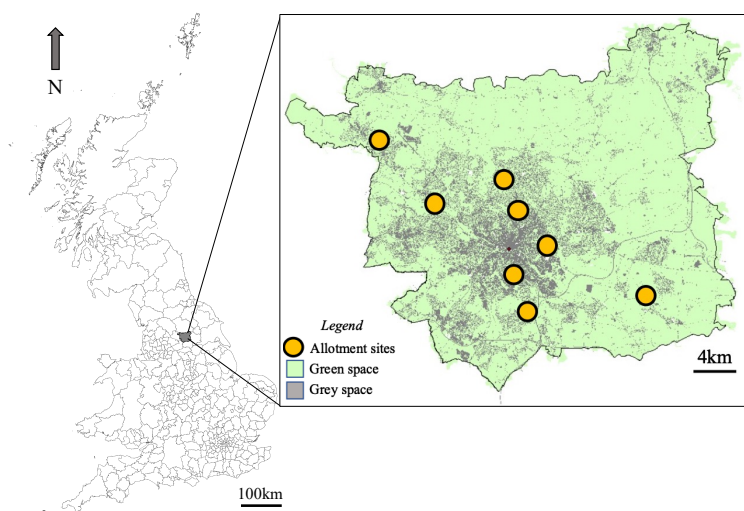


Figure S3. 1 Location of Leeds within the U.K. and location of the sites within the city, showing the area of grey and green space.

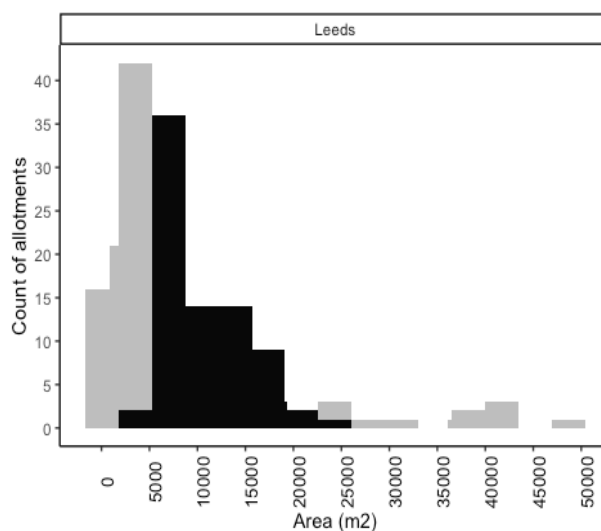


Figure S3. 2 Size (m²) distributions of allotments in the city of Leeds. Black depicts the range of allotments sizes that were included in this study (range = 5192m² – 22639m²).

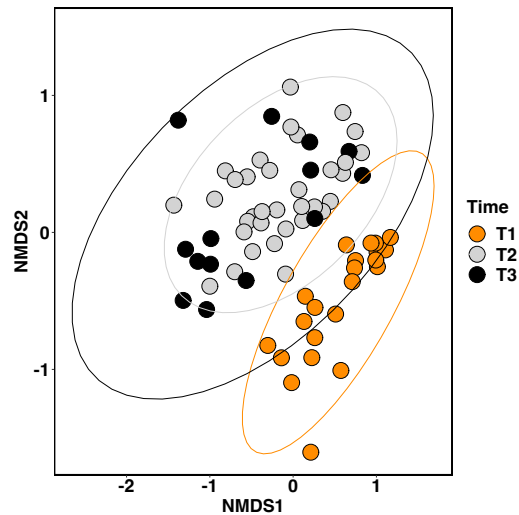


Figure S3. 3 Non-metric multidimensional scaling (NMDS) plot showing the plant-visitation patterns of bees and moths are distinct across time (ANOSIM $R^2 = 0.46$, stress = 0.19, $p < 0.001$). T1 = early summer, T2 = midsummer, T3 = late summer.

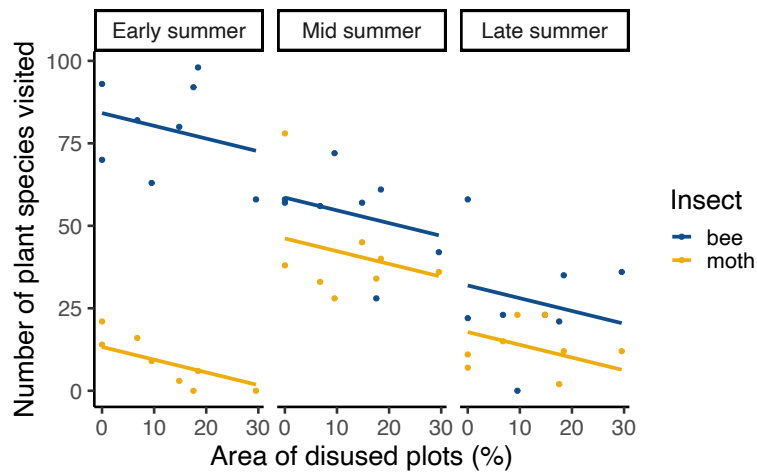


Figure S3. 4 The number of plant species visited by bees and moths across the season along an allotment site cultivation gradient (% cover of disused plots within each site). Fitted line based on a generalized linear model shows some evidence that numbers of plants visited by bees and moths across time are negatively affected by increasing areas of disused plots ($\chi^2 = 4.13$, $df = 1$, $p = 0.042$). Lines represent linear relationships between predictor (area of disused plots) and response (number of plant species visited), showing a significant insect*time interactions and non-significant cultivation*insect nor cultivation*time interaction (i.e., same slopes).

Supplementary Text S3:

Supplementary Text S3.1: Lab protocols.

- Pollen removal from insect:** Insects were shaken (in a lysis buffer for five minutes (250µl- 3mL Digsol (recipe below)) and Proteinase K (10mg/ml).

Reagent recipes

Digsol recipe (for 500mL)	Low TE (for 500mL)	Ammonium acetate
20mL 0.5M EDTA* (ph8.0)	5mL 1M Tris-HCl** (ph 8.0)	
3.425g NaCl	100mL 0.5M EDTA*(ph8.0)	
25mL 1M Tris-HCl** (ph 8.0)	495mL ddH2O	
430ml ddH2O		
25ml SDS***		

2. Ammonium acetate precipitation protocol for DNA extraction:

Due to the hard pollen exines we digested the pollen over night at 55°C in a rotating oven. Once digested, we used an ammonium acetate precipitation method.

- Once digested add 4M ammonium acetate (300µl) to each sample
- Vortex several times over a period of at least 15 mins at room temperature to precipitate the proteins.
- Centrifuge for 10 minutes at 13,000rpm
- Aspirate supernatant (clear liquid containing the DNA) into clean labelled 1.5ml flip-top tubes (discard the gunky protein stuff which usually pellets on the bottom although could be floating on the top).
- Add 1ml 100% ethanol
- Invert tubes gently several times to precipitate DNA
- Centrifuge for 10 minutes at 13,000rpm
- Pour off ethanol taking care not to lose DNA pellet
- Add 500µl 70% ethanol and invert several times to rinse pellet
- Centrifuge for 5 minutes at 15,000rpm in case the pellet has dislodged from the bottom of the tube.
- Pour off ethanol in a smooth movement or using a 200µl pipette gently draw off the supernatant if fear of losing pellet. Stand tubes upside-down on clean tissue (approx. 30-60minutes). This can be speeded up by using the heat of a lamp from above.
- Once fully dry add approx. 15µl-30µl Low TE (recipe Table1). Obviously add less if a very tiny pellet or no pellet is observed.
- Flick sample to dislodge pellet
- Place tubes in hotblock for 30 minutes (65 °C) to dissolve pellet (flicking every 10 mins). Tubes can also be placed at 4°C overnight or weekend which also allows for the pellet to dissolve.
- Store at -20 °C (long term) or 4 °C (short term)

3. Amplicon PCR and library preparation for Illumina sequencing:

PCR-1

Primers used:

ITS2 forward = TGTGAATTGCARRATYCMG

ITS2 reverse = CCCGHYTGAYYTGRGGTDCDC

rbcl forward = ATGTCACCACAAACAGAGACTAAAGC

rbcl reverse = AGGGGACGACCATACTTGTTC

PCR-1 programmes:

ITS2: 95°C for 15 minutes, then 40 cycles of the following; 95 °C for 30 seconds, 56 °C for 30 seconds, 72 °C. for 1 minute. Once cycled through, finish with 72 °C for 10 minutes.

rbcl: 95°C for 15 minutes, then 40 cycles of the following; 95 °C for 30 seconds, 50 °C for 30 seconds, 72 °C. for 45 seconds. Once cycled through, finish with 72 °C for 10 minutes.

4. Agrose gels

4µl of PCR-1 product was run on 1% agrose gel to ensure the samples had amplified successfully and that pollen was present.

5. Bead cleaning using AMPure XP Beads:

1. PCR1 samples were eluted to 25µl with Low TE (recipe above).
2. 25µl of beads was added to samples
3. Samples were then placed on magnetic rack to separate the beads from the solution.
4. Once clear, the supernatant was aspirated and discarded
5. 200µl of 80% ethanol was added to beads (still on magnetic rack) for 30 seconds to clean off any remaining supernatant.
6. Ethanol was aspirated and discarded.
7. Steps 5-7 were repeated once
8. While on the magnetic rack beads were dried
9. Once dry, samples were removed from plate and beads eluted with 15µl of Low TE
10. Beads were placed back on magnetic rack to separate the beads and solution.
11. Solution was aspirated off and put in clean tubes for next stages (i.e. PCR-2).

1. PCR-2

Using i7- and i5-tailed indexed primers to add unique identifier sequences and Illumina sequencing sites to the amplicon sequences.

Plates were loaded with a unique index primer in each well.

PCR programme: 95 °C for 15 mins. Followed by 12 cycles of: 98 °C for 10 seconds, 65 °C for 30 seconds, 72 °C for 30 seconds. Then finish with 72 °C for 5 minutes.

2. Tapestation

Each run was checked on the Tapestation before and after PCR-2 to ensure the samples have increased in size from the addition of PCR-2 primers.

3. Fluorimeter

To check the DNA concentration, 2 μ l of each sample using the fluorimeter.

4. Purification with AMPure XP beads (2)

1. Using 0.5x bead concentration: 50 μ l of each pool of PCR2 products with 25 μ l resuspended AMPure XP beads.
2. Place on magnetic rack to separate beads from the solution and transfer the supernatant (75 μ l) to a new plate/tube and discard the beads.
3. Mix a further 67.5 μ l (0.9x) of resuspended AMPure XP beads with the transferred supernatant
4. Place on magnetic rack to separate beads from the solution and aspirate the supernatant and discard.
5. Add 200 μ l 80% ethanol then carefully aspirate out and discard.
6. Repeat step 5.
7. Allow the beads to dry.
8. Remove samples from the magnetic plate and elute with 15 μ l of low TE.
9. Place on magnetic rack to separate beads from the solution (~ 1 minute).

5. Quantification with qPCR

1. Make a serial dilution of each library: 100, 1000 and 10000 -fold.
2. Prepare SYBR® Green master mix.
3. Add 2 μ l of the SYBR kit standards, diluted sample libraries, or dilution buffer (no template control) to appropriate wells in 96-well plate.
4. Dispense 8 μ l of the master mix to the appropriate wells in the 96-well plate.
5. Set the reaction volume to 10 μ l and the following qPCR profile:
5 min at 95°C
35 cycles of the following:
30 sec at 95°C
45 sec at 60°C
6. Pool samples in equimolar amounts – aim for 4 nM.
7. The final pool is now ready to submit for Illumina sequencing.

Supplementary Text S3.2: Bioinformatic pipeline code:

Raw sequences were put through a metabarcoding analysis pipeline using R v4.0.0 using packages 'dada2', 'Biostrings' and 'ShortRead'. A BLAST was carried out through Linux HPC against the GenBank nucleotide database (nt). BLAST results were filtered based on measures of read quality and the presence of uncultured/environmental matches. Then, using MEtaGenome ANalyzer (MEGAN), the BLAST results were given a taxonomic assignment using the Lowest Common Ancestor (LCA) algorithm (threshold 6). The assignments were then manually checked to ensure all Amplicon Sequence Variants (ASVs) had no obviously spurious matches

This is the raw sequence processing pipeline, the script below is processing the rbcl amplicons, the same code was used for ITS2 sequences, but with changes to primer input.

```
library(dada2)
library(Biostrings)
library(ShortRead)
input.path <- "/fastdata/bop18eee/rbcl"
output.path <- "/fastdata/bop18eee/rbcl/rbcl_out2"
##### Inputting the forward and reverse reads#####
#The raw sequences are sent as reverse and forward reads so first, we assign samples as a forward or a reverse
read based on their file names.
fnFs <- sort(list.files(input.path, pattern = "_L001_1_R1.fastq.gz", full.names = TRUE))
fnRs <- sort(list.files(input.path, pattern = "_L001_1_R2.fastq.gz", full.names = TRUE))
FWD <- "ATGTCACCACAAACAGAGACTAAAGC"
REV <- "AGGGGACGACCATACTTGTTC"
#### Primer orientation checking ####
#The orientation of primers may not be in the position we expect, this is due the fact that the amplicons between
species vary in length and in some cases the sequencing machine can cycle through the full region and into the f
orward/reverse primer. Therefore, we search for Forward, Compliment, Reverse and Reverse Compliments orien
tations of the primers in our dataset.

allOrients <- function(primer) {
  # Create all orientations of the input sequence
  require(Biostrings)
  dna <- DNASTring(primer) # The Biostrings works w/ DNASTring
  #objects rather than character vectors
  orients <- c(Forward = dna, Complement = complement(dna), Reverse = reverse(dna),
              RevComp = reverseComplement(dna))
  return(sapply(orients, toString)) # Convert back to character vector
}

FWD.orients <- allOrients(FWD)
FWD.orients # print all orientations of the forward primer to the console
REV.orients <- allOrients(REV)
REV.orients # print all orientations of the reverse primer to the console

#### Filter and trim ####
#The first step of filtering and trimming the sequences is a pre-filter step which removes all sequences with Ns us
ing the filterAndTrim function. We removed all sequences with Ns in them and saved said sequences into a new f
ile called filtN

fnFs.filtN <- file.path(output.path, "filtN", basename(fnFs))
fnRs.filtN <- file.path(output.path, "filtN", basename(fnRs))
filterAndTrim(fnFs, fnFs.filtN, fnRs, fnRs.filtN, maxN = 0, multithread = FALSE)

primerHits <- function(primer, fn) {
  # Counts number of reads in which the primer is found
  nhits <- vcountPattern(primer, sread(readFastq(fn)), fixed = FALSE)
  return(sum(nhits > 0))
}

rbind(FWD.ForwardReads = sapply(FWD.orients, primerHits, fn = fnFs.filtN[[1]]),
      FWD.ReverseReads = sapply(FWD.orients, primerHits, fn = fnRs.filtN[[1]]),
      REV.ForwardReads = sapply(REV.orients, primerHits, fn = fnFs.filtN[[1]]),
      REV.ReverseReads = sapply(REV.orients, primerHits, fn = fnRs.filtN[[1]])

#### cutadapt ####
#Using cutadapt software (through system 2 in R shell) the primers were trimmed off; this is a necessary step to
use dada2
cutadapt <- "/usr/local/community/Genomics/apps/miniconda/envs/py36cutadapt/bin/cutadapt"
```

```

path.cut <- file.path(output.path, "cutadapt")
if(!dir.exists(path.cut)) dir.create(path.cut)
fnFs.cut <- file.path(path.cut, basename(fnFs))
fnRs.cut <- file.path(path.cut, basename(fnRs))

FWD.RC <- dada2::rc(FWD)
REV.RC <- dada2::rc(REV)
# Trim FWD and the reverse-complement of REV off of R1 (forward reads)
R1.flags <- paste("-g", FWD, "-a", REV.RC)
# Trim REV and the reverse-complement of FWD off of R2 (reverse reads)
R2.flags <- paste("-G", REV, "-A", FWD.RC)

for(i in seq_along(fnFs)) {
  system2(cutadapt, args = c(R1.flags, R2.flags, "-n", 2,
    # -n 2 required to remove FWD and REV
    "-o", fnFs.cut[i], "-p", fnRs.cut[i], # output files
    fnFs.filtN[i], fnRs.filtN[i], # input files
    "--discard-untrimmed",
    "--minimum-length 60"))
}

rbind(FWD.ForwardReads = sapply(FWD.oriens, primerHits, fn = fnFs.cut[[1]]),
  FWD.ReverseReads = sapply(FWD.oriens, primerHits, fn = fnRs.cut[[1]]),
  REV.ForwardReads = sapply(REV.oriens, primerHits, fn = fnFs.cut[[1]]),
  REV.ReverseReads = sapply(REV.oriens, primerHits, fn = fnRs.cut[[1]])

# we should have no primers remaining in our file

#### Checking the quality of your data ####
#using dada2's quality control function 'plotQualityProfile' we plotted figures to examine the similar read length by
quality (Figure 1)

# Specify the paths and file names the forward and reverse primer cleaned files
cutFs <- sort(list.files(path.cut, pattern = "_L001_1_R1.fastq.gz", full.names = TRUE))
cutRs <- sort(list.files(path.cut, pattern = "_L001_1_R2.fastq.gz", full.names = TRUE))

# Extract sample names
get.sample.name <- function(fname) strsplit(basename(fname), "-")[[1]][1]
sample.names <- unname(sapply(cutFs, get.sample.name))
head(sample.names)

# check the quality for the first file
pdf("quality_profile_rbcl_cutfs1.pdf")
# 2. Create a plot
plotQualityProfile(cutFs[1:12])
# Close the pdf file
dev.off()

# check the quality for the rev file
pdf("quality_profile_rbcl_cutrs1.pdf")
# 2. Create a plot
plotQualityProfile(cutRs[1:12])
# Close the pdf file
dev.off()

#### Cleaning your data ####
# this step is done to filter the data and remove any poor quality reads. Poor quality reads here are defined 5 criteria:
# 1. Ns: any sequences with more than 0 Ns will be discarded (a requirement for dada2);
# 2. A quality score of less than or equal to two;
# 3. Discards any reads that match phiX genome;

