



**This electronic thesis or dissertation has been
downloaded from Explore Bristol Research,
<http://research-information.bristol.ac.uk>**

Author:
Tew, Nick E

Title:
Floral resources and insect pollinator populations in urban landscapes

General rights

Access to the thesis is subject to the Creative Commons Attribution - NonCommercial-No Derivatives 4.0 International Public License. A copy of this may be found at <https://creativecommons.org/licenses/by-nc-nd/4.0/legalcode>. This license sets out your rights and the restrictions that apply to your access to the thesis so it is important you read this before proceeding.

Take down policy

Some pages of this thesis may have been removed for copyright restrictions prior to having it been deposited in Explore Bristol Research. However, if you have discovered material within the thesis that you consider to be unlawful e.g. breaches of copyright (either yours or that of a third party) or any other law, including but not limited to those relating to patent, trademark, confidentiality, data protection, obscenity, defamation, libel, then please contact collections-metadata@bristol.ac.uk and include the following information in your message:

- Your contact details
- Bibliographic details for the item, including a URL
- An outline nature of the complaint

Your claim will be investigated and, where appropriate, the item in question will be removed from public view as soon as possible.

Floral resources and insect pollinator populations in urban landscapes

Nicholas Tew



The ashy mining bee (*Andrena cineraria*) is a common insect pollinator in urban landscapes. Here, it is collecting floral resources from thrift (*Armeria maritima*) on a balcony in the city of Bristol. A dense nesting aggregation of the species was seen in a mown lawn on the same street (Photo: N. Tew).

A dissertation submitted to the University of Bristol in accordance with the requirements for award of the Degree of Philosophy in the Faculty of Life Sciences

March 2022

Word count: c. 32,000

Abstract

A diverse assortment of insects act as pollinators for plants, performing a valuable role in maintaining healthy functioning ecosystems as well as improving the yields of many agricultural crops. Given the overwhelming importance of pollination to plants and people, pollinator declines are of widespread concern and have led to an increased focus on pollinator conservation. One of the main drivers of pollinator loss in the countryside is the decrease in floral resources which has accompanied intensive farming practices. Meanwhile, urbanised landscapes contain some flower-rich green spaces, such as parks and gardens, which can support diverse pollinator communities, but have received less research attention. These urban pollinators could act as source populations for subsequent spread into the surrounding countryside, but even within urban landscapes they deliver an important service by pollinating wild plants and food crops.

The first aim of this thesis is to quantify floral resources in urban landscapes. Combining nectar sugar measurements with pre-existing floral abundance data, I compared nectar supplies between urban areas, farmland and nature reserves in the UK. Although the magnitude of nectar sugar production did not differ significantly among the three landscape types, urban nectar supplies were more diverse in floral origin and predominantly derived from non-native plants. Within cities, gardens provided an average of 85% of all nectar sugar and, along with allotments, produced the most diverse supplies. This shows that urban landscapes are hotspots of floral resource diversity, and that residential gardens play a critical role in feeding urban pollinator communities. Following on from these findings, I focused in detail on UK residential gardens, measuring nectar supplies through the year. I found substantial variation in the magnitude of nectar sugar production in different gardens, and this was not significantly predicted by their size. Temporal patterns in nectar supply also varied from garden to garden, but complementarity among different flowering periods led to a relatively smooth and continuous overall supply of nectar through time. These results show that the independent management of many small gardens scales up to provide a food supply for urban pollinators which is both diverse and stable through the year.

The second aim was to compare pollinator populations between urban and agricultural landscapes. Focusing on the buff-tailed bumblebee (*Bombus terrestris*), a widespread and commercially important crop pollinator in the UK, I estimated colony density using molecular markers to identify bees from the same nest. Colony density was twice as high in urbanised sites than farmed sites, with urban bees also significantly greater in body size. These results indicate that towns and cities act as population hotspots for this bumblebee species within regions dominated by intensive agriculture.

Overall, this thesis demonstrates the value of urban landscapes, and in particular of residential gardens, in providing floral resources to insect pollinators, emphasising the importance of including these areas when planning pollinator conservation strategies.