```

```

# 4. If expected errors are higher than two sequences will be removed;
# 5. Finally, if the read length is less than 60 it will be removed.

filtFs <- file.path(path.cut, "../filtered", basename(cutFs))
filtRs <- file.path(path.cut, "../filtered", basename(cutRs))

out <- filterAndTrim(cutFs, filtFs, cutRs, filtRs, maxN = 0, maxEE = c(2, 2),
                    truncQ = 2, minLen = 60, rm.phix = TRUE, compress = TRUE,
                    multithread = FALSE)

#out

#### Identification of ASVs ####
#Generating an error model: Each dataset will have a specific error-signature with errors introduced by PCR ampli-
fication and sequencing, there error models were made using "plotErrors" function to examine the error rates of o-
ur dataset
errF <- learnErrors(filtFs, multithread = FALSE)
errR <- learnErrors(filtRs, multithread = FALSE)

#### saving error plot
pdf("errorplot_rbcl_errf.pdf")
# 2. Create a plot
plotErrors(errF, nominalQ = TRUE)
# Close the pdf file
dev.off()

#reverse
pdf("errorplot_rbcl_errr.pdf")
# 2. Create a plot
plotErrors(errR, nominalQ = TRUE)
# Close the pdf file
dev.off()

#### Dereplication ####
#to increase processing power identical reads are collapsed together
exists <- file.exists(filtFs)
# check that all the samples are still present after filtering
derepFs <- derepFastq(filtFs[exists], verbose=TRUE)
derepRs <- derepFastq(filtRs[exists], verbose=TRUE)
# Name the derep-class objects by the sample names
names(derepFs) <- sample.names[exists]
names(derepRs) <- sample.names[exists]

#### Inference of ASVs ####
# as insect samples were collected in the field (i.e. not a sterile environment), we opted to use the Independent S-
ample Inference algorithm over the Pseudo-Pooling algorithm as the latter, despite being more sensitive to sampl-
es with low reads, comes with an increased risk of false-positive ASV inference (e.g. reporting contamination as
ASVs). Dada2 using the error models (above) to infer the true sample composition.
dadaFs <- dada(derepFs, err = errF, multithread = FALSE)
dadaRs <- dada(derepRs, err = errR, multithread = FALSE)

#### Merging paired end reads ####
#forward and reverse reads combined with a default minimum overlap of 12 bps.
mergers <- mergePairs(dadaFs, derepFs, dadaRs, derepRs, verbose=TRUE)

#### Making our ASV matrix ####
#simply using 'makeSequenceTable' function, creates a matrix with each column representing a single ASV and
each row an individual sample.
seqtab <- makeSequenceTable(mergers)
dim(seqtab)

#### Chimera detection and removal ####
#all Chimeric sequences were removed, using dada2 function 'removeBimerDenovo' which compares the left an-
d right segments of abundant reads and compares these with lower abundant sequences, and removes any low
abundant sequences that match.

seqtab.nochim <- removeBimeraDenovo(seqtab, method="consensus",

```

```

                                multithread=FALSE, verbose=TRUE)

dim(seqtab.nochim)

sum(seqtab.nochim)/sum(seqtab)

table(nchar(getSequences(seqtab.nochim)))

write.table(seqtab.nochim, "rbcl_seqtab.nochim.tsv", sep="\t", quote=F, col.names=NA)
#### Sequence tracking sanity check ####
getN <- function(x) sum(getUniques(x))
track <- cbind(out, sapply(dadaFs, getN),
              sapply(dadaRs, getN),
              sapply(mergers, getN),
              rowSums(seqtab.nochim))
colnames(track) <- c("input", "filtered",
                  "denoisedF", "denoisedR",
                  "merged", "nonchim")
rownames(track) <- sample.names
track
write.csv(track, "rbcl_track.csv" )
# The column names of seqtab.nochim are actually the ASV sequences
mifish_seqs <- colnames(seqtab.nochim)
# Make a new variable for ASV names, `mifish_headers`
mifish_headers <- vector(dim(seqtab.nochim)[2], mode="character")
# Fill the vector with names formatted for a fasta header (>ASV_1, >ASV_2, etc.)
for (i in 1:dim(seqtab.nochim)[2]) {mifish_headers[i] <- paste(">ASV", i, sep="_")}
mifish_fasta <- c(rbind(mifish_headers, mifish_seqs))
write(mifish_fasta, "rbcl_MiSeq_asv.fa")
mifish_tab <- t(seqtab.nochim)
# Name each row with the ASV name, omitting the '>' used in the fasta file
row.names(mifish_tab) <- sub(">", "", mifish_headers)
write.table(mifish_tab, "rbcl_MiSeq_asv_counts.tsv", sep="\t", quote=F, col.names=NA)

```

Supplementary Text S3.3: Geographic information system (GIS) urbanisation analysis

Using ArcGIS (version 10.1.7) the area of impervious surface were extracted from UK Ordnance Survey MasterMap© (<https://digimap.edina.ac.uk/>). All land-types described as 'manmade' which include buildings and roads were selected. Circular buffers surrounding the allotment site, with the centre of the circle being the centre of the site, were drawn with radii of 250m, 500m and 1000m. The area of surfaces were then exported as csv and used for subsequent analysis.

Supplementary Tables S3:

Table S3.1: Size, distance from the city centre, area of disused plots, and 2019 sampling dates for eight allotments sites in Leeds.

Site ID	Size m ²	Distance (km)	Area of disused (%)	Early summer (Day/month)	Mid summer (Day/month)	Late summer (Day/month)	
				Bees Moths	Bees Moths	Bees	Moths
LD1	11499.7	1.8	29.5	22/05 24/05	16/07 19/07	20/9	21/9
LD2	11774.6	2.32	18.4	23/05 24/05	18/07 19/07	19/9	21/9
LD3	5192.1	3.33	9.5	24/05 24/05	16/07 19/07	20/9	21/9
LD4	22639.5	4.49	6.8	22/05 24/05	18/07 19/07	19/9	21/9
LD5	14037.9	5.9	17.5	22/05 24/05	18/07 19/07	19/9	21/9
LD6	14857.3	5.06	0	21/05 24/05	17/07 19/07	20/9	21/9
LD7	11127.2	12.12	0	21/05 24/05	17/07 19/07	20/9	21/9
LD8	8288.6	11.73	14.8	22/05 24/05	16/07 19/07	19/9	21/9

Table S3.2: R packages used and associated citations.

Package	Usage	Reference
Biostrings	Bioinformatics pipeline	(Pagès, Aboyoun, Gentleman, & DebRoy, 2021)
bipartite	Network analysis	(Dormann et al., 2021)
car	Statistical analysis	(Fox, 2021)
dada2	Bioinformatics pipeline	(Callahan, McMurdie, & Holmes, 2018)
dplyr	Data frame manipulation	(Wickham & Francois, 2018)
emmeans	Post-hoc tests	(Lenth, 2018)
ggfortify	Statistical analysis	(Tang, Horikoshi, & Li, 2016)
ggplot2	Graphing	(Valero-Mora, 2010)
lme4	Statistical analysis	(Bates, Maechler, Bolker, & Walker, 2015)
MCMCglmm	Statistical analysis	(Hadfield, 2017)
modelr	Data frame manipulation	(Wickham, 2020)
phyloseq	Graphing	(McMurdie, Holmes, with contributions from Gregory Jordan, & Chamberlain, 2020)
ShortRead	Bioinformatics pipeline	(Morgan, Lawrence, & Anders, 2021)
tidyr	Data frame manipulation	(Wickham & Henry, 2019)
tidyverse	Data frame manipulation	(Wickham, 2011)
vegan	Community analysis	(Oksanen, Blanchet, Kindt, & Legendre, 2006)
visreg	Graphing	(Breheny, P. and Burchett, 2015)

Table S3.3: Species list of moths caught in eight allotments sites in Leeds 2019. The number of individuals (abundance) in each site (LD1-LD8) and the number of these individuals carrying pollen on their proboscis.

Family	Species	Number carrying pollen	Number carrying pollen								
			LD1	LD2	LD3	LD4	LD5	LD6	LD7	LD8	
Blastobasidae	<i>Blastobasis adustella</i>	0	0	2	0	0	0	0	0	1	1
Crambidae	<i>Agriphila straminella</i>	0	0	0	1	1	0	0	0	0	1
Crambidae	<i>Anania coronata</i>	1	0	0	2	0	1	0	0	1	0
Crambidae	<i>Catoptria pinella</i>	0	0	0	0	0	0	0	0	0	1
Crambidae	<i>Chrysoteuchia culmella</i>	3	3	2	2	1	10	3	0	0	1
Crambidae	<i>Cranbus perella</i>	0	0	0	0	0	1	0	0	0	0
Crambidae	<i>Eudonia delunella</i>	0	0	0	0	3	0	0	0	0	0
Crambidae	<i>Eudonia lacustrata</i>	0	1	4	2	1	1	0	0	0	5
Erebidae	<i>Calliteara pudibunda</i>	0	0	1	0	0	0	0	0	0	0
Erebidae	<i>Eilema complana</i>	0	0	0	0	0	0	0	0	0	1
Erebidae	<i>Manulea lurideola</i>	8	0	7	0	1	0	0	0	1	7
Geometridae	<i>Biston betularia</i>	0	0	0	0	0	0	1	0	0	0
Geometridae	<i>Campaea margaritata</i>	0	0	0	0	0	0	0	0	0	1
Geometridae	<i>Crocallis elinguaris</i>	0	0	2	0	0	0	0	0	1	0
Geometridae	<i>Dysstroma truncata</i>	0	0	0	0	0	1	0	0	1	0
Geometridae	<i>Eulithis prunata</i>	0	0	0	0	0	0	0	0	1	0
Geometridae	<i>Eupithecia centaureata</i>	0	0	1	0	0	0	0	0	0	0
Geometridae	<i>Eupithecia spp.</i>	0	1	0	0	0	0	0	0	0	1
Geometridae	<i>Hemithea aestivaria</i>	0	0	0	0	0	0	0	0	1	0
Geometridae	<i>Idaea aversata</i>	0	1	2	1	0	1	1	4	4	1
Geometridae	<i>Idaea biselata</i>	0	0	1	0	0	0	0	0	0	0
Geometridae	<i>Odontopera bidentata</i>	1	0	0	0	0	0	0	0	2	0
Geometridae	<i>Ourapteryx sambucaria</i>	1	1	1	0	0	0	0	0	0	3
Geometridae	<i>Selenia dentaria</i>	0	0	0	0	0	0	0	0	0	1
Hepialidae	<i>Korscheltellus lupulina</i>	0	0	0	0	1	0	0	0	0	0
Noctuidae	<i>Agrotis exclamationis</i>	27	2	2	7	4	1	10	7	7	7
Noctuidae	<i>Agrotis puta</i>	3	0	2	2	1	0	0	0	0	2
Noctuidae	<i>Amphipyra pyramidea</i>	3	0	0	1	2	0	2	0	0	0
Noctuidae	<i>Apamea lithoxylaea</i>	1	0	0	0	0	1	0	0	0	0
Noctuidae	<i>Apamea monoglypha</i>	22	4	6	6	5	3	6	12	6	6
Noctuidae	<i>Aporophyla nigra</i>	1	1	0	0	0	0	0	0	0	1
Noctuidae	<i>Axylia putris</i>	1	0	1	1	0	0	0	0	1	0
Noctuidae	<i>Caradrina morpheus</i>	1	0	2	0	0	0	0	0	1	0
Noctuidae	<i>Cosmia trapezina</i>	4	0	3	0	0	1	0	0	0	0
Noctuidae	<i>Cydalima perspectalis</i>	0	0	0	0	1	0	0	0	0	0
Noctuidae	<i>Diachrysis chrysitis</i>	1	0	0	0	0	0	0	0	0	1
Noctuidae	<i>Diarsia mendica</i>	0	0	0	0	0	0	0	0	0	1

Noctuidae	<i>Hoplodrina octogenaria/blanda</i>	29	0	10	6	11	6	6	1	4
Noctuidae	<i>Hypena proboscidalis</i>	0	0	0	0	0	0	0	1	0
Noctuidae	<i>Lacanobia oleracea</i>	3	0	3	0	0	0	1	0	1
Noctuidae	<i>Mesapamea secalis agg.</i>	6	3	1	1	8	1	2	2	1
Noctuidae	<i>Mormo maura</i>	0	1	0	0	0	0	0	0	0
Noctuidae	<i>Mythimna conigera</i>	3	2	0	0	0	0	2	0	2
Noctuidae	<i>Mythimna ferrago</i>	1	1	1	0	0	0	1	0	0
Noctuidae	<i>Mythimna impura</i>	15	9	4	7	1	1	1	4	9
Noctuidae	<i>Naenia typica</i>	1	0	1	0	0	0	1	0	0
Noctuidae	<i>Noctua comes</i>	5	0	1	2	3	0	1	1	4
Noctuidae	<i>Noctua janthe</i>	1	0	1	0	0	0	0	0	0
Noctuidae	<i>Noctua pronuba</i>	17	6	7	15	6	5	8	4	4
Noctuidae	<i>Oegoconia spp.</i>	0	0	0	0	0	1	0	0	0
Noctuidae	<i>Oligia strigilis agg.</i>	1	1	1	0	0	0	0	0	3
Noctuidae	<i>Xestia c-nigrum</i>	7	0	0	0	4	1	0	0	3
Noctuidae	<i>Xestia ditrapezium</i>	0	0	1	0	0	0	0	0	0
Noctuidae	<i>Xestia triangulum</i>	1	0	0	0	0	0	1	0	0
Noctuidae	<i>Xestia xanthographa</i>	2	0	0	1	0	0	0	0	2
Notodontidae	<i>Pheosia tremula</i>	0	0	0	0	1	0	0	0	0
Oecophoridae	<i>Crassa unitella</i>	0	0	0	0	0	0	0	0	1
Oecophoridae	<i>Hofmannophila pseudospretella</i>	0	0	0	0	0	0	1	1	0
Pterophoridae	<i>Emmelina monodactyla</i>	0	0	0	0	0	0	1	0	0
Pyralidae	<i>Aphomia sociella</i>	0	0	0	0	0	0	0	0	1
Pyralidae	<i>Endotricha flammealis</i>	0	0	0	0	0	0	1	0	1
Pyralidae	<i>Xestia xanthographa</i>	0	0	1	0	0	0	0	0	0
Sphingidae	<i>Laothoe populi</i>	0	0	0	0	1	0	0	0	0
Tortricidae	<i>Celypha striana</i>	0	0	0	1	0	0	0	0	0
Tortricidae	<i>Cydia pomonella</i>	1	0	3	0	0	1	0	0	1
Tortricidae	<i>Pandemis cerasana</i>	0	1	0	0	0	0	0	1	0
Yponomeutidae	<i>Yponomeuta spp.</i>	0	0	0	0	0	0	0	0	2

Family	Species	Total abundance	Number carrying pollen	LD1	LD2	LD3	LD4	LD5	LD6	LD7	LD8
Blastobasidae	<i>Blastobasis adustella</i>	4	0	0	2	0	0	0	0	1	1
Crambidae	<i>Agriphila straminella</i>	3	0	0	0	1	1	0	0	0	1
Crambidae	<i>Anania coronata</i>	3	0	0	0	2	0	1	0	0	0
Crambidae	<i>Anania coronata</i>	1	1	0	0	0	0	0	0	1	0
Crambidae	<i>Catoptria pinella</i>	1	0	0	0	0	0	0	0	0	1
Crambidae	<i>Chrysoteuchia culmella</i>	12	0	3	2	2	1	0	3	0	1
Crambidae	<i>Chrysoteuchia culmella</i>	10	3	0	0	0	0	10	0	0	0
Crambidae	<i>Cranbus perella</i>	1	0	0	0	0	0	1	0	0	0

Crambidae	<i>Eudonia delunella</i>	3	0	0	0	0	3	0	0	0	0
Crambidae	<i>Eudonia lacustrata</i>	14	0	1	4	2	1	1	0	0	5
Erebidae	<i>Calliteara pudibunda</i>	1	0	0	1	0	0	0	0	0	0
Erebidae	<i>Eilema complana</i>	1	0	0	0	0	0	0	0	0	1
Erebidae	<i>Manulea lurideola</i>	7	4	0	7	0	0	0	0	0	0
Erebidae	<i>Manulea lurideola</i>	1	1	0	0	0	1	0	0	0	0
Erebidae	<i>Manulea lurideola</i>	1	0	0	0	0	0	0	0	1	0
Erebidae	<i>Manulea lurideola</i>	7	3	0	0	0	0	0	0	0	7
Geometridae	<i>Biston betularia</i>	1	0	0	0	0	0	0	1	0	0
Geometridae	<i>Campaea margaritata</i>	1	0	0	0	0	0	0	0	0	1
Geometridae	<i>Crocallis elinguaris</i>	3	0	0	2	0	0	0	0	1	0
Geometridae	<i>Dysstroma truncata</i>	2	0	0	0	0	0	1	0	1	0
Geometridae	<i>Eulithis prunata</i>	1	0	0	0	0	0	0	0	1	0
Geometridae	<i>Eupithecia centaureata</i>	1	0	0	1	0	0	0	0	0	0
Geometridae	<i>Eupithecia spp.</i>	2	0	1	0	0	0	0	0	0	1
Geometridae	<i>Hemithea aestivaria</i>	1	0	0	0	0	0	0	0	1	0
Geometridae	<i>Idaea aversata</i>	11	0	1	2	1	0	1	1	4	1
Geometridae	<i>Idaea biselata</i>	1	0	0	1	0	0	0	0	0	0
Geometridae	<i>Odontopera bidentata</i>	2	1	0	0	0	0	0	0	2	0
Geometridae	<i>Ourapteryx sambucaria</i>	2	1	1	1	0	0	0	0	0	0
Geometridae	<i>Ourapteryx sambucaria</i>	3	0	0	0	0	0	0	0	0	3
Geometridae	<i>Selenia dentaria</i>	1	0	0	0	0	0	0	0	0	1
Hepialidae	<i>Korscheltellus lupulina</i>	1	0	0	0	0	1	0	0	0	0
Noctuidae	<i>Agrotis exclamationis</i>	3	1	2	0	0	0	1	0	0	0
Noctuidae	<i>Agrotis exclamationis</i>	2	2	0	2	0	0	0	0	0	0
Noctuidae	<i>Agrotis exclamationis</i>	14	6	0	0	7	0	0	0	0	7
Noctuidae	<i>Agrotis exclamationis</i>	4	3	0	0	0	4	0	0	0	0
Noctuidae	<i>Agrotis exclamationis</i>	10	8	0	0	0	0	0	10	0	0
Noctuidae	<i>Agrotis exclamationis</i>	7	7	0	0	0	0	0	0	7	0
Noctuidae	<i>Agrotis puta</i>	3	1	0	2	0	1	0	0	0	0
Noctuidae	<i>Agrotis puta</i>	4	2	0	0	2	0	0	0	0	2
Noctuidae	<i>Amphipyra pyramidea</i>	1	1	0	0	1	0	0	0	0	0
Noctuidae	<i>Amphipyra pyramidea</i>	2	0	0	0	0	2	0	0	0	0
Noctuidae	<i>Amphipyra pyramidea</i>	2	2	0	0	0	0	0	2	0	0
Noctuidae	<i>Apamea lithoxyloa</i>	1	1	0	0	0	0	1	0	0	0
Noctuidae	<i>Apamea monoglypha</i>	7	3	4	0	0	0	3	0	0	0
Noctuidae	<i>Apamea monoglypha</i>	12	6	0	6	0	0	0	0	0	6