Acknowledgements

My PhD journey has lasted four and a half years, during which time I have lived in four different English counties, attended conferences in the UK and overseas, taught undergraduates, enjoyed three field seasons, given talks and presentations, attended courses, conducted an internship and much more besides. Throughout, I have received a great deal of support and encouragement from others, which really helped to keep me motivated.

My supervisory team of Jane, Kath, Ian and Steph was wonderfully balanced, with different perspectives and fields of expertise complementing each other beautifully. Jane has provided great enthusiasm and optimism throughout, especially during periods of uncertainty and frustration, along with a talent for thinking up creative research ideas. Kath's regular support, even after she moved institutions, has been invaluable, while her attention to detail and methodological expertise helped bring ideas to fruition. I am also very lucky to have had Ian's statistical advice and Steph's horticultural and entomological perspectives, which improved my thesis considerably.

I was fortunate to receive generous financial support for my work, from the Natural Environment Research Council (NERC) and the Royal Horticultural Society (RHS). The RHS funding ensured I could employ two field assistants, helping me collect important data, and a NERC grant to work at their Environmental Omics Facility in Sheffield provided molecular training and analysis. I am also grateful to UK Research and Innovation, the NERC GW4+ DTP and the University of Bristol for coordinating an extension to my stipend funding, supporting me during the disruption caused by COVID-19.

I know how envious other PhD students in the LSB are of the Community Ecology Group. While COVID-19 restricted some of my social experiences, I will always remember winter trips to the Gower, potluck dinners, cakes in the Sky Lounge and post-viva drinks very fondly. Thanks to everyone in the group, and the wider LSB, for providing such a friendly atmosphere. Bristol will always hold a special place in my heart.

I cannot possibly thank everyone by name who helped to ensure my experience of a doing PhD was predominantly positive, the list is simply too long. But thanks to my supervisors; my friends; my university colleagues in Bristol and Sheffield; Stuart, and other staff at the Avon Wildlife Trust; my family; my resilient field assistants Jo and Anna; academics I met at conferences; journal editors and reviewers; paper co-authors; gardeners; farmers and so many other people.

Author's declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's Regulations and Code of Practice for Research Degree Programmes and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

Nicholas Tew, 15 March 2022

COVID-19 statement

Due to restrictions brought about by the COVID-19 pandemic, I did not conduct the field and molecular work for Chapter 4 in 2020, as initially planned, but instead postponed it by 12 months to 2021. As a result, I was awarded a six-month extension to my stipend funding (coordinated by UK Research and Innovation, the NERC GW4+ DTP and the University of Bristol) and a corresponding six-month extension to my thesis submission deadline (granted by the University of Bristol). With the allowance of this extra time, no planned research activities were cancelled due to the COVID-19 pandemic. However, the location of the field sites chosen for sampling in Chapter 4 were partially determined based on pandemic-associated university restrictions and the period between the completion of laboratory work for Chapter 4 and the thesis submission deadline was reduced from ten months to four months. In addition, there was a necessary ten-day break in sampling during the 2021 field season due to a period of self-isolation.

Publications and co-author contributions

An adapted version of Chapter 2 was published in *Journal of Ecology* on 26 January 2021.

Reference: Tew, N.E., Memmott, J., Vaughan, I.P., Bird, S., Stone, G.N., Potts, S.G. and Baldock, K.C., 2021. Quantifying nectar production by flowering plants in urban and rural landscapes. *Journal of Ecology*, 109(4), pp.1747-1757.

Authors' contributions: N.T., J.M. and K.B. conceived the ideas and designed the methodology; N.T. collected the data; N.T. analysed the data with input from I.V. and K.B.; N.T. wrote the manuscript with input from K.B., J.M., I.V., S.B., G.S. and S.P.

An adapted version of Chapter 3 was published in *Journal of Applied Ecology* on 04 January 2022.

Reference: Tew, N.E., Baldock, K.C., Vaughan, I.P., Bird, S. and Memmott, J., 2022. Turnover in floral composition explains species diversity and temporal stability in the nectar supply of urban residential gardens. *Journal of Applied Ecology*, 59, pp.801-811.