Noctuidae	<i>Apamea monoglypha</i>	17	5	0	0	6	5	0	6	0	0
Noctuidae	<i>Apamea monoglypha</i>	12	8	0	0	0	0	0	0	12	0
Noctuidae	<i>Aporophyla nigra</i>	1	1	1	0	0	0	0	0	0	0
Noctuidae	<i>Aporophyla nigra</i>	1	0	0	0	0	0	0	0	0	1
Noctuidae	<i>Axylia putris</i>	3	1	0	1	1	0	0	0	1	0
Noctuidae	<i>Caradrina morpheus</i>	3	1	0	2	0	0	0	0	1	0
Noctuidae	<i>Cosmia trapezina</i>	3	3	0	3	0	0	0	0	0	0
Noctuidae	<i>Cosmia trapezina</i>	1	1	0	0	0	0	1	0	0	0
Noctuidae	<i>Cydalima perspectalis</i>	1	0	0	0	0	1	0	0	0	0
Noctuidae	<i>Diachrysis chrysitis</i>	1	1	0	0	0	0	0	0	0	1
Noctuidae	<i>Diarsia mendica</i>	1	0	0	0	0	0	0	0	0	1
Noctuidae	<i>Hoplodrina octogenaria/blanda</i>	10	8	0	10	0	0	0	0	0	0
Noctuidae	<i>Hoplodrina octogenaria/blanda</i>	6	4	0	0	6	0	0	0	0	0
Noctuidae	<i>Hoplodrina octogenaria/blanda</i>	11	9	0	0	0	11	0	0	0	0
Noctuidae	<i>Hoplodrina octogenaria/blanda</i>	12	5	0	0	0	0	6	6	0	0
Noctuidae	<i>Hoplodrina octogenaria/blanda</i>	1	1	0	0	0	0	0	0	1	0
Noctuidae	<i>Hoplodrina octogenaria/blanda</i>	4	2	0	0	0	0	0	0	0	4
Noctuidae	<i>Hypena proboscidalis</i>	1	0	0	0	0	0	0	0	1	0
Noctuidae	<i>Lacanobia oleracea</i>	3	2	0	3	0	0	0	0	0	0
Noctuidae	<i>Lacanobia oleracea</i>	2	1	0	0	0	0	0	1	0	1
Noctuidae	<i>Mesapamea secalis</i> agg.	3	2	3	0	0	0	0	0	0	0
Noctuidae	<i>Mesapamea secalis</i> agg.	5	1	0	1	0	0	1	0	2	1
Noctuidae	<i>Mesapamea secalis</i> agg.	3	0	0	0	1	0	0	2	0	0
Noctuidae	<i>Mesapamea secalis</i> agg.	8	3	0	0	0	8	0	0	0	0
Noctuidae	<i>Mormo maura</i>	1	0	1	0	0	0	0	0	0	0
Noctuidae	<i>Mythimna conigera</i>	4	1	2	0	0	0	0	0	0	2
Noctuidae	<i>Mythimna conigera</i>	2	2	0	0	0	0	0	2	0	0
Noctuidae	<i>Mythimna ferrago</i>	2	1	1	1	0	0	0	0	0	0
Noctuidae	<i>Mythimna ferrago</i>	1	0	0	0	0	0	0	1	0	0
Noctuidae	<i>Mythimna impura</i>	18	7	9	0	0	0	0	0	0	9
Noctuidae	<i>Mythimna impura</i>	8	2	0	4	0	0	0	0	4	0
Noctuidae	<i>Mythimna impura</i>	7	5	0	0	7	0	0	0	0	0
Noctuidae	<i>Mythimna impura</i>	1	1	0	0	0	1	0	0	0	0
Noctuidae	<i>Mythimna impura</i>	2	0	0	0	0	0	1	1	0	0
Noctuidae	<i>Naenia typica</i>	2	1	0	1	0	0	0	1	0	0
Noctuidae	<i>Noctua comes</i>	3	0	0	1	0	0	0	1	1	0
Noctuidae	<i>Noctua comes</i>	5	1	0	0	2	3	0	0	0	0
Noctuidae	<i>Noctua comes</i>	4	4	0	0	0	0	0	0	0	4
Noctuidae	<i>Noctua janthe</i>	1	1	0	1	0	0	0	0	0	0

Noctuidae	<i>Noctua pronuba</i>	16	4	6	0	0	6	0	0	4	0
Noctuidae	<i>Noctua pronuba</i>	15	6	0	7	0	0	0	8	0	0
Noctuidae	<i>Noctua pronuba</i>	15	5	0	0	15	0	0	0	0	0
Noctuidae	<i>Noctua pronuba</i>	5	0	0	0	0	0	5	0	0	0
Noctuidae	<i>Noctua pronuba</i>	4	2	0	0	0	0	0	0	0	4
Noctuidae	<i>Oegoconia spp.</i>	1	0	0	0	0	0	1	0	0	0
Noctuidae	<i>Oligia strigilis agg.</i>	5	1	1	1	0	0	0	0	0	3
Noctuidae	<i>Xestia c-nigrum</i>	4	4	0	0	0	4	0	0	0	0
Noctuidae	<i>Xestia c-nigrum</i>	1	1	0	0	0	0	1	0	0	0
Noctuidae	<i>Xestia c-nigrum</i>	3	2	0	0	0	0	0	0	0	3
Noctuidae	<i>Xestia ditrapezium</i>	1	0	0	1	0	0	0	0	0	0
Noctuidae	<i>Xestia triangulum</i>	1	1	0	0	0	0	0	1	0	0
Noctuidae	<i>xanthographa</i>	1	0	0	0	1	0	0	0	0	0
Noctuidae	<i>Xestia</i>	1	0	0	0	1	0	0	0	0	0
Noctuidae	<i>xanthographa</i>	2	2	0	0	0	0	0	0	0	2
Notodontidae	<i>Pheosia tremula</i>	1	0	0	0	0	1	0	0	0	0
Oecophoridae	<i>Crassa unitella</i>	1	0	0	0	0	0	0	0	0	1
Oecophoridae	<i>Hofmannophila</i>	1	0	0	0	0	0	0	0	0	1
Oecophoridae	<i>pseudospretella</i>	2	0	0	0	0	0	0	1	1	0
Oecophoridae	<i>Emmelina</i>	2	0	0	0	0	0	0	1	1	0
Pterophoridae	<i>monodactyla</i>	1	0	0	0	0	0	0	1	0	0
Pyralidae	<i>Aphomia sociella</i>	1	0	0	0	0	0	0	0	0	1
Pyralidae	<i>Endotricha</i>	1	0	0	0	0	0	0	0	0	1
Pyralidae	<i>flammealis</i>	2	0	0	0	0	0	0	1	0	1
Pyralidae	<i>Xestia</i>	1	0	0	1	0	0	0	0	0	0
Pyralidae	<i>xanthographa</i>	1	0	0	1	0	0	0	0	0	0
Sphingidae	<i>Laothoe populi</i>	1	0	0	0	0	1	0	0	0	0
Tortricidae	<i>Celypha striana</i>	1	0	0	0	1	0	0	0	0	0
Tortricidae	<i>Cydia pomonella</i>	4	1	0	3	0	0	0	0	0	1
Tortricidae	<i>Cydia pomonella</i>	1	0	0	0	0	0	1	0	0	0
Tortricidae	<i>Pandemis</i>	1	0	0	0	0	0	1	0	0	0
Tortricidae	<i>cerasana</i>	2	0	1	0	0	0	0	0	1	0
Yponomeutidae	<i>Yponomeuta spp.</i>	2	0	0	0	0	0	0	0	0	2

Table S3.4: Species list and abundances of bees caught in eight allotments sites in Leeds 2019 (LD1-LD8). All bees carried pollen

Family	Species	LD1	LD2	LD3	LD4	LD5	LD6	LD7	LD8
Andrenidae	<i>Andrena haemorrhoa</i>	0	0	0	0	0	0	1	0
Andrenidae	<i>Andrena minutula</i>	0	2	0	0	0	0	0	0
Andrenidae	<i>Andrena nitida</i>	0	0	0	0	0	0	0	1
Andrenidae	<i>Andrena scotica</i>	0	1	0	0	0	0	0	0
Apidae	<i>Apis mellifera</i>	17	15	25	35	18	20	14	21
Apidae	<i>Bombus hortorum</i>	1	1	2	3	0	0	1	0
Apidae	<i>Bombus hypnorum</i>	3	7	11	3	4	5	6	1
Apidae	<i>Bombus lapidarius</i>	5	3	2	3	0	2	2	2
Apidae	<i>Bombus pascorum</i>	9	15	5	17	7	17	10	14
Apidae	<i>Bombus pratorum</i>	6	3	4	7	3	2	3	13
Apidae	<i>Bombus terrestris</i>	20	14	7	8	8	3	7	8

Apidae	Bombus terrestris	0	0	0	1	0	0	0	0
Apidae	Nomada flava	0	0	0	0	0	2	2	1
Colletidae	Colletes daviesanus	0	0	0	0	0	0	1	0
Colletidae	Hylaeus communis	0	0	0	0	0	0	1	0
Halictidae	Lasioglossum xanthopus	0	0	0	0	0	1	0	1
Halictidae	Lasioglossum cupromicans	0	0	0	0	0	1	0	0
Megachilidae	Megachile centuncularis	0	1	1	1	1	0	0	0
Megachilidae	Osmia bicornis	4	0	5	3	3	1	2	0
Megachilidae	Osmia caerulescens	0	0	0	1	0	0	0	0
Megachilidae	Osmia leaiana	0	1	0	0	0	2	0	0
Megachilidae	Osmia leaniana	1	1	0	0	0	0	0	0

Table S3.5: Species list of plant assignments from pollen loads of bees and moths in urban allotments in Leeds 2019, the primer that identified the plant assignment and the number of insect interactions recorded with the plant across the dataset. Ranked from most interacted with to least interacted with.

Primer	Family	Assignment	Interactions
both	Rosaceae	<i>Rubus</i>	138
its2	Boraginaceae	<i>Borago officinalis</i>	117
both	Urticaceae	<i>Urtica dioica</i>	98
both	Brassicaceae	<i>Brassica oleracea</i>	95
its2	Boraginaceae	<i>Symphytum</i>	91
both	Oleaceae	<i>Ligustrum vulgare</i>	80
both	Boraginaceae	<i>Myosotis arvensis</i>	73
both	Solanaceae	<i>Solanum</i>	68
both	Balsaminaceae	<i>Impatiens</i>	64
its2	Scrophulariaceae	<i>Buddleja</i>	61
its2	Sapindaceae	<i>Acer</i>	58
both	Sapindaceae	<i>Acer campestre</i>	58
its2	Limnanthaceae	<i>Limnanthes douglasii</i>	57
its2	Ranunculaceae	<i>Ranunculus repens</i>	56
both	Brassicaceae	<i>Brassica</i>	55
both	Ericaceae	<i>Vaccinium</i>	54
its2	Asteraceae	<i>Taraxacum</i>	50
both	Ranunculaceae	<i>Aquilegia vulgaris</i>	45
both	Fabaceae	<i>Trifolium</i>	39
both	Amaryllidaceae	<i>Allium</i>	38
both	Malvaceae	<i>Tilia</i>	37
both	Tropaeolaceae	<i>Tropaeolum</i>	36
both	Fabaceae	<i>Vicia</i>	34
its2	Plantaginaceae	<i>Plantago lanceolata</i>	33
its2	Boraginaceae	<i>Pentaglottis sempervirens</i>	30
its2	Plantaginaceae	<i>Linaria repens</i>	30
its2	Apiaceae	<i>Anthriscus sylvestris</i>	29
its2	Rhamnaceae	<i>Ceanothus</i>	29
its2	Malvaceae	<i>Tilia platyphyllos</i>	28
its2	Sapindaceae	<i>Aesculus</i>	28
its2	Adoxaceae	<i>Sambucus nigra</i>	27

its2	Asteraceae	<i>Senecio</i>	27
its2	Onagraceae	<i>Epilobium</i>	27
both	Aquifoliaceae	<i>Ilex aquifolium</i>	26
its2	Brassicaceae	<i>Capsella bursa pastoris</i>	26
both	Fabaceae	<i>Vicia sepium</i>	26
its2	Rosaceae	<i>Geum urbanum</i>	26
both	Rosaceae	<i>Fragaria</i>	26
both	Hypericaceae	<i>Hypericum</i>	25
rbcl	Rhamnaceae	<i>Rhamnus cathartica</i>	25
its2	Asteraceae	<i>Cirsium arvense</i>	23
both	Ranunculaceae	<i>Ranunculus</i>	23
both	Asteraceae	<i>Senecio jacobaea</i>	22
both	Papaveraceae	<i>Papaver rhoeas</i>	22
both	Grossulariaceae	<i>Ribes rubrum</i>	21
its2	Plantaginaceae	<i>Plantago major</i>	21
both	Rosaceae	<i>Prunus</i>	21
its2	Fagaceae	<i>Castanea</i>	20
its2	Grossulariaceae	<i>Ribes</i>	20
both	Lamiaceae	<i>Salvia</i>	20
its2	Papaveraceae	<i>Meconopsis cambrica</i>	20
its2	Rutaceae	<i>Citrus</i>	20
its2	Myrtaceae	<i>Eucalyptus</i>	19
its2	Oleaceae	<i>Fraxinus</i>	19
its2	Papaveraceae	<i>Papaver somniferum</i>	19
its2	Fabaceae	<i>Trifolium repens</i>	18
its2	Sapindaceae	<i>Acer pseudoplatanus</i>	18
its2	Asteraceae	<i>Sonchus</i>	17
both	Rosaceae	<i>Rosa</i>	17
its2	Amaryllidaceae	<i>Allium schoenoprasum</i>	16
both	Betulaceae	<i>Betula</i>	16
rbcl	Boraginaceae	<i>Symphytum officinale</i>	16
its2	Brassicaceae	<i>Diplotaxis tenuifolia</i>	15
its2	Brassicaceae	<i>Erysimum cheiri</i>	15
its2	Hydrangeaceae	<i>Hydrangea</i>	15
its2	Plantaginaceae	<i>Veronica chamaedrys</i>	15
both	Araliaceae	<i>Hedera helix</i>	13
its2	Asteraceae	<i>Bellis perennis</i>	13
its2	Asteraceae	<i>Helianthus</i>	13
its2	Asteraceae	<i>Lapsana communis</i>	12
its2	Fagaceae	<i>Quercus</i>	12
its2	Lamiaceae	<i>Salvia rosmarinus</i>	12
both	Plantaginaceae	<i>Veronica agrestis</i>	12
its2	Ranunculaceae	<i>Clematis</i>	12
both	Rosaceae	<i>Sorbus</i>	12
both	Salicaceae	<i>Salix</i>	12
its2	Convolvulaceae	<i>Calystegia silvatica</i>	11
both	Hydrangeaceae	<i>Philadelphus</i>	11
rbcl	Lamiaceae	<i>Lamium album</i>	11
both	Plantaginaceae	<i>Linaria</i>	11

its2	Solanaceae	<i>Solanum tuberosum</i>	11
its2	Chenopodiaceae	<i>Beta</i>	10
both	Geraniaceae	<i>Geranium</i>	10
rbcl	Hyacinthaceae	<i>Hyacinthoides non scripta</i>	10
both	Lamiaceae	<i>Lamium</i>	10
both	Onagraceae	<i>Chamaenerion angustifolium</i>	10
rbcl	Plantaginaceae	<i>Veronica</i>	10
rbcl	Ranunculaceae	<i>Clematis vitalba</i>	10
its2	Ranunculaceae	<i>Aquilegia</i>	10
its2	Asteraceae	<i>Centaurea montana</i>	9
its2	Brassicaceae	<i>Alliaria petiolata</i>	9
its2	Brassicaceae	<i>Sisymbrium officinale</i>	8
its2	Fagaceae	<i>Fagus sylvatica</i>	8
its2	Lamiaceae	<i>Lavandula</i>	8
rbcl	Onagraceae	<i>Fuchsia</i>	8
both	Plantaginaceae	<i>Digitalis purpurea</i>	8
rbcl	Polygonaceae	<i>Rumex</i>	8
rbcl	Ranunculaceae	<i>Thalictrum</i>	8
its2	Ranunculaceae	<i>Ranunculus acris</i>	8
its2	Adoxaceae	<i>Sambucus</i>	7
rbcl	Caprifoliaceae	<i>Lonicera periclymenum</i>	7
its2	Hydrophyllaceae	<i>Phacelia tanacetifolia</i>	7
both	Hypericaceae	<i>Hypericum androsaemum</i>	7
rbcl	Rosaceae	<i>Rosoideae incertae sedis</i>	7
both	Adoxaceae	<i>Viburnum</i>	6
its2	Apiaceae	<i>Aethusa cynapium</i>	6
its2	Asteraceae	<i>Artemisia</i>	6
its2	Asteraceae	<i>Calendula</i>	6
its2	Asteraceae	<i>Calendula officinalis</i>	6
its2	Asteraceae	<i>Hypochaeris</i>	6
rbcl	Brassicaceae	<i>Brassica sp 3 KS 2019</i>	6
its2	Caryophyllaceae	<i>Stellaria</i>	6
its2	Fabaceae	<i>Trifolium pratense</i>	6
both	Hydrangeaceae	<i>Deutzia</i>	6
rbcl	Plantaginaceae	<i>Plantago</i>	6
both	Ranunculaceae	<i>Anemone</i>	6
both	Rosaceae	<i>Prunus padus</i>	6
its2	Rosaceae	<i>Prunus avium</i>	6
its2	Solanaceae	<i>Capsicum</i>	6
both	Apiaceae	<i>Astrantia major</i>	5
its2	Apiaceae	<i>Heracleum</i>	5
its2	Asteraceae	<i>Tanacetum</i>	5
both	Asteraceae	<i>Cirsium</i>	5
its2	Betulaceae	<i>Alnus</i>	5
its2	Boraginaceae	<i>Echium plantagineum</i>	5
its2	Boraginaceae	<i>Glandora prostrata</i>	5
its2	Brassicaceae	<i>Aubrieta</i>	5
both	Campanulaceae	<i>Lobelia erinus</i>	5
its2	Caprifoliaceae	<i>Centranthus</i>	5

both	Chenopodiaceae	<i>Atriplex</i>	5
its2	Chenopodiaceae	<i>Chenopodium album</i>	5
both	Ericaceae	<i>Calluna vulgaris</i>	5
rbcl	Fabaceae	<i>Lathyrus</i>	5
its2	Juglandaceae	<i>Juglans</i>	5
both	Malvaceae	<i>Malva</i>	5
its2	Plantaginaceae	<i>Antirrhinum</i>	5
its2	Polygonaceae	<i>Rumex acetosa</i>	5
both	Ranunculaceae	<i>Anemone nemorosa</i>	5
rbcl	Rosaceae	<i>Rosaceae sp KS 2019</i>	5
rbcl	Rubiaceae	<i>Galium</i>	5
its2	Rubiaceae	<i>Galium aparine</i>	5
its2	Amaryllidaceae	<i>Allium scorodoprasum</i>	4
its2	Asteraceae	<i>Achillea</i>	4
its2	Asteraceae	<i>Matricaria</i>	4
its2	Asteraceae	<i>Centaurea nigra</i>	4
its2	Boraginaceae	<i>Cerithe major</i>	4
its2	Brassicaceae	<i>Sisymbrium orientale</i>	4
both	Cornaceae	<i>Cornus sanguinea</i>	4
its2	Cucurbitaceae	<i>Cucurbita</i>	4
rbcl	Lamiaceae	<i>Stachys</i>	4
its2	Plantaginaceae	<i>Cymbalaria</i>	4
rbcl	Rosaceae	<i>Dryas octopetala</i>	4
rbcl	Rosaceae	<i>Rubus hispidus</i>	4
both	Rosaceae	<i>Potentilla</i>	4
its2	Rosaceae	<i>Spiraea japonica</i>	4
its2	Scrophulariaceae	<i>Buddleja lindleyana</i>	4
its2	Ulmaceae	<i>Ulmus</i>	4
its2	Asteraceae	<i>Leucanthemum vulgare</i>	3
its2	Asteraceae	<i>Centaurea</i>	3
its2	Asteraceae	<i>Crepis vesicaria</i>	3
its2	Betulaceae	<i>Corylus avellana</i>	3
its2	Boraginaceae	<i>Symphytum asperum</i>	3
its2	Brassicaceae	<i>Brassica rapa</i>	3
its2	Brassicaceae	<i>Barbarea vulgaris</i>	3
rbcl	Brassicaceae	<i>Brassicaceae sp KS 2019</i>	3
its2	Cucurbitaceae	<i>Cucumis</i>	3
both	Ericaceae	<i>Rhododendron</i>	3
its2	Ericaceae	<i>Vaccinium myrtillus</i>	3
both	Fabaceae	<i>Vicia hirsuta</i>	3
its2	Fabaceae	<i>Vicia sativa</i>	3
rbcl	Fabaceae	<i>Lotus corniculatus</i>	3
its2	Fabaceae	<i>Phaseolus</i>	3
its2	Hydrangeaceae	<i>Deutzia gracilis</i>	3
its2	Hypericaceae	<i>Hypericum calycinum</i>	3
both	Papaveraceae	<i>Papaver</i>	3
rbcl	Polygonaceae	<i>Fallopia</i>	3
its2	Rosaceae	<i>Sorbus torminalis</i>	3
its2	Rosaceae	<i>Filipendula ulmaria</i>	3

its2	Saxifragaceae	<i>Tellima grandiflora</i>	3
its2	Solanaceae	<i>Solanum lycopersicum</i>	3
rbcl	Urticaceae	<i>Urtica</i>	3
rbcl	Adoxaceae	<i>Viburnum opulus</i>	2
its2	Amaryllidaceae	<i>Allium ursinum</i>	2
its2	Apiaceae	<i>Levisticum officinale</i>	2
its2	Apiaceae	<i>Meum athamanticum</i>	2
both	Asparagaceae	<i>Asparagus officinalis</i>	2
its2	Asteraceae	<i>Symphyotrichum</i>	2
its2	Asteraceae	<i>Cirsium vulgare</i>	2
both	Asteraceae	<i>Crepis</i>	2
its2	Asteraceae	<i>Pilosella flagellaris</i>	2
its2	Asteraceae	<i>Scorzoneroides autumnalis</i>	2
rbcl	Asteraceae	<i>Crepis capillaris</i>	2
rbcl	Asteraceae	<i>Hypochaeris glabra</i>	2
its2	Asteraceae	<i>Dahlia</i>	2
its2	Asteraceae	<i>Cosmos bipinnatus</i>	2
its2	Asteraceae	<i>Galinsoga</i>	2
its2	Asteraceae	<i>Galinsoga parviflora</i>	2
both	Asteraceae	<i>Jacobaea</i>	2
its2	Asteraceae	<i>Senecio aquaticus</i>	2
its2	Brassicaceae	<i>Arabidopsis thaliana</i>	2
its2	Brassicaceae	<i>Cardamine hirsuta</i>	2
its2	Brassicaceae	<i>Erysimum</i>	2
both	Campanulaceae	<i>Campanula</i>	2
rbcl	Campanulaceae	<i>Lobelia</i>	2
its2	Caprifoliaceae	<i>Symphoricarpos</i>	2
its2	Caprifoliaceae	<i>Centranthus lecoqii</i>	2
rbcl	Caprifoliaceae	<i>Centranthus ruber</i>	2
its2	Caryophyllaceae	<i>Stellaria holostea</i>	2
rbcl	Caryophyllaceae	<i>Silene</i>	2
rbcl	Cistaceae	<i>Helianthemum nummularium</i>	2
its2	Crassulaceae	<i>Hylotelephium</i>	2
rbcl	Cucurbitaceae	<i>Cucurbita pepo</i>	2
its2	Fagaceae	<i>Castanea crenata</i>	2
its2	Hypericaceae	<i>Hypericum hircinum</i>	2
rbcl	Iridaceae	<i>Iris</i>	2
its2	Lamiaceae	<i>Lamium purpureum</i>	2
its2	Lamiaceae	<i>Melissa officinalis</i>	2
its2	Lamiaceae	<i>Origanum vulgare</i>	2
its2	Malvaceae	<i>Althaea officinalis</i>	2
its2	Myrtaceae	<i>Callistemon citrinus</i>	2
its2	Platanaceae	<i>Plantanus</i>	2
both	Oxalidaceae	<i>Oxalis</i>	2
rbcl	Paeoniaceae	<i>Paeonia</i>	2
its2	Paeoniaceae	<i>Paeonia veitchii</i>	2
rbcl	Papaveraceae	<i>Chelidonium majus</i>	2
rbcl	Papaveraceae	<i>Glaucium flavum</i>	2
its2	Plantaginaceae	<i>Veronica fruticans</i>	2

rbcl	Plantaginaceae	<i>Veronica subgen Pseudoveronica</i>	2
its2	Ranunculaceae	<i>Ranunculus bulbosus</i>	2
its2	Resedaceae	<i>Reseda luteola</i>	2
its2	Rosaceae	<i>Chaenomeles speciosa</i>	2
rbcl	Rosaceae	<i>Malus sylvestris</i>	2
its2	Rutaceae	<i>Balfourodendron riedelianum</i>	2
its2	Salicaceae	<i>Salix alba</i>	2
its2	Scrophulariaceae	<i>Nemesia</i>	2
its2	Scrophulariaceae	<i>Verbascum thapsus</i>	2
its2	Solanaceae	<i>Lycium</i>	2
its2	Solanaceae	<i>Petunia</i>	2
its2	Solanaceae	<i>Solanum crispum</i>	2
its2	Verbenaceae	<i>Verbena officinalis</i>	2
its2	Adoxaceae	<i>Viburnum plicatum</i>	1
both	Amaranthaceae	<i>Amaranthus</i>	1
its2	Amaryllidaceae	<i>Allium rosenorum</i>	1
its2	Apiaceae	<i>Foeniculum vulgare</i>	1
its2	Apiaceae	<i>Apium graveolens</i>	1
its2	Apiaceae	<i>Aegopodium podagraria</i>	1
its2	Apiaceae	<i>Conium maculatum</i>	1
its2	Apiaceae	<i>Chaerophyllum temulum</i>	1
its2	Asteraceae	<i>Tripleurospermum maritimum</i>	1
its2	Asteraceae	<i>Symphotrichum novae angliae</i>	1
its2	Asteraceae	<i>Calendula arvensis</i>	1
its2	Asteraceae	<i>Arctium</i>	1
its2	Asteraceae	<i>Centaurea mollis</i>	1
its2	Asteraceae	<i>Centaurea scabiosa</i>	1
its2	Asteraceae	<i>Cynara cardunculus</i>	1
its2	Asteraceae	<i>Pilosella</i>	1
its2	Asteraceae	<i>Helminthotheca echioides</i>	1
its2	Asteraceae	<i>Rudbeckia hirta</i>	1
its2	Asteraceae	<i>Telekia speciosa</i>	1
both	Begoniaceae	<i>Begonia</i>	1
rbcl	Boraginaceae	<i>Mertensia maritima</i>	1
its2	Boraginaceae	<i>Pontechium maculatum</i>	1
its2	Brassicaceae	<i>Erophila verna</i>	1
its2	Brassicaceae	<i>Lunaria annua</i>	1
its2	Brassicaceae	<i>Diplotaxis erucooides</i>	1
its2	Brassicaceae	<i>Rapistrum rugosum</i>	1
its2	Brassicaceae	<i>Iberis amara</i>	1
rbcl	Brassicaceae	<i>Lepidium</i>	1
both	Caprifoliaceae	<i>Linnaea</i>	1
its2	Caprifoliaceae	<i>Dipsacus fullonum</i>	1
its2	Caprifoliaceae	<i>Symphoricarpos albus</i>	1
its2	Caryophyllaceae	<i>Silene dioica</i>	1
its2	Caryophyllaceae	<i>Silene flos cuculi</i>	1
its2	Caryophyllaceae	<i>Silene pendula</i>	1
its2	Caryophyllaceae	<i>Silene subgen Behenantha</i>	1
its2	Convolvulaceae	<i>Merremia</i>	1

its2	Crassulaceae	<i>Phedimus spurius</i>	1
its2	Cucurbitaceae	<i>Cucurbita ficifolia</i>	1
its2	Ericaceae	<i>Erica arborea</i>	1
its2	Euphorbiaceae	<i>Euphorbia amygdaloides</i>	1
rbcl	Fabaceae	<i>Lathyrus sylvestris</i>	1
its2	Fabaceae	<i>Galega officinalis</i>	1
rbcl	Fabaceae	<i>Lotus</i>	1
rbcl	Fabaceae	<i>Fabaceae sp KS 2019</i>	1
its2	Fabaceae	<i>Glycine</i>	1
its2	Fabaceae	<i>Melilotus altissimus</i>	1
its2	Fagaceae	<i>Quercus petraea</i>	1
its2	Geraniaceae	<i>Geranium dissectum</i>	1
its2	Hydrangeaceae	<i>Philadelphus mexicanus</i>	1
rbcl	Iridaceae	<i>Gladiolus</i>	1
both	Lamiaceae	<i>Ajuga reptans</i>	1
both	Lamiaceae	<i>Teucrium</i>	1
its2	Malvaceae	<i>Gossypium</i>	1
its2	Malvaceae	<i>Malva moschata</i>	1
its2	Oleaceae	<i>Fraxinus ornus</i>	1
its2	Pedaliaceae	<i>Sesamum indicum</i>	1
its2	Plantaginaceae	<i>Linaria alpina</i>	1
its2	Plantaginaceae	<i>Veronica sect Hebe</i>	1
its2	Polemoniaceae	<i>Polemonium</i>	1
rbcl	Polygonaceae	<i>Bistorta</i>	1
its2	Polygonaceae	<i>Rheum</i>	1
its2	Ranunculaceae	<i>Actaea simplex</i>	1
its2	Ranunculaceae	<i>Aconitum</i>	1
its2	Ranunculaceae	<i>Aconitum napellus</i>	1
its2	Ranunculaceae	<i>Ranunculus verna</i>	1
its2	Ranunculaceae	<i>Ranunculus sardous</i>	1
its2	Rosaceae	<i>Chaenomeles</i>	1
its2	Rosaceae	<i>Crataegus</i>	1
its2	Rosaceae	<i>Malus</i>	1
its2	Rosaceae	<i>Chaenomeles japonica</i>	1
its2	Rubiaceae	<i>Spermacoce</i>	1
both	Salicaceae	<i>Populus</i>	1
its2	Saxifragaceae	<i>Bergenia</i>	1
its2	Saxifragaceae	<i>Heuchera</i>	1
its2	Solanaceae	<i>Petunia axillaris</i>	1
its2	Solanaceae	<i>Solanum tubersum cultivar 1</i>	1
its2	Solanaceae	<i>Solanum tubersum cultivar 2</i>	1
its2	Solanaceae	<i>Solanum tubersum cultivar 3</i>	1
its2	Solanaceae	<i>Solanum tubersum cultivar 4</i>	1
its2	Solanaceae	<i>Solanum tubersum cultivar 5</i>	1
its2	Solanaceae	<i>Solanum lyratum</i>	1
its2	Solanaceae	<i>Solanum nigrum</i>	1
its2	Thymelaeaceae	<i>Daphne laureola</i>	1
its2	Tropaeolaceae	<i>Tropaeolum majus</i>	1
its2	Verbenaceae	<i>Verbena rigida</i>	1

Table S3.6: The top 6 plants that bees interacted with in eight allotments in Leeds, based on analysis of their pollen load (aggregated across eight sites and three sampling points of early, mid and late summer).

Plant species	Total visits
<i>Rubus</i>	96
<i>Symphytum</i>	80
<i>Borago officinalis</i>	80
<i>Myosotis arvensis</i>	65
<i>Brassica oleracea</i>	63
<i>Urtica dioica</i>	57

Table S3.7: The top 6 plants that moths interacted with in eight allotments in Leeds, based on analysis of their pollen load (aggregated across eight sites and three sampling points of early, mid and late summer).

Plant species	Total visits
<i>Buddleja</i>	53
<i>Solanum</i>	51
<i>Ligustrum vulgare</i>	47
<i>Rubus</i>	42
<i>Urtica dioica</i>	41
<i>Borago officinalis</i>	37

Table S3.8: Contrast of linear model: Number of plant species visited by insects ~ (Insect group * Time) + (Insect group * Plant type). Showing that bees foraged more frequently on non-woody flowering vegetation whereas moths foraged on woody and non-wood vegetation equally.

Insect:	Model term	df1	df2	F ratio	p value
Bee	Plant type (non-woody flowering)	1	82	85.7	<0.0001
	Time	2	82	100.85	<0.0001
Moth	Plant type (non-woody flowering)	1	82	0.02	0.895
	Time	2	82	17.81	<.0001

Table S3.9: Contrast of generalised linear mixed effect models comparing the species richness, abundance of bees and moths across the season (model 1 and model 2). The foraging patterns of bees and moths are then compared by testing the total number of plant species richness (found in their pollen loads) and the total number of plant species richness found on each insect species (model 3 and model 4).

Model 1:
 Dependent variable: Insect species richness
 Random effects: Site
 Type: Generalised linear mixed effect model
 Family: poisson

Contrasts:

Time:	Model term	df1	df2	F ratio	p value
Early summer	Insect type	1	Inf	23.525	1.23E-06
Mid summer	Insect type	1	Inf	51.587	6.85E-13
Late summer	Insect type	1	Inf	2.825	0.09

Model 3:
 Dependent variable: Total plant species richness
 Random effects: Site
 Type: Linear mixed effect model
 Family: gaussian

Contrasts:

Time:	Model term	df1	df2	F ratio	p value
Early summer	Insect type	1	35	149.619	3.40E-14
Mid summer	Insect type	1	35	4.561	0.04
Late summer	Insect type	1	35	5.943	0.02

Model 2:
 Dependent variable: Insect abundance
 Random effects: Site
 Type: Generalised linear mixed effect model
 Family: poisson

Contrasts:

Time:	Model term	df1	df2	F ratio	p value
Early summer	Insect type	1	Inf	106.437	5.91E-25
Mid summer	Insect type	1	Inf	77.825	1.13E-18
Late summer	Insect type	1	Inf	8.093	0.004

Model 4:
 Dependent variable: No. of plants species per insect species
 Random effects: Site
 Type: Linear mixed effect model
 Family: gaussian

Contrasts:

Time:	Model term	df1	df2	F ratio	p value
Early summer	Insect type	1	35	71.037	6.08E-10
Mid summer	Insect type	1	35	21.265	5.16E-05
Late summer	Insect type	1	35	6.085	0.02

Table S3.10: Model summaries testing the network structural differences of bee and moth pollen-transport networks. Eight pairs (each pair containing moth and bee data) of networks (pooled by site).

Model: Testing the effects of insect type (bees or moths) on the nestedness of the networks

Dependent variable: Nestedness

Independent variable: Insect type (bees vs moths)

Type: Linear model

Family: gaussian

Summary table (Anova type II)

Coefficients	Estimate	Std. Error	t value	p value
Intercept	30.71	2.253	13.056	3.15E-09
Insect type (moth)	-3.254	3.327	-0.978	3.45E-01

Residuals:619.86 on 14 degrees of freedom

Model: Testing the effects of insect type (bees or moths) on the insect niche overlap of the networks

Dependent variable: Niche overlap of insects

Independent variable: Insect type (bees vs moths)

Type: Generalized Linear model

Family: quasipoisson

Summary table (Anova type II)

Coefficients	Estimate	Std. Error	t value	p value
Intercept	-1.1	0.073	-15.064	4.81E-10
Insect type (moth)	-0.22	0.109	-2.038	0.061

Residuals:0.205 on 14 degrees of freedom

Model 5: Testing the effects of insect type (bees or moths) on the robustness (lower level) of the networks

Dependent variable: Robustness of plants

Independent variable: Insect type (bees vs moths)

Type: Generalized Linear model

Family: quasipoisson

Summary table (Anova type II)

Coefficients	Estimate	Std. Error	t value	p value
Intercept	-0.043	0.009	-4.77	2.97E-04
Insect type (moth)	-0.073	0.013	-5.624	6.27E-05

Residuals:0.0089 on 14 degrees of freedom

Model: Testing the effects of insect type (bees or moths) on the linkage density of the networks

Dependent variable: Linkage density

Independent variable: Insect type (bees vs moths)

Type: Linear model

Family: gaussian

Summary table (Anova type II)

Coefficients	Estimate	Std. Error	t value	p value
Intercept	19.96	0.687	29.06	6.48E-14
Insect type (moth)	-12.05	0.972	-12.4	6.12E-09

Residuals:52.869 on 14 degrees of freedom

Model: Testing the effects of insect type (bees or moths) on the robustness (higher level) of the networks

Dependent variable: Robustness of insects

Independent variable: Insect type (bees vs moths)

Type: Generalized Linear model

Family: quasipoisson

Summary table (Anova type II)

Coefficients	Estimate	Std. Error	t value	p value
Intercept	-0.44	0.016	-27.07	1.72E-13
Insect type (moth)	-0.029	0.023	-1.26	0.228

Residuals:0.019 on 14 degrees of freedom

Table S11: Model summaries testing the effect of urbanisation (models: 1,2,3 and 5) and cultivation (percentage of disused plots; model 4) on the total number of plant species richness visited by bees and moths in urban allotments across the season.

Model 1: Testing the effects of urbanisation (scale = 250m) on the plant species richness visited by bees and moths across the season
 Dependent variable: Total plant species richness
 Type: Linear model
 Family: gaussian

Coefficients	Estimate	Std. Error	t value	p value
Intercept	100.09	10.24	9.77	<0.00001
Urbanisation (250m)	-0.38	0.15	-2.53	0.02
Site size	-1.59E-04	3.76E-04	-0.42	0.67
Insect (moth)	-70.88	6.21	-11.41	<0.00001
Mid summer	-25.63	6.21	-4.13	1.82E-04
Late summer	-52.25	6.21	-8.41	<0.00001
Insect (moth): Mid summer	58.50	8.78	6.66	1.00E-07
Insect (moth): Late summer	56.75	8.78	6.46	1.00E-07

Model 2: Testing the effects of urbanisation (scale = 500m) on the plant species richness visited by bees and moths across the season
 Dependent variable: Total plant species richness
 Type: Linear model
 Family: gaussian

Coefficients	Estimate	Std. Error	t value	p value
Intercept	95.57	9.57	9.98	<0.00001
Urbanisation (500m)	-0.36	0.16	-2.24	0.03
Site size	-2.87E-04	3.96E-04	-0.72	0.47
Insect (moth)	-70.88	6.31	-11.24	<0.00001
Mid summer	-25.63	6.31	-4.06	2.20E-04
Late summer	-52.25	6.31	-8.28	<0.00001
Insect (moth): Mid summer	58.50	8.92	6.56	1.00E-07
Insect (moth): Late summer	56.75	8.92	6.36	1.00E-07

Model 3: Testing the effects of urbanisation (scale = 1000m) on the plant species richness visited by bees and moths across the season
 Dependent variable: Total plant species richness
 Type: Linear model
 Family: gaussian

Coefficients	Estimate	Std. Error	t value	p value
Intercept	86.017	9.009	9.548	<0.00001
Urbanisation (1000m)	-0.132	0.126	-1.046	0.302
Site size	-1.09E-04	4.04E-04	-0.270	0.789
Insect (moth)	-70.875	6.600	-10.738	<0.00001
Mid summer	-25.625	6.600	-3.883	3.78E-04
Late summer	-52.250	6.600	-7.917	<0.00001
Insect (moth): Mid summer	58.500	9.334	6.267	2.00E-07
Insect (moth): Late summer	56.750	9.334	6.080	4.00E-07

Model 4: Testing the effects of cultivation (percent of disused plots) on the plant species richness visited by bees and moths across the season
 Dependent variable: Total plant species richness
 Type: Linear model
 Family: gaussian

Coefficients	Estimate	Std. Error	t value	p value
Intercept	86.67	7.36	11.77	<0.00001
Cultivation	-0.41	0.20	-2.03	0.05
Site size	-1.84E-04	3.90E-04	-0.47	0.64
Insect (moth)	-70.88	6.37	-11.13	<0.00001
Mid summer	-25.63	6.37	-4.02	2.48E-04
Late summer	-52.25	6.37	-8.20	<0.00001
Insect (moth): Mid summer	58.50	9.01	6.50	1.00E-07
Insect (moth): Late summer	56.75	9.01	6.30	2.00E-07

Model 5: Testing the effects of urbanisation (distance from the city centre (km) on the plant species richness visited by bees and moths across the season
 Dependent variable: Total plant species richness
 Type: Linear model
 Family: gaussian

Coefficients	Estimate	Std. Error	t value	p value
Intercept	70.91	7.37	9.62	<0.00001
Distance from city centre (km)	1.20	0.49	2.44	0.02
Site size	0.00	0.00	0.34	0.74
Insect (moth)	-70.88	6.24	-11.36	<0.00001
Mid summer	-25.63	6.24	-4.11	1.93E-04
Late summer	-52.25	6.24	-8.37	<0.00001
Insect (moth): Mid summer	58.50	8.82	6.63	1.00E-07
Insect (moth): Late summer	56.75	8.82	6.43	1.00E-07

Table S3.12: Model summaries testing the effect of urbanisation (models: 1,2,3 + 5) and cultivation (percentage of disused plots) on insect species richness of bees and moths in urban allotments across the season.

Model 1: Testing the effects of urbanisation (scale = 250m) on the insect species richness of bees and moths across the season
 Dependent variable: Insect species richness
 Type: Generalized linear model
 Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	2.62	0.30	8.67	<0.00001
Urbanisation (250m)	-0.01	0.00	-1.80	0.08
Site size	-6.80E-06	1.14E-05	-0.60	0.56
Insect (moth)	-1.26	0.24	-5.17	6.80E-06
Mid summer	-0.62	0.19	-3.21	2.64E-03
Late summer	-1.26	0.24	-5.17	6.80E-06
Insect (moth): Mid summer	2.60	0.30	8.67	<0.00001
Insect (moth): Late summer	1.75	0.37	4.78	2.37E-05

Model 2: Testing the effects of urbanisation (scale = 500m) on the insect species richness of bees and moths across the season
 Dependent variable: Insect species richness
 Type: Generalized linear model
 Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	2.51	0.27	9.23	<0.00001
Urbanisation (500m)	-0.01	0.00	-1.62	0.11
Site size	-9.50E-06	1.18E-05	-0.80	0.43
Insect (moth)	-1.26	0.25	-5.13	7.80E-06
Mid summer	-0.62	0.20	-3.18	2.83E-03
Late summer	-1.26	0.25	-5.13	7.80E-06
Insect (moth): Mid summer	2.60	0.30	8.61	<0.00001
Insect (moth): Late summer	1.75	0.37	4.74	2.67E-05

Model 3: Testing the effects of urbanisation (scale = 1000m) on the insect species richness of bees and moths across the season
 Dependent variable: Insect species richness
 Type: Generalized linear model
 Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	2.261	0.252	8.972	<0.00001
Urbanisation (1000m)	-0.002	0.004	-0.502	0.618
Site size	-5.20E-06	1.18E-05	-0.436	0.665
Insect (moth)	-1.260	0.254	-4.969	1.31E-05
Mid summer	-0.621	0.202	-3.081	3.73E-03
Late summer	-1.260	0.254	-4.969	1.31E-05
Insect (moth): Mid summer	2.604	0.313	8.333	<0.00001
Insect (moth): Late summer	1.750	0.381	4.593	4.29E-05

Model 4: Testing the effects of cultivation (percent of disused plots) on the insect species richness of bees and moths across the season
 Dependent variable: Insect species richness
 Type: Generalized linear model
 Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	2.18	0.21	10.24	<0.00001
Cultivation	-0.00009	0.01	-0.01	0.99
Site size	-4.00E-06	1.19E-05	-0.34	0.74
Insect (moth)	-1.26	0.25	-4.95	1.39E-05
Mid summer	-0.62	0.20	-3.07	3.86E-03
Late summer	-1.26	0.25	-4.95	1.39E-05
Insect (moth): Mid summer	2.60	0.31	8.30	<0.00001
Insect (moth): Late summer	1.75	0.38	4.57	4.55E-05

Model 5: Testing the effects of urbanisation (distance from the city centre (km)) on the insect species richness of bees and moths across the season
 Dependent variable: Insect species richness
 Type: Generalized linear model
 Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	2.02	0.22	9.27	<0.00001
Distance from city centre (km)	0.02	0.01	1.40	0.17
Site size	0.0000011	0.00001	-0.10	0.92
Insect (moth)	-1.26	0.25	-5.06	9.90E-06
Mid summer	-0.62	0.20	-3.14	3.21E-03
Late summer	-1.26	0.25	-5.06	9.90E-06
Insect (moth): Mid summer	2.60	0.31	8.48	<0.00001
Insect (moth): Late summer	1.75	0.37	4.67	3.32E-05

Table S3.13: Model summaries testing the effect of urbanisation (models: 1,2,3 and 5) and cultivation (percentage of disused plots, model 4) on insect abundance of bees and moths in urban allotments across the season.

Model 1: Testing the effects of urbanisation (scale = 250m) on the insect abundance of bees and moths across the season

Dependent variable: Insect abundance

Type: Generalized linear model

Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	3.42	0.30	11.57	<0.00001
Urbanisation (250m)	0.00	0.00	-0.47	0.64
Site size	-4.00E-07	1.12E-05	-0.03	0.97
Insect (moth)	-2.26	0.35	-6.40	1.00E-07
Mid summer	-0.40	0.17	-2.32	2.57E-02
Late summer	-0.72	0.19	-3.80	4.83E-04
Insect (moth): Mid summer	3.12	0.39	8.08	<0.00001
Insect (moth): Late summer	1.82	0.43	4.22	1.37E-04

Model 2: Testing the effects of urbanisation (scale = 500m) on the insect abundance of bees and moths across the season

Dependent variable: Insect abundance

Type: Generalized linear model

Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	3.32	0.27	12.29	<0.00001
Urbanisation (500m)	0.00	0.00	-0.07	0.95
Site size	1.00E-07	1.16E-05	0.01	0.99
Insect (moth)	-2.26	0.35	-6.39	1.00E-07
Mid summer	-0.40	0.17	-2.31	2.61E-02
Late summer	-0.72	0.19	-3.79	4.98E-04
Insect (moth): Mid summer	3.12	0.39	8.06	<0.00001
Insect (moth): Late summer	1.82	0.43	4.21	1.43E-04

Model 3: Testing the effects of urbanisation (scale = 1000m) on the insect abundance of bees and moths across the season

Dependent variable: Insect abundance

Type: Generalized linear model

Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	3.206	0.242	13.234	<0.00001
Urbanisation (1000m)	0.002	0.003	0.624	0.536
Site size	1.80E-06	1.13E-05	0.157	0.876
Insect (moth)	-2.258	0.352	-6.412	1.00E-07
Mid summer	-0.396	0.171	-2.320	2.55E-02
Late summer	-0.721	0.189	-3.805	4.76E-04
Insect (moth): Mid summer	3.122	0.386	8.091	<0.00001
Insect (moth): Late summer	1.819	0.431	4.223	1.35E-04

Model 4: Testing the effects of cultivation (percent of disused plots) on the insect abundance of bees and moths across the season

Dependent variable: Insect abundance

Type: Generalized linear model

Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	3.29	0.20	16.34	<0.00001
Cultivation	0.00139	0.01	0.24	0.81
Site size	9.00E-07	1.13E-05	0.08	0.94
Insect (moth)	-2.26	0.35	-6.39	1.00E-07
Mid summer	-0.40	0.17	-2.31	2.59E-02
Late summer	-0.72	0.19	-3.79	4.92E-04
Insect (moth): Mid summer	3.12	0.39	8.07	<0.00001
Insect (moth): Late summer	1.82	0.43	4.21	1.40E-04

Model 5: Testing the effects of urbanisation (distance from the city centre (km)) on the insect abundance of bees and moths across the season)

Dependent variable: Insect abundance

Type: Generalized linear model

Family: quasipoisson

Coefficients	Estimate	Std. Error	t value	p value
Intercept	3.33	0.21	16.19	<0.00001
Distance from city centre (km)	0.00	0.01	-0.15	0.89
Site size	1.00E-07	0.00001	0.01	0.99
Insect (moth)	-2.26	0.35	-6.39	1.00E-07
Mid summer	-0.40	0.17	-2.31	2.61E-02
Late summer	-0.72	0.19	-3.79	4.97E-04
Insect (moth): Mid summer	3.12	0.39	8.06	<0.00001
Insect (moth): Late summer	1.82	0.43	4.21	1.42E-04

Table S3.14: Plant species list of common ‘weedy’ plants visited by moths and bees in the pollen-transport network analysis in allotments.

Common name	Scientific name
Field forget-me-nots	<i>Myosotis arvensis</i>
Creeping buttercup	<i>Ranunculus reopens</i>
Stinging nettles	<i>Urtica dioica</i>
Dandelions	<i>Taraxacum</i> spp.
Daisy	<i>Bellis perennis</i>
Ragwort	<i>Jacobaea</i> spp.
Clover	<i>Trifolium</i>

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Supplementary Material Chapter 4:

Supplementary Figures S4:

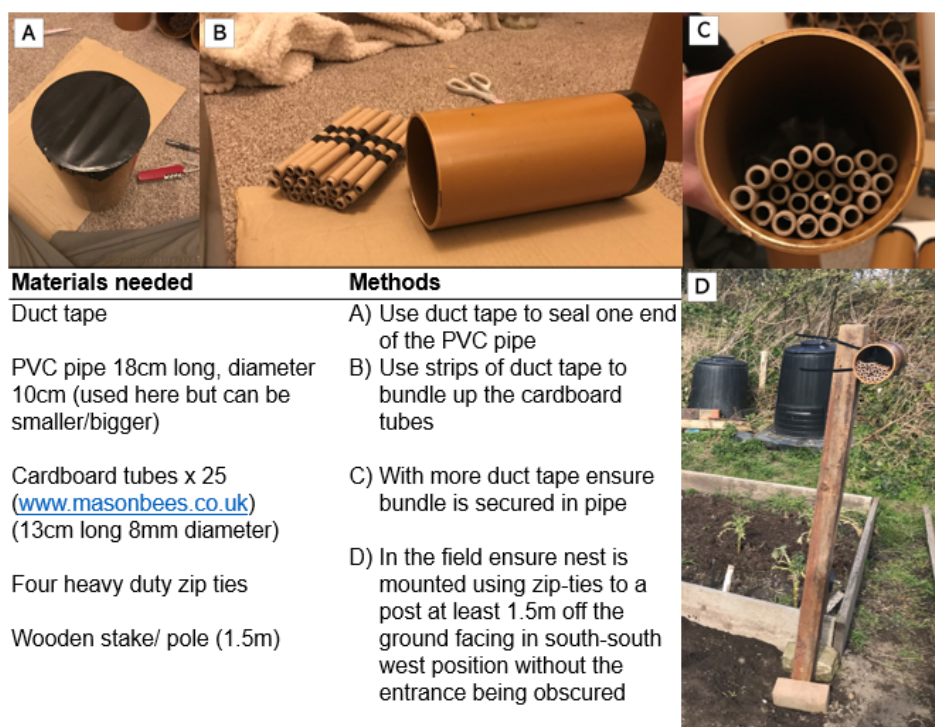


Figure S4. 1 Materials and methods for creating trap nest with cardboard tubing.

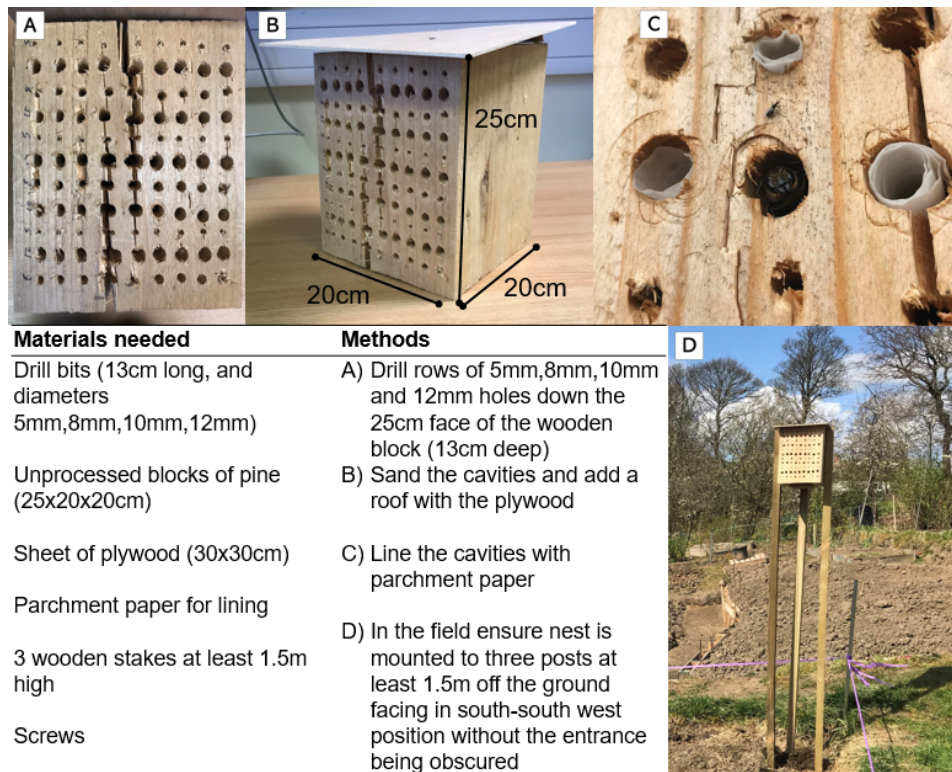


Figure S4. 2 Materials and methods for creating trap nest from wooden block.

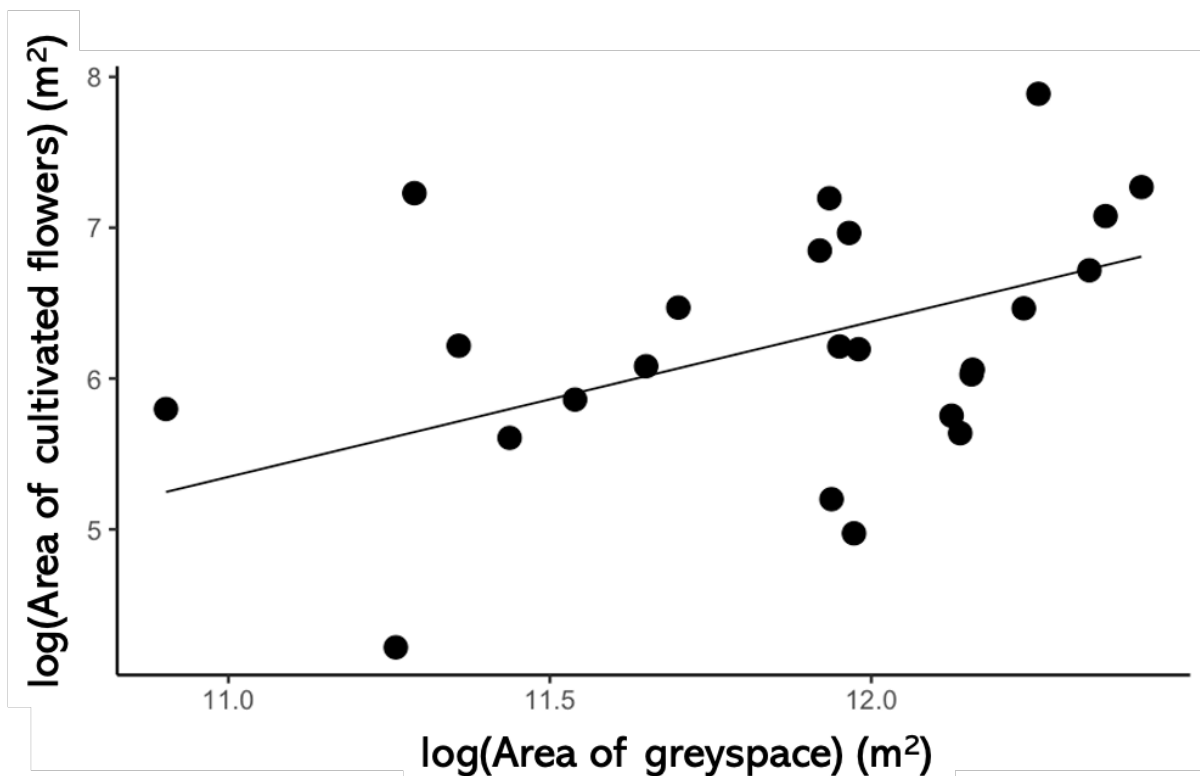


Figure S4. 3 Area of cultivated flowering plants recorded during visual surveys in 24 allotment sites in Leeds increases as area of grey space surround each site (m² log) increases. Line represents linear model fitted ($F_{(1,23)} = 6.15$, $df = 1$, $p = 0.022$).

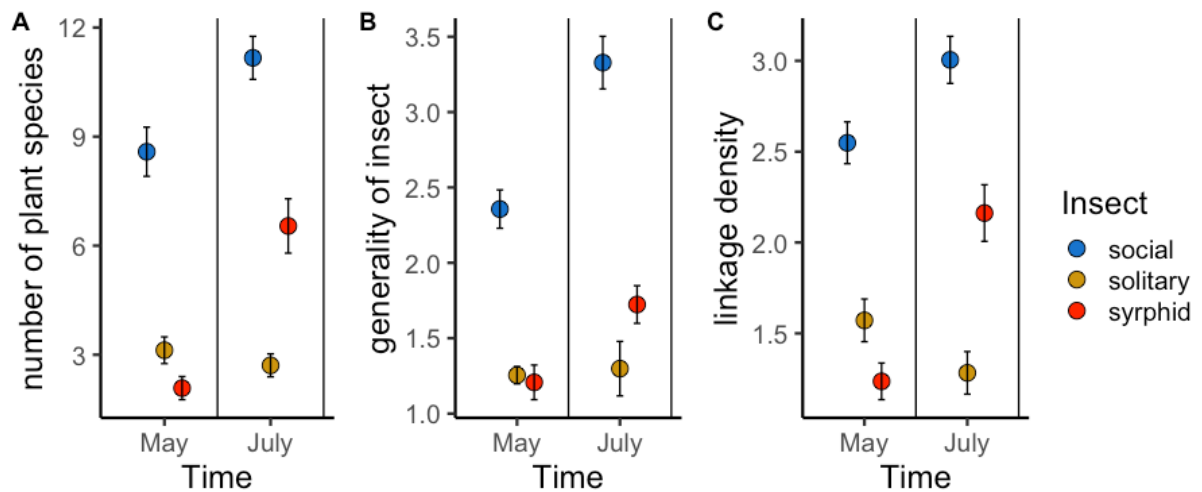


Figure S4. 4 Insect community visiting patterns across time of social bees, solitary bees and hoverflies (a) number of plant species visited by each insect group, b) host range of insect species (average number of plant species visited by each insect species) and c) the linkage density of networks. Data are means \pm SE of twenty-four allotment sites in Leeds visited in June and July in 2020.

Supplementary Text S4:

Text S4.1 Flower patch addition methodology:

Site preparation (March):

- Cut vegetation down to 5-10cm and turn the soil over in an area of 100m²
- Remove persistent weeds

Seed bed preparation and sowing (April-May):

- Rake over soil and remove debris and stones.
- Sow 3g/m² of seeds evening throughout the patch (on a calm, dry day).
- Roll over the seeds lightly to maximise germination

Supplementary Tables S4:

Table S4. 1 Species list of seed mix of EuroFlor and Rigby Taylor Native pollinator and Banquet seed mix (for a more complete list directly contact authors)

Species
<i>Lotus corniculatus</i>
<i>Trifolium pratense</i>
<i>Centaurea cyanus</i>
<i>Vicia sativa</i>
<i>Daucus carota</i>
<i>Papaver rhoeas</i>
<i>Achillea millefolium</i>
<i>Myosotis alpestris</i>
<i>Digitalis purpurea</i>
<i>Allium schoenoprasum</i>
<i>Aquilegia vulgaris</i>
<i>Borago officinalis</i>
<i>Calendula officinalis</i>

Table S4. 2 A list of plant species recorded in twenty-four allotments in Leeds observed along insect-pollinator transects conducted in June and July of 2020, the sugar per floral unit (ug) (Tew et al. 2019) of each species and the number of recorded interactions (total).

Plant species	Sugar per floral unit (ug)	Number of recorded interactions
<i>Achillea millefolium</i>	34.62	1
<i>Anthriscus sylvestris</i>	95.17	6
<i>Antirrhinum majus</i>	1079.17	4
<i>Bellis perennis</i>	64.75	7
<i>Borago officinalis</i>	1843.88	243
<i>Calendula officinalis</i>	469.52	110
<i>Calystegia sepium</i>	1800.78	5
<i>Campanula persicifolia</i>	185.63	13
<i>Capsella bursa-pastoris</i>	3.67	6
<i>Centaurea cyanus</i>	895.83	295
<i>Centaurea montana</i>	17945.11	63
<i>Centaurea nigra</i>	6089.74	2
<i>Centranthus ruber</i>	908.18	13
<i>Cirsium vulgare</i>	12024.29	237
<i>Clarkia amoena</i>	234.15	1
<i>Convolvulus arvensis</i>	351.82	2
<i>Coriandrum sativum</i>	69.91	4
<i>Daucus carota</i>	573.1	1
<i>Digitalis purpurea</i>	1273.88	22
<i>Diploaxis tenuifolia</i>	14.21	2
<i>Dipsacus fullonum</i>	1058.33	17
<i>Eschscholzia californica</i>	10.32	32
<i>Euphorbia helioscopia</i>	120.34	1
<i>Foeniculum vulgare</i>	423.24	5
<i>Geranium pyrenaicum</i>	82.31	6
<i>Geum urbanum</i>	29.8	9
<i>Glebionis coronaria</i>	931.21	4
<i>Lamium purpureum</i>	58.01	11
<i>Lapsana communis</i>	54.12	42
<i>Leucanthemum vulgare</i>	1416.49	48
<i>Ligustrum ovalifolium</i>	66.75	2
<i>Limnanthes douglasii</i>	231.84	131

<i>Linaria purpurea</i>	180.13	24
<i>Lotus corniculatus</i>	60.91	1
<i>Matricaria chamomilla</i>	84.48	1
<i>Nepeta cataria</i>	328.9	9
<i>Origanum vulgare</i>	83.28	365
<i>Papaver rhoeas</i>	3.92	17
<i>Papaver somniferum</i>	3.92	13
<i>Phacelia tanacetifolia</i>	469.27	84
<i>Phaseolus coccineus</i>	53.44	5
<i>Phaseolus vulgaris</i>	53.44	1
<i>Polemonium caeruleum</i>	264.2	4
<i>Polygonum aviculare</i>	3.05	2
<i>Ribes rubrum</i>	600.26	1
<i>Salvia officinalis</i>	2133.87	1
<i>Senecio vulgaris</i>	7.71	1
<i>Solanum tuberosum</i>	27.29	2
<i>Sonchus oleraceus</i>	501.17	37
<i>Stachys byzantina</i>	640.27	8
<i>Tanacetum parthenium</i>	45.04	1
<i>Thlaspi arvense</i>	4.16	1
<i>Thymus vulgaris</i>	24.65	63
<i>Trifolium pratense</i>	2226.84	11
<i>Trifolium repens</i>	1015.14	35
<i>Tripleurospermum inodorum</i>	1415.79	14
<i>Tropaeolum majus</i>	1181.43	22
<i>Valeriana officinalis</i>	271.42	1
<i>Verbena bonariensis</i>	18.57	9
<i>Veronica longifolia</i>	282.14	9
<i>Veronica serpyllifolia</i>	2.83	1
<i>Vicia cracca</i>	409.56	1
<i>Vicia faba</i>	300.34	11
<i>Vicia sepium</i>	117.07	20
<i>Vinca major</i>	854	1

Table S4. 3 A list of hoverfly (Diptera:Syrphidae) species recorded in 24 allotments in Leeds (U.K.) in 2020 along insect-pollinator transects and using pan traps and the number of individuals observed (total) across two collection (June and July).

name	Insect species	+Nesting resources	Control	+Nesting +Floral resources
Syrphidae	<i>Melanostomas scalare</i> <i>Platycheirus sculatus</i>	2	0	1
Syrphidae	agg.	2	0	0
Syrphidae	<i>Syrphidae</i> spp.	32	31	15
Syrphidae	<i>Eristalis inticaria</i>	0	0	1
Syrphidae	<i>Sphaerophoria indet</i>	0	0	1
Syrphidae	<i>Spherophoria</i> spp.	0	0	1
Syrphidae	<i>Chrysotoxum bicinctum</i>	1	0	0
Syrphidae	<i>Chrysotoxum festivum</i>	1	0	3
Syrphidae	<i>Episyrphus balteatus</i>	23	23	28
Syrphidae	<i>Eristalis arbustorum</i>	7	0	1
Syrphidae	<i>Eristalis tenax</i>	3	1	2
Syrphidae	<i>Eumerus funeralis</i>	2	0	0

Syrphidae	<i>Eupeodes corollae</i>	5	3	4
Syrphidae	<i>Eupeodes luniger</i>	2	5	7
Syrphidae	<i>Merodon equestris</i>	4	4	4
Syrphidae	<i>Neoascia podagrica</i>	1	0	0
Syrphidae	<i>Platycheirus albimanus</i>	9	6	23
Syrphidae	<i>Scaeva pyrastris</i>	5	1	2
Syrphidae	<i>Sphaerophoria scripta</i>	14	5	29
Syrphidae	<i>Syrpitta pipiens</i>	15	21	12
Syrphidae	<i>Syrphus ribesii</i>	6	13	19
Syrphidae	<i>Syrphus vitripennis</i>	4	9	18
Syrphidae	<i>Volucella bombylans</i>	1	1	0
Syrphidae	<i>Xylota segnis</i>	1	0	0
Syrphidae	<i>Epistrophe eligans</i>	0	1	0
Syrphidae	<i>Eristalis nemorum</i>	0	1	0
Syrphidae	<i>Eristalis pertinax</i>	0	1	1
Syrphidae	<i>Helophilus pendulus</i>	0	3	3
Syrphidae	<i>Heringia vitripennis</i>	0	1	0
Syrphidae	<i>Meliscaeva auricollis</i>	0	1	0
Syrphidae	<i>Myathropa florea</i>	0	2	0
Syrphidae	<i>Pipizella viduata</i>	0	1	0
Syrphidae	<i>Platycheirus angustatus</i>	0	4	1
Syrphidae	<i>Platycheirus clypeatus</i>	0	2	0
Syrphidae	<i>Dasysyrphus albostriatus</i>	0	0	3
Syrphidae	<i>Epistrophe grossulariae</i>	0	0	1
Syrphidae	<i>Melanostoma mellinum</i>	0	0	1
				+Nesting
		+Nesting	Control	+Floral
Family	Species	resources		resources
Syrphidae	<i>Melanostomas scalare</i>	2	0	1
Syrphidae	<i>Platycheirus sculatus</i>			
Syrphidae	agg.	2	0	0
Syrphidae	<i>Syrphidae spp.</i>	32	31	15
Syrphidae	<i>Eristalis inticaria</i>	0	0	1
Syrphidae	<i>Sphaerophoria indet</i>	0	0	1
Syrphidae	<i>Spherophoria spp.</i>	0	0	1
Syrphidae	<i>Chrysotoxum bicinctum</i>	1	0	0
Syrphidae	<i>Chrysotoxum festivum</i>	1	0	3
Syrphidae	<i>Episyrphus balteatus</i>	23	23	28
Syrphidae	<i>Eristalis arbustorum</i>	7	0	1
Syrphidae	<i>Eristalis tenax</i>	3	1	2
Syrphidae	<i>Eumerus funeralis</i>	2	0	0
Syrphidae	<i>Eupeodes corollae</i>	5	3	4

Syrphidae	<i>Eupeodes luniger</i>	2	5	7
Syrphidae	<i>Merodon equestris</i>	4	4	4
Syrphidae	<i>Neoscia podagrica</i>	1	0	0
Syrphidae	<i>Platycheirus albimanus</i>	9	6	23
Syrphidae	<i>Scaeva pyrastris</i>	5	1	2
Syrphidae	<i>Sphaerophoria scripta</i>	14	5	29
Syrphidae	<i>Syritta pipiens</i>	15	21	12
Syrphidae	<i>Syrphus ribesii</i>	6	13	19
Syrphidae	<i>Syrphus vitripennis</i>	4	9	18
Syrphidae	<i>Volucella bombylans</i>	1	1	0
Syrphidae	<i>Xylota segnis</i>	1	0	0
Syrphidae	<i>Epistrophe eligans</i>	0	1	0
Syrphidae	<i>Eristalis nemorum</i>	0	1	0
Syrphidae	<i>Eristalis pertinax</i>	0	1	1
Syrphidae	<i>Helophilus pendulus</i>	0	3	3
Syrphidae	<i>Heringia vitripennis</i>	0	1	0
Syrphidae	<i>Meliscaeva auricollis</i>	0	1	0
Syrphidae	<i>Myathropa florea</i>	0	2	0
Syrphidae	<i>Pipizella viduata</i>	0	1	0
	<i>Platycheirus</i>			
Syrphidae	<i>angustatus</i>	0	4	1
Syrphidae	<i>Platycheirus clypeatus</i>	0	2	0
	<i>Dasysyrphus</i>			
Syrphidae	<i>albostriatus</i>	0	0	3
	<i>Epistrophe</i>			
Syrphidae	<i>grossulariae</i>	0	0	1
Syrphidae	<i>Melanostoma mellinum</i>	0	0	1

Table S4. 4 A list of nocturnal moth (Lepidoptera) species recorded in 24 allotments in Leeds (U.K.) in 2020 using light traps (Heath) traps and the number of individuals observed in the experimental treatments aggregated across two collection (June and July).

Family	Species	+Nesting resources	Control	+Nesting +Floral resources
Adelidae	Adelidae spp.	4	13	4
Blastobasidae	<i>Blastobasis adustella</i>	0	0	1
Crambidae	<i>Agriphila straminella</i>	3	2	1
Crambidae	<i>Anania coronata</i>	1	0	0
Crambidae	<i>Anania hortulata</i>	1	1	2
Crambidae	<i>Chrysoteuchia culmella</i>	6	42	19
Crambidae	<i>Pyrausta aurata</i>	1	0	0

Crambidae	<i>Eudonia lacustrata</i>	0	9	11
Crambidae	<i>Eudonia mercurella</i>	0	1	1
Crambidae	<i>Patania ruralis</i>	0	1	1
Crambidae	<i>Crambus perlella</i>	0	0	1
Crambidae	<i>Eudonia spp.</i>	0	1	1
Erebidae	<i>Eilema lurideola</i>	2	4	7
Erebidae	<i>Spilarctia luteum</i>	1	0	1
Erebidae	<i>Herminia grisealis</i>	0	1	0
Erebidae	<i>Herminia tarsipennalis</i>	0	1	1
Erebidae	<i>Rivula sericealis</i>	0	1	0
Erebidae	<i>Tyria jacobaeae</i>	0	2	1
Erebidae	<i>Hypena proboscidalis</i>	0	0	1
Erebidae	<i>Phragmatobia fuliginosa</i>	0	0	1
Gelechiidae	<i>Helcytogramma rufescens</i>	1	0	2
Gelechiidae	<i>Pseudotelphisa scallella</i>	0	1	0
Geometridae	<i>Crocallis elinguaris</i>	5	4	0
Geometridae	<i>Eulithis prunata</i>	1	1	2
Geometridae	<i>Idaea aversata</i>	2	7	10
Geometridae	<i>Ourapteryx sambucaria</i>	1	0	0
Geometridae	<i>Peribatodes rhomboidaria</i>	1	0	2
Geometridae	<i>Scotopteryx chenopodiata</i>	1	0	0
Geometridae	<i>Xanthorhoe fluctuata</i>	3	2	2
Geometridae	<i>Ecliptopera silaceata</i>	0	1	0
Geometridae	<i>Eulithis populata</i>	0	1	0
Geometridae	<i>Eupithecia pulchellata</i>	0	1	0
Geometridae	<i>Lampropteryx suffumata</i>	0	1	1
Geometridae	<i>Opisthograptis luteolata</i>	0	2	1
Geometridae	<i>Thera britannica</i>	0	1	1
Geometridae	<i>Dysstroma truncata</i>	0	0	1
Geometridae	<i>Eupithecia exiguata</i>	0	0	1
Geometridae	<i>Hydriomena furcata</i>	0	0	3
Geometridae	<i>Idaea biselata</i>	0	0	1
Geometridae	<i>Idaea dimidiata</i>	0	0	1
Geometridae	<i>Biston butularia</i>	0	1	2
Geometridae	<i>Eupithecia sp.</i>	0	8	5
Geometridae	Geometrid spp.	0	1	0
Glyphipterigidae	<i>Glypjopterix spp.</i>	5	0	0
Hepialidae	<i>Triodia sylvina</i>	0	4	0
Lasiocampidae	<i>Euthrix potatoria</i>	0	0	1
Noctuidae	<i>Apamea sp.</i>	1	0	0
Noctuidae	<i>Hoplodrina spp.</i>	7	47	29
Noctuidae	Noctuididae	1	0	0
Noctuidae	<i>Oligia strigillis agg.</i>	14	18	10
Noctuidae	<i>Mesapamea secalis agg.</i>	0	8	13
Noctuidae	<i>Agrotis exclamationis</i>	36	48	53

Noctuidae	<i>Agrotis segetum</i>	1	0	0
	<i>Aporophyla</i>			
Noctuidae	<i>lueneburgensis</i>	1	1	1
Noctuidae	<i>Autographa gamma</i>	1	0	4
Noctuidae	<i>Axylia putris</i>	3	13	5
Noctuidae	<i>Bryophila domestica</i>	1	1	2
Noctuidae	<i>Caradrina morpheus</i>	1	1	3
Noctuidae	<i>Cosmia trapezina</i>	1	0	3
Noctuidae	<i>Diarsia mendica</i>	1	1	0
Noctuidae	<i>Lacanobia oleracea</i>	3	9	3
Noctuidae	<i>Mythimna impura</i>	5	18	32
Noctuidae	<i>Mythimna pallens</i>	1	0	0
Noctuidae	<i>Noctua pronuba</i>	16	108	122
Noctuidae	<i>Oligia fasciuncula</i>	1	0	0
Noctuidae	<i>Photodes fluxa</i>	1	0	0
Noctuidae	<i>Xestia xanthographa</i>	2	1	1
Noctuidae	<i>Agrotis puta</i>	0	1	0
Noctuidae	<i>Apamea monoglypha</i>	0	13	11
Noctuidae	<i>Autographa jota</i>	0	1	0
Noctuidae	<i>Mythimna ferrago</i>	0	2	2
Noctuidae	<i>Xestia triangulum</i>	0	3	2
Noctuidae	<i>Amphipyra pyramidea</i>	0	0	1
Noctuidae	<i>Diachrysia chrysitis</i>	0	0	1
Noctuidae	<i>Hadena compta</i>	0	0	1
Noctuidae	<i>Mormo maura</i>	0	0	1
Noctuidae	<i>Naenia typica</i>	0	0	1
Noctuidae	<i>Noctua janthina</i>	0	0	1
Noctuidae	<i>Xestia c nigrum</i>	0	0	1
Oecophoridae	<i>Borkhausenia fuscescens</i>	0	1	0
	<i>Hofmannophila</i>			
Oecophoridae	<i>pseudospretella</i>	0	0	2
Pterophoridae	<i>Emmelina monodactyla</i>	0	1	1
Pterophoridae	<i>Pterophorus pentadactyla</i>	0	1	0
Sphingidae	<i>Smerinthus ocellatus</i>	0	1	0
Sphingidae	<i>Deilephila elpenor</i>	1	0	3
Sphingidae	<i>Laothoe populi</i>	0	1	0
Tortricidae	<i>Ephiphyas postvittana</i>	0	1	1
Tortricidae	<i>Ryacionia buliana</i>	0	1	0
Tortricidae	<i>Celypha striana</i>	1	7	5
Tortricidae	<i>Acleris forsskaleana</i>	0	1	0
Tortricidae	<i>Agapeta hamana</i>	0	1	1
Tortricidae	<i>Clepsis consimilana</i>	0	1	0
Tortricidae	<i>Cydia pomonella</i>	0	3	4
Tortricidae	<i>Dichrorampha alpinana</i>	0	1	0
Tortricidae	<i>Hedya nubiferana</i>	0	1	1

Tortricidae	<i>Hedya pruniana</i>	0	1	0
Tortricidae	<i>Lozotaenia forsterana</i>	0	1	0
Tortricidae	<i>Tortricidae</i>	0	2	0
Tortricidae	<i>Eucosma cana</i>	0	0	4
Tortricidae	<i>Notocelia uddmanniana</i>	0	0	1
	<i>Pseudosciaphila</i>			
Tortricidae	<i>branderiana</i>	0	0	1
Ypsolophidae	<i>Ypsolopha dentella</i>	0	6	3
	Micro 1	1	13	16
	Micro 2	1	1	1
	Micro 3	1	0	0
	Micro 4	0	6	6
	Micro 5	0	4	3

Table S4. 5 A list of bee (Hymenoptera) species recorded in 24 allotments in Leeds (U.K.) in 2020 along insect-pollinator transects and using pan traps and the number of individuals observed (total) across two collection (June and July).

Family	Species	+Nesting resources	Control	+Nesting +Floral resources
Andrenidae	<i>Andrena minutula</i>	1	1	0
Andrenidae	<i>Andrena bicolor</i>	0	2	1
Andrenidae	<i>Andrena cineraria</i>	0	0	4
Andrenidae	<i>Andrena haemorrhoa</i>	0	0	1
Andrenidae	<i>Andrena semilaevis</i>	0	0	1
Andrenidae	<i>Andrena albipes</i>	0	0	1
Apidae	<i>Anthophora furcata</i>	5	0	0
Apidae	<i>Apis mellifera</i>	390	633	639
Apidae	<i>Bombus hortorum</i>	6	16	22
Apidae	<i>Bombus hypnorum</i>	65	46	100
Apidae	<i>Bombus lapidarius</i>	86	81	111
Apidae	<i>Bombus pascuorum</i>	133	140	128
Apidae	<i>Bombus pratorum</i>	75	85	97
Apidae	<i>Bombus vestalis</i>	1	0	0
Apidae	<i>Bombus jonellus</i>	0	1	0
Apidae	<i>Bombus sylvestris</i>	0	3	0
Apidae	<i>Bombus terrestris</i> agg.	222	237	281
Apidae	<i>Nomada ruuficornis</i>	0	1	0
Apidae	<i>Anthophora plumpies</i>	0	0	2
Apidae	<i>Nomada</i> spp.	0	0	1
Colletidae	<i>Colletes daviesanus</i>	11	2	6
Colletidae	<i>Hylaeus communis</i>	66	68	47
Colletidae	<i>Hylaeus hyalinatus</i>	9	2	10

Colletidae	<i>Hylaeus signatus</i>	1	0	0
Halictidae	<i>Halictus tumulorum</i>	1	0	3
Halictidae	<i>Lasioglossum albipes</i>	1	0	0
	<i>Lasioglossum</i>			
Halictidae	<i>cupromicans</i>	3	3	3
Halictidae	<i>Lasioglossum leucopus</i>	9	1	3
Halictidae	<i>Halictus rubicundus</i>	0	1	1
Halictidae	<i>Lasioglossum fratellum</i>	0	0	1
	<i>Lasioglossum</i>			
Halictidae	<i>smeathmanellum</i>	0	0	4
Halictidae	<i>Lasioglossum villosulum</i>	0	0	4
Halictidae	<i>Lasioglossum calcetum</i>	0	23	4
Halictidae	<i>Lasioglossum spp.</i>	0	1	3
Megachilidae	<i>Megachile centuncularis</i>	4	5	4
Megachilidae	<i>Megachile willughbiella</i>	3	1	1
Megachilidae	<i>Osmia bicornis</i>	7	4	4
Megachilidae	<i>Osmia caerulescens</i>	6	2	0
Megachilidae	<i>Osmia leaiana</i>	6	4	6
Megachilidae	<i>Megachile versicolor</i>	0	0	1
Megachilidae	<i>Osmia spp.</i>	5	1	1
	<i>Solitary bee spp.</i>	2	5	5

Table S4. 6 Plant species recorded during transects and focal surveys in 24 allotments in Leeds (U.K.) and the total number of visits by bees and hoverflies during two collections (June and July 2020).

Species	Number of visits
<i>Origanum vulgare</i>	368
<i>Centaurea cyanus</i>	302
<i>Jacobaea vulgaris</i>	251
<i>Borago officinalis</i>	244
<i>Symphytum officinale</i>	243
<i>Cirsium vulgare</i>	240
<i>Rubus spp. (bramble)</i>	238
<i>Rubus spp. (raspberry)</i>	233
<i>Allium schoenoprasum</i>	168
<i>Symphytum officinale</i>	167
<i>Limnanthes douglasii</i>	132
<i>Lavandula angustifolia</i>	120
<i>Ranunculus spp.</i>	114
<i>Calendula officinalis</i>	113
<i>Phacelia tanacetifolia</i>	84
<i>Rubus spp. (bramble)</i>	78
<i>Centaurea montana</i>	63
<i>Thymus vulgaris</i>	63
<i>Allium sphaerocephalon</i>	57
<i>Leucanthemum vulgare</i>	55
<i>Lapsana communis</i>	44
<i>Fragaria ananassa</i>	43
<i>Sonchus oleraceus</i>	37
<i>Trifolium repens</i>	35
<i>Nepeta spp.</i>	33
<i>Eschscholzia californica</i>	32

<i>Lupinus polyphyllus</i>	32
<i>Geranium palustre</i>	29
<i>Myosotis sylvatica</i>	28
<i>Rubus</i> spp. (logan)	28
<i>Aquilegia vulgaris</i>	27
<i>Allium nigrum</i>	25
<i>Rapistrum rugosum</i>	25
<i>Linaria purpurea</i>	24
<i>Digitalis purpurea</i>	22
<i>Epilobium ciliatum</i>	22
<i>Taraxacum</i> spp.	22
<i>Tropaeolum majus</i>	22
<i>Leucanthemum x superbum</i>	20
<i>Silene dioica</i>	20
<i>Vicia sepium</i>	20
<i>Malva arborea</i>	18
<i>Brassica oleracea</i>	17
<i>Buddleja</i>	17
<i>Dipsacus fullonum</i>	17
<i>Papaver rhoeas</i>	17
<i>Salvia rosmarinus</i>	16
<i>Allium ampeloprasum</i>	15
<i>Helenium</i> spp.	15
<i>Sinapis arvensis</i>	15
<i>Centranthus ruber</i>	14
<i>Tripleurospermum inodorum</i>	14
<i>Anthriscus sylvestris</i>	13
<i>Campanula persicifolia</i>	13
<i>Geranium pyrenaicum</i>	13
<i>Papaver somniferum</i>	13
<i>Veronica persica</i>	13
<i>Bellis perennis</i>	12
<i>Chamaenerion angustifolium</i>	12
<i>Crocsmia crocosmiiflora</i>	12
<i>Epilobium hirsutum</i>	12
<i>Helianthus</i> spp.	12
<i>Helichrysum italicum</i>	12
<i>Lamium purpureum</i>	12
<i>Geum urbanum</i>	11
<i>Trifolium pratense</i>	11
<i>Vicia faba</i>	11
<i>Capsella bursa-pastoris</i>	10
<i>Dahlia</i> spp.	9
<i>Geranium phaeum</i>	9
<i>Nepeta cataria</i>	9
<i>Raphanus raphanistrum</i>	9
<i>Verbena bonariensis</i>	9
<i>Veronica longifolia</i>	9
<i>Echium vulgare</i>	8
<i>Geranium endressii</i>	8
<i>Papaver alpinum</i>	8
<i>Stachys byzantina</i>	8
<i>Ammi majus</i>	7
<i>Chenopodium album</i>	7
<i>Carduus crispus</i>	6
<i>Fumaria officinalis</i>	6
<i>Hypericum cerastoides</i>	6
<i>Monarda punctata</i>	6
<i>Papaver orientale</i>	6
<i>Schizanthus pinnatus</i>	6
<i>Arabis blepharophylla</i>	5
<i>Calystegia sepium</i>	5
<i>Foeniculum vulgare</i>	5
<i>Iris pseudacorus</i>	5
<i>Knautia arvensis</i>	5
<i>Persicaria maculos</i>	5
<i>Phaseolus coccineus</i>	5

<i>Rosa canina</i>	5
<i>Allium giganteum</i>	4
<i>Anemone tomentosa</i>	4
<i>Antirrhinum majus</i>	4
<i>Brassica rapa</i>	4
<i>Coriandrum sativum</i>	4
<i>Dietes iridioides</i>	4
<i>Geranium himalayense</i>	4
<i>Glebionis coronaria</i>	4
<i>Polemonium caeruleum</i>	4
<i>Rosa rugosa</i>	4
<i>Inula helenium</i>	3
<i>Lamium hybridum</i>	3
<i>Myosotis arvensis</i>	3
<i>Penstemon campanulatus</i>	3
<i>Rudbeckia hirta</i>	3
<i>Senecio vulgaris</i>	3
<i>Weigela florida</i>	3
<i>Centaurea nigra</i>	2
<i>Convolvulus arvensis</i>	2
<i>Dimorphotheca pluvialis</i>	2
<i>Diplotaxis tenuifolia</i>	2
<i>Epilobium montanum</i>	2
<i>Eucosma sp.</i>	2
<i>Fumaria capreolata</i>	2
<i>Geranium macrorrhizum</i>	2
<i>Graptophyllum pictum</i>	2
<i>Gypsophila spp.</i>	2
<i>Hypericum perforatum</i>	2
<i>Ligustrum ovalifolium</i>	2
<i>Lonicera caprifolium</i>	2
<i>Oenothera glazioviana</i>	2
<i>Polygonum aviculare</i>	2
<i>Psilostrophe cooperi</i>	2
<i>Rosa californica</i>	2
<i>Rosa spp.</i>	2
<i>Solanum tuberosum</i>	2
<i>Spirea douglasii</i>	2
<i>Stachys sylvatica</i>	2
<i>Thlaspi arvense</i>	2
<i>Veronica officinalis</i>	2
<i>Achillea millefolium</i>	1
<i>Allium cepa</i>	1
<i>Amsinckia menziesii</i>	1
<i>Anthemis cotula</i>	1
<i>Clarkia amoena</i>	1
<i>Daucus carota</i>	1
<i>Dianthus barbatus</i>	1
<i>Euphorbia helioscopia</i>	1
<i>Fuchsia magellanica</i>	1
<i>Heuchera micrantha</i>	1
<i>Iberis amara</i>	1
<i>Lathyrus tuberosus</i>	1
<i>Lobelia erinus</i>	1
<i>Lotus corniculatus</i>	1
<i>Lysimachia punctata</i>	1
<i>Malus (apple)</i>	1
<i>Matricaria chamomilla</i>	1
<i>Melilotus officinalis</i>	1
<i>Mercurialis annua</i>	1
<i>Oenothera biennis</i>	1
<i>Oxalis corniculata</i>	1
<i>Papaver nudicaule</i>	1
<i>Phaseolus vulgaris</i>	1
<i>Pyracantha spp.</i>	1
<i>Rheum spp.</i>	1
<i>Ribes rubrum</i>	1

<i>Rosa multiflora</i>	1
<i>Rubus</i> spp. (<i>logan</i>)	1
<i>Rumex obtusifolius</i>	1
<i>Salvia officinalis</i>	1
<i>Symphoricarpos albus</i>	1
<i>Tanacetum parthenium</i>	1
<i>Valeriana officinalis</i>	1
<i>Valerianella locusta</i>	1
<i>Veronica serpyllifolia</i>	1
<i>Vicia cracca</i>	1
<i>Vinca major</i>	1

Table S4. 7 Species list of plant assignments from 16 pollen loads of moths (all individuals aggregated by site) in 16 urban allotments in Leeds 2020 using the ITS2 primer. Showing the number of occurrences across the dataset. Ranked from most interacted with to the least interacted with.

Species	Number of visits (max = 16)
<i>Ligustrum vulgare</i>	16
<i>Buddleja</i>	16
<i>Rubus</i>	16
<i>Acer</i>	15
<i>Solanum</i>	15
<i>Tilia platyphyllos</i>	14
<i>Sambucus nigra</i>	13
<i>Tilia</i>	13
<i>Agrostis</i>	12
<i>Eucalyptus</i>	11
<i>Sambucus</i>	11
<i>Betula</i>	10
<i>Castanea</i>	10
<i>Quercus</i>	10
<i>Taraxacum</i>	10
<i>Fraxinus</i>	9
<i>Aegilops</i>	8
<i>Epilobium</i>	8
<i>Philadelphus</i>	8
<i>Salix</i>	8
<i>Borago officinalis</i>	7
<i>Plantago lanceolata</i>	7
<i>Poa trivialis</i>	7
<i>Alnus</i>	6
<i>Cirsium arvense</i>	6
<i>Buddleja lindleyana</i>	5
<i>Fagaceae</i>	5
<i>Hydrangea</i>	5
<i>Acer pseudoplatanus</i>	4
<i>Centranthus</i>	4
<i>Corylus avellana</i>	4
<i>Lapsana communis</i>	4
<i>Papaver rhoeas</i>	4
<i>Plantago major</i>	4
<i>Aurantioideae</i>	3
<i>Betulaceae</i>	3
<i>Brassica oleracea</i>	3
<i>Calystegia silvatica</i>	3
<i>Capsicum</i>	3
<i>Castanea crenata</i>	3
<i>Chamaenerion angustifolium</i>	3
<i>Cirsium</i>	3
<i>Digitalis purpurea</i>	3
<i>Festuca</i>	3
<i>Fragaria</i>	3
<i>Hypochaeris</i>	3

<i>Impatiens</i>	3
<i>Linaria repens</i>	3
<i>Prunus</i>	3
<i>Prunus avium</i>	3
<i>Ranunculus repens</i>	3
<i>Silene dioica</i>	3
<i>Sonchus</i>	3
<i>Taxus</i>	3
<i>Tropaeolum</i>	3
<i>Anemone</i>	2
<i>Atriplex</i>	2
<i>Avena</i>	2
<i>Beta</i>	2
<i>Brassicaceae</i>	2
<i>Campanula poscharskyana</i>	2
<i>Cardueae</i>	2
<i>Centaurea nigra</i>	2
<i>Chenopodium album</i>	2
<i>Clematis</i>	2
<i>Conium maculatum</i>	2
<i>Fagus sylvatica</i>	2
<i>Geum urbanum</i>	2
<i>Hypericum androsaemum</i>	2
<i>Ilex aquifolium</i>	2
<i>Limnanthes douglasii</i>	2
<i>Linaria</i>	2
<i>Myosotis arvensis</i>	2
<i>Prunus salicina</i>	2
<i>Rosa</i>	2
<i>Salvia</i>	2
<i>Silene latifolia</i>	2
<i>Solanum lycopersicum</i>	2
<i>Solanum tuberosum</i>	2
<i>Symphytum</i>	2
<i>Ulmus</i>	2
<i>Verbascum thapsus</i>	2
<i>Verbena officinalis</i>	2
<i>Veronica chamaedrys</i>	2
<i>Acer campestre</i>	1
<i>Alliaria petiolata</i>	1
<i>Amaranthus</i>	1
<i>Anthyllis vulneraria</i>	1
<i>Armoracia rusticana</i>	1
<i>Bellis perennis</i>	1
<i>Brassica</i>	1
<i>Bromus</i>	1
<i>Calenduleae</i>	1
<i>Callitropsis</i>	1
<i>Calluna vulgaris</i>	1
<i>Campanula</i>	1
<i>Campanula fenestrellata</i>	1
<i>Cannabaceae</i>	1
<i>Cardamine hirsuta</i>	1
<i>Cardamine pratensis</i>	1
<i>Carduus</i>	1
<i>Centranthus lecoqii</i>	1
<i>Cirsium vulgare</i>	1
<i>Citrus</i>	1
<i>Clematis integrifolia</i>	1
<i>Coreopsidaeae</i>	1
<i>Cornus sanguinea</i>	1
<i>Cotoneaster frigidus</i>	1
<i>Cucurbita</i>	1
<i>Cupressaceae</i>	1
<i>Cymbalaria</i>	1
<i>Dactylis glomerata</i>	1
<i>Dahlia</i>	1

<i>Delphinium</i>	1
<i>Dianthus</i>	1
<i>Erysimum cheiri</i>	1
<i>Galium aparine</i>	1
<i>Glandularia subincana</i>	1
<i>Heracleum</i>	1
<i>Hypericum</i>	1
<i>Jacobaea</i>	1
<i>Lavandula</i>	1
<i>Leucanthemum vulgare</i>	1
<i>Linum</i>	1
<i>Lonicera</i>	1
<i>Lunaria annua</i>	1
<i>Myrteae</i>	1
<i>Nothofagaceae</i>	1
<i>Oenanthe</i>	1
<i>Papaver somniferum</i>	1
<i>Parietaria</i>	1
<i>Parietaria officinalis</i>	1
<i>Phleum pratense</i>	1
<i>Plantanus</i>	1
<i>Populus</i>	1
<i>Potentilla</i>	1
<i>Primula</i>	1
<i>Ribes</i>	1
<i>Rumex acetosella</i>	1
<i>Saponaria</i>	1
<i>Saponaria officinalis</i>	1
<i>Scorzoneroides autumnalis</i>	1
<i>Senecio</i>	1
<i>Sesamum indicum</i>	1
<i>Silene coronaria</i>	1
<i>Silene vulgaris</i>	1
<i>Solanum dulcamara</i>	1
<i>Solanum nitidum</i>	1
<i>Sorbus</i>	1
<i>Telekia speciosa</i>	1
<i>Trachelospermum</i>	1
<i>Trifolium pratense</i>	1
<i>Urtica urens</i>	1
<i>Veronica arvensis</i>	1
<i>Veronica serpyllifolia</i>	1
<i>Viburnum</i>	1
<i>Vicia sepium</i>	1
<i>Weigela</i>	1

Table S4. 8 Linear mixed effect model output. Type II Analysis of Variance Table with Satterthwaite's method testing the species richness of bees (social and solitary), moths and hoverflies, and if the mean species richness differs across habitat supplement treatments, and how urbanisation influences insect species richness. Anova type II

Response	Terms	Coefficients	Estimate	t value	p value
Species richness					
	Treatment				
		Treatment - Nesting addition (intercept)	0.28	0.245	0.81
		Treatment - Control	0.28	-5.023	0.137
		Treatment - Flower addition	0.1	-6.662	0.081
	Insect taxa				
		Moths (intercept)	0.28	0.245	0.81
		Social	-0.34	-5.023	<0.001
		Solitary	-0.48	-6.662	<0.001
		Hoverfly	-0.33	-4.847	<0.001
	Urbanisation				
			0.044	0.44	0.66

Table S4. 9 Linear mixed effect model output. Type II Analysis of Variance Table with Satterthwaite's method testing the species richness of bees (social and solitary), moths and hoverflies, and if the mean species richness differs across habitat supplement treatments, and how site level area of cultivated flowers influences insect species richness

Response	Terms	Coefficients	Estimate	t value	p value
<u>Species richness</u>					
	<u>Treatment</u>				
		Treatment - Nesting addition (intercept)	0.65	2.65	0.01
		Treatment - Control	0.08	1.2	0.23
		Treatment - Flower addition	0.11	1.61	0.11
	<u>Insect taxa</u>				
		Moths (intercept)	0.65	2.65	0.01
		Social	-0.34	-5.023	<0.001
		Solitary	-0.48	-6.662	<0.001
		Hoverfly	-0.33	-4.847	<0.001
	<u>Cultivated flowers</u>				
			0.023	0.60	0.54

Table S4. 10 Linear mixed effect model output. Type II Analysis of Variance Table with Satterthwaite's method testing the abundance of bees (social and solitary), moths and hoverflies, and if the mean abundance differs across habitat supplement treatments, and how urbanisation influences insect abundance.

Response	Terms	Coefficients	Estimate	t value	p value
<u>Abundance</u>					
	<u>Treatment</u>				
		Treatment - Nesting addition (intercept)	47.58	0.227	0.81
		Treatment - Control	17.21	2.013	0.047
		Treatment - Flower addition	14.4	1,724	0.086
	<u>Insect taxa</u>				
		Moths (intercept)	47.58	0.227	0.81
		Social	137.1	0.489	0.62
		Solitary	-157.635	-0.056	0.58
		Hoverfly	-138.89	-0.49	0.62
	<u>Urbanisation</u>				
			-1.24	-0.071	0.94

Table S4. 11 Linear mixed effect model output. Type II Analysis of Variance Table with Satterthwaite's method testing the abundance of bees (social and solitary), moths and hoverflies, and if the mean abundance differs across habitat supplement treatments, and how area of cultivated flowers influences insect abundance.

Response	Terms	Coefficients	Estimate	t value	p value
<u>Abundance</u>					
	<u>Treatment</u>				
		Treatment - Nesting addition (intercept)	7.33	0.148	0.882

	Treatment - Control	12.54	1.53	0.129
	Treatment - Flower addition	12.15	1.535	0.122
<hr/>				
<i>Insect taxa</i>				
<hr/>				
	Moths (intercept)	7.33	0.15	0.81
	Social	-48.44	-0.712	0.47
	Solitary	-1.83	-0.171	0.87
	Hoverfly	5.529	0.081	0.93
<hr/>				
<i>Cultivated flowers</i>				
<hr/>				
		4.51	0.57	0.56
<hr/>				
<i>Cultivated flowers: Insect taxa</i>				
<hr/>				
	Moths (intercept)	7.33	0.15	0.81
	Social	24.22	2.24	0.028
	Solitary	-2.59	-0.24	0.811
	Hoverfly	-4.69	-0.433	0.66

Table S4. 12 Linear mixed effect model output. Type II Analysis of Variance Table with Satterthwaite's method testing the host range of bees (social and solitary) and hoverflies, and if the mean number of plants per species (host range) differs across habitat supplement treatments, and how area of cultivated flowers influences the host range of each insect species.

Terms	Coefficients	Estimate	Std. Error	t value	p value
Host range of insect					
<i>Insect taxa</i>					
<hr/>					
	Social (intercept)	1.20	0.48	2.50	0.01
	Solitary	-1.10	0.19	-5.81	<0.001
	Hoverfly	-1.15	0.19	-6.07	<0.001
<hr/>					
<i>Time</i>					
<hr/>					
	June (intercept)	1.20	0.48	2.50	0.01
	July	0.97	0.19	5.13	<0.001
<hr/>					
<i>Cultivated flowers</i>					
<hr/>					
		0.17	0.07	2.39	0.02
<hr/>					
<i>Treatment</i>					
<hr/>					
	Treatment - Control (intercept)	1.20	0.48	2.50	0.01
	Treatment - Nesting addition	0.22	0.14	1.55	0.12
	Treatment - Flower addition	0.12	0.13	0.91	0.37
<hr/>					
	<i>Insect:Time</i>	-0.93	0.27	-3.46	<0.001

Table S4. 13 Linear mixed effect model output. Type II Analysis of Variance Table with Satterthwaite's method testing the linkage density of pollinator-plant networks of bees (social and solitary) and hoverflies, and if the mean linkage density differs across habitat supplement treatments, and how area of cultivated flowers influences the linkage density

Terms	Coefficients	Estimate	Std. Error	t value	p value
Linkage density					
<i>Insect taxa</i>					
<hr/>					
	Social (intercept)	1.05	0.53	2.00	0.05
	Solitary	-0.98	0.17	-5.70	<0.001
	Hoverfly	-1.31	0.17	-7.66	<0.001
<hr/>					
<i>Time</i>					
<hr/>					
	June (intercept)	1.05	0.53	2.00	0.05
	July	0.46	0.17	2.66	0.01
<hr/>					
<i>Cultivated flowers</i>					
<hr/>					
		0.20	0.07	2.72	0.01
<hr/>					
<i>Treatment</i>					
<hr/>					
	Treatment - Control (intercept)	1.05	0.53	2.00	0.05
	Treatment - Nesting addition	0.11	0.13	0.85	0.40

	Treatment - Flower addition	0.10	0.12	0.83	0.41
<i>Insect:Time</i>		-0.75	0.24	-3.07	<0.001

Table S4. 14 Linear mixed effect model output. Type II Analysis of Variance Table with Satterthwaite's method testing the total number of plants species in the pollinator-plant networks of bees (social and solitary) and hoverflies, and if the mean number of plants differs across habitat supplement treatments, and how area of cultivated flowers influences the number of plants interacted with.

Terms	Coefficients	Estimate	Std. Error	t value	p value
Total number of plants					
<i>Insect taxa</i>					
	Social (intercept)	3.19	2.04	1.56	0.12
	Solitary	-1.01	0.13	-7.69	<0.001
	Hoverfly	-1.42	0.15	-9.21	<0.001
<i>Time</i>					
	June (intercept)	3.19	2.04	1.56	0.12
	July	0.26	0.09	2.91	<0.001
<i>Cultivated flowers</i>					
		0.27	0.08	3.51	<0.001
<i>Treatment</i>					
	Treatment - Control (intercept)	3.19	2.04	1.56	0.12
	Treatment - Nesting addition	0.20	0.11	1.87	0.06
	Treatment - Flower addition	0.15	0.09	1.70	0.09
<i>Insect:Time</i>		-0.41	0.19	-2.16	0.03

Supplementary Material Chapter 5:

Supplementary Tables S5:

Table S5. 1 Species list and the abundance of cavity nesting bees that colonised artificial trap nests during 2020 and 2021 in sixteen allotment sites in Leeds (eight with nesting resources and eight with both floral and nesting resources added).

Year	Family	Species	+Nesting resources	+Floral resources +Nesting resources
2020				
	Megachilidae	<i>Osmia bicornis</i>	17	25
	Megachilidae	<i>Osmia leaiana</i>	19	0
2021				
	Megachilidae	<i>Megachile lignisea</i>	137	159
	Colletidae	<i>Hylaeus hyalinatus</i>	128	71
	Megachilidae	<i>Osmia leaiana</i>	59	89
	Colletidae	<i>Hylaeus communis</i>	9	121
	Megachilidae	<i>Osmia bicornis</i>	27	47
	Megachilidae	<i>Megachile centuncularis</i>	16	4
	Megachilidae	<i>Coelioxys inermis</i>	2	0

Table S5. 2 List of morphotypes,(identified to genus where possible), their feeding behaviours and the abundance of cavity nesting wasps that colonised artificial trap nests during 2020 and 2021 in sixteen allotment sites in Leeds (eight with nesting resources and eight with both floral and nesting resources added).

Year	Family	Morphotype	Genus	Feeding behaviour	+Nesting resources	+Floral resources +Nesting resources
2020						
	Vespidae	Mason wasp 1	<i>Ancistrocerus</i> sp.	Lepidoptera caterpillars	17	14
	Crabronidae	Resin sealing wasp 1	<i>Passaloecus/Pemphredon</i>	Spider/ aphid hunter	1	2
	Chrysididae	Ruby tailed wasp	<i>Chrysis ignita</i> agg.	Kleptoparasites	1	0
2021						
	Torymidae	Chalcid wasp 1	<i>Monodontomerus</i> sp.	Bee parasitoid	163	935
	Torymidae	Chalcid wasp 2	<i>Monodontomerus</i> sp.	Bee parasitoid	1	127

Crabronidae	Resin sealing wasp 1	<i>Passaloecus/Pemphredon</i>	Spider/ aphid hunter	46	58
Gasteruptiidae	<i>Gasteruption jaculator</i>	<i>Gasteruption jaculator</i>	Bee parasitoid	4	17
Chrysididae	Ruby tailed wasp	<i>Chrysis ignita</i> agg.	Kleptoparasites	3	11
Ichneumonidae	Ichneumon 1		Bee parasitoid	0	10
Vespidae	Mason wasp 1	<i>Ancistrocerus</i> sp.	Lepidoptera	5	3
Ichneumonidae	Ichneumon 2		Bee parasitoid	0	2
Ichneumonidae	Ichneumon 3		Bee parasitoid	1	1
Vespidae	Mason wasp 2	<i>Ancistrocerus</i> sp.	Lepidoptera caterpillars	1	0
Vespidae	Mason wasp 3	<i>Ancistrocerus</i> sp.	Lepidoptera caterpillars	0	1
Ichneumonidae	Ichneumon 4		Bee parasitoid	1	0
Ichneumonidae	Ichneumon 5		Bee parasitoid	0	1
Ichneumonidae	Ichneumon 6		Bee parasitoid	0	1
Ichneumonidae	Ichneumon 7		Bee parasitoid	0	1
Crabronidae	Resin sealing wasp 2	<i>Passaloecus/Pemphredon</i>	Spider/ aphid hunter	0	1

Table S5. 3 Anova Type II table of generalised linear models (glm) fitted with quasipoisson distribution for the analysis of the effect of urbanisation and area of flowering plants in an allotment site on the number of larvae laid per nest by species of bees and wasps. Including testing the effect of the addition of floral resources (treatment), trap nest type (cardboard or wooden), experimental pair (n = 8) and the year which the data was collected (2020/2021). Significant terms are in bold.

Number of larva per tube			
Terms	Chisq	df	p-value
Year	0.66	1	0.42
Log(Urbanisation)	0.60	1	0.44
Species	263.15	7	<0.0001
Nest type	6.67	1	0.01
Treatment	0.59	1	0.44
Log(Urbanisation) x Species	13.74	7	0.06
Pair	4.47	7	0.61
Not included:			
log(Area of log cultivated flowers)	0.12	1	0.73
log(Area of wild flowers)	1.52	1	0.22
log(Total area of flowers)	2.16	1	0.14

Table S5. 4 Anova Type II table of generalised linear models (glm) fitted with quasipoisson distribution for the analysis of the effect of urbanisation and area of flowering plants in an allotment site on the total number of cavities filled in each allotment site. Including testing the effect of the addition of floral

resources (treatment), experimental pair (n = 8) and the year which the data was collected (2020/2021). Significant terms are in bold.

Number of tubes (nests) per site			
Terms	Chisq	df	p-value
Year	43.70	1	<0.0001
Log(Urbanisation)	5.64	1	0.02
Treatment	0.18	1	0.67
Pair	12.06	7	0.06
Not included:			
log(Area of cultivated flowers)	1.38	1	0.24
log(Area of wild flowers)	0.75	1	0.39
log(Total area of flowers)	3.02	1	0.08

Table S5. 5 Summary from generalised linear mixed effect models (MCMCglmm) for the analysis of the effect area of cultivated flowers in an allotment site on the abundance of bees and wasps (insect group) found to uptake two types of trap nests (wooden blocks and cardboard) during two years (2020,2021) and testing if floral additions (Treatment) had main or interactive effects. Significant terms are in bold.

Terms	Abundance of insects				
	Post mean	95% CI	u-95%CI	effective sample	p-value
Intercept	2.71	-9.29	14.61	5103.00	0.66
Year (2021)	4.13	2.23	6.14	2283.00	<0.0001
Nest type (Cardboard)	-2.29	-4.09	-0.51	4284.00	0.01
Log(Cultivated flowers)	-0.90	-2.79	1.03	4807.00	0.35
Insect group (wasp)	-0.37	-2.08	1.41	5716.00	0.67
Treatment (nesting+floral addition)	0.55	-1.25	2.41	5939.00	0.54
Non-significant interactions excluded from final model:					
	Log(Cultivated flowers) flowers:	Insect group:	Treatment		0.64
	Log(Cultivated flowers) flowers:	Insect group			0.37
	Log(Cultivated flowers) flowers:	Treatment			0.16
	Insect group:	Treatment			0.64

Table S5. 6 Summary from generalised linear mixed effect models (MCMCglmm) for the analysis of the effect area of cultivated flowers)in an allotment site on the species richness of bees and wasps (insect group) found to uptake two types of trap nests (wooden blocks and cardboard) during two years (2020,2021) and testing if floral additions (Treatment) had main or interactive effects. Significant terms are in bold.

Terms	Species richness				
	Post mean	95% CI	u-95%CI	effective sample	p-value
Intercept	0.80	-2.59	4.19	840.00	0.61
Year (2021)	2.00	1.40	2.67	283.00	<0.0001
Nest type (Cardboard)	-1.38	-1.90	-0.81	393.80	<0.0001
Log(Cultivated flowers)	-0.35	-0.94	0.15	794.60	0.18
Insect group (wasp)	-0.06	-0.51	0.46	630.90	0.80

Treatment (nesting+floral addition)	0.29	-0.22	0.78	614.50	0.25
Non-significant interactions excluded from final model:					
Log(Cultivated flowers) flowers:Insect group:Treatment					0.21
Log(Cultivated flowers) flowers:Insect group					0.64
Log(Cultivated flowers) flowers:Treatment					0.64
Insect group: Treatment					0.21

Table S5. 7 Summary from generalised linear mixed effect models (MCMCglmm) for the analysis of the effect urbanisation (area of impervious surface surrounding an allotment at a 250m buffer) on the abundance of bees and wasps (insect group) found to uptake two types of trap nests (wooden blocks and cardboard) during two years (2020, 2021) and testing if floral additions (Treatment) had main or interactive effects. Significant terms are in bold.

Terms	Abundance of insects				
	Post mean	95% CI	u-95%CI	effective sample	p-value
Intercept	2.1	-13.53	17.9	6440	0.78
Year (2021)	4.1821	2.3051	6.2377	2057	<0.0001
Nest type (Cardboard)	-2.42	-4.29	-0.66	3901	0.005
Log(Urbanisation)	-2.66	-5.32	-0.14	4323	0.039
Insect group (wasp)	-0.41	-2.13	1.42	5568	0.633
Treatment (nesting+floral addition)	-0.12	-1.85	1.73	5413	0.902
Non-significant interactions excluded from final model:					
Log(Urbanisation):Insect group:Treatment					0.61
Log(Urbanisation):Insect group					0.93
Log(Urbanisation):Treatment					0.63
Insect group: Treatment					0.61

Table S5. 8 Summary from generalised linear mixed effect models (MCMCglmm) for the analysis of the effect urbanisation (area of impervious surface surrounding an allotment at a 250m buffer) on the species richness of bees and wasps (insect group) found to uptake two types of trap nests (wooden blocks and cardboard) during two years (2020, 2021) and testing if floral additions (Treatment) had main or interactive effects. Significant terms are in bold.

Terms	Species richness of insects				
	Post mean	95% CI	u-95%CI	effective sample	p-value
Intercept	5.50	-3.29	15.03	908.30	0.20
Year (2021)	2.01	1.42	2.66	689.30	<0.0001
Nest type (Cardboard)	-1.38	-1.92	-0.85	722.70	<0.0001
Log(Urbanisation) (log)	-0.57	-1.38	0.15	854.10	0.11
Insect group (wasp)	-0.06	-0.52	0.45	1187.10	0.75
Treatment (nesting+floral addition)	0.09	-0.44	0.60	826.80	0.68
Non-significant interactions excluded from final model:					
Log(Urbanisation):Insect group:Treatment					0.63
Log(Urbanisation):Insect group					0.71
Log(Urbanisation):Treatment					0.74
Insect group: Treatment					0.63

Table S5. 9 Summary from generalised linear mixed effect models (MCMCglmm) for the analysis of the effect urbanisation (area of impervious surface surrounding an allotment at a 250m buffer) on the total abundance of individual species of bees and wasps found to uptake trap nests) during two years (aggregated) and testing if floral additions (Treatment) had main or interactive effects. Significant terms are in bold.

Insect species	Abundance of insects				
	Post mean	95% CI	u-95%CI	effective sample	p-value
<i>Osmia leaiana</i>					
Intercept	20.67	5.13	37.72	2556	0.016 *
Log(Urbanisation)	-1.49	-2.82	-0.15	12574 991	0.027
Treatment (nesting+floral)	-0.62	-1.80	0.64	2454	0.29
Log(Urbanisation):Treatment	-0.55	-5.72	4.86	5378	0.78
<i>Osmia bicornis</i>					
Intercept	4.34	-14.22	22.53	6711	0.52
Log(Urbanisation)	-0.16	-1.72	1.31	6792	0.80
Treatment (nesting+floral)	-0.10	-1.28	1.08	6858	0.77
Log(Urbanisation):Treatment	2.26	-7.86	12.51	8121	0.54
<i>Megachile ligniseca</i>					
Intercept	-0.01289	-40.45193	43.29041	4863	0.9757
Log(Urbanisation)	0.19338	-3.47191	3.52372	4882	0.8680
Treatment (nesting+floral)	39.62138	-7.24015	83.79068	5358	0.0899
Log(Urbanisation):Treatment	-3.38235	-7.09802	0.60458	5341	0.0878
<i>Hylaeus spp.</i>					
Intercept	-3.86832	-37.28294	23.13805	9378	0.811
Log(Urbanisation)	0.50744	-1.75999	3.28396	9398	0.682
Treatment (nesting+floral)	0.01489	-1.66528	1.84290	9700	0.985
Log(Urbanisation):Treatment	-2.204	-11.553	7.049	9700	0.604
<i>Monodontomerus spp.</i>					
Intercept	35.1105	10.5059	57.3698	6863	0.0188
Log(Urbanisation)	-2.5924	-4.3380	-0.4626	6981	0.0272
Treatment (nesting+floral)	-0.3017	-1.9174	1.6864	5467	0.5779
Log(Urbanisation):Treatment	-2.38510	-12.43157	8.85146	8607	0.465