Authors' contributions: N.T., J.M. and K.B. conceived the ideas and designed the methodology; N.T. collected the data; N.T. analysed the data with input from I.V.; N.T. wrote the manuscript with input from J.M., K.B., I.V. and S.B.

Table of contents

Chapter 1: Introduction	1
1.1 The diversity of animals that pollinate	2
1.2 The importance of pollinators to plants and people.....	2
1.3 The resources required by insect pollinators	4
1.4 Threats to insect pollinators.....	6
1.5 Insect pollinators in urban landscapes	7
1.6 Conserving insect pollinators	8
1.7 Knowledge gaps and thesis aims	10
Chapter 2: Quantifying the floral nectar supply in urban and rural landscapes	11
2.1 Introduction	12
2.2 Materials and methods.....	13
2.3 Results	21
2.4 Discussion.....	26
Chapter 3: Spatial and temporal variation in the floral nectar supply of urban residential gardens	30
3.1 Introduction	31
3.2 Materials and methods.....	32
3.3 Results	37
3.4 Discussion.....	44
Chapter 4: Comparing buff-tailed bumblebee populations between urban and farmland landscapes	48
4.1 Introduction	49
4.2 Materials and methods.....	50
4.3 Results	58
4.4 Discussion.....	61
Chapter 5: Discussion	67
5.1 Summary of research findings.....	68
5.2 The supply of floral resources in urban landscapes and its consequences for pollinating insects.....	69
5.3 Thesis outputs and applications to conservation	74
5.4 Limitations of this thesis and recommendations for future research	75
5.5 Concluding remarks.....	79
References	80
Appendix 1: Supplementary information for Chapter 2	104
Appendix 1: Supplementary information for Chapter 3	110

List of figures

2.1 Nectar quantification methods.....	16
2.2 Relationship between nectar production of taxa measured in two locations	20
2.3 Relationship between predicted and empirical values of nectar production	21
2.4 Comparison of nectar supplies among landscapes	22
2.5 The composition of nectar supplies among landscapes	23
2.6 Comparison of nectar supplies among urban land uses.....	24
2.7 The relationship between floral abundance and nectar production	25
3.1 Survey regions.....	33
3.2 Spatial and temporal patterns in the magnitude of garden nectar supplies.....	38
3.3 Patterns of temporal stability in garden nectar supplies	39
3.4 Flowering plant richness through the year.....	40
3.5 The contribution of plant taxa to monthly nectar sugar production	41
3.6 Nectar supply by native status	42
3.7 Nectar supply by plant life form.....	42
3.8 Nectar supply by flower structure	43
4.1 Sampling sites.....	51
4.2 Maps of sampling areas	56
4.3 Body size for urban and farmland bumblebees	59
4.4 Colony density for urban and farmland bumblebees.....	61
4.5 A visual comparison of two fields classified as improved grassland	63
5.1 Cities are home to many novel ecological interactions	72

List of tables

2.1 Research questions addressed in this study	14
2.2 Nectar sampling locations	16
2.3 Nectar production of urban land uses	25
3.1 Survey regions	33
3.2 Statistical models for analysing nectar production	35
3.3 Statistical models for analysing floral richness	36
3.4 The most common flowering plants	41
3.5 Validation of stratified sampling method	44
3.6 Recommended plants for different seasonal periods in UK gardens	47
4.1 The composition of urban sampling sites	51
4.2 The composition of farmland sampling sites	52
4.3 A description of farmland sampling sites	53
4.4 Dates of sampling visits to sites	54
4.5 Details of the 11 microsatellite loci used for genotyping	55
4.6 The most visited plant taxa by bumblebees collected in urban and farmland landscapes	59
4.7 Bumblebee numbers and colony density estimates	60

Chapter 1

Introduction



The tree bumblebee (*Bombus hypnorum*) is a relatively new member of the UK pollinator fauna, first recorded in 2001. Here, a newly emerged queen explores an early crocus flower (*Crocus tommasinianus*) in the University of Bristol Botanic Garden (Photo: N. Tew).

1.1 The diversity of animals that pollinate

From a metre-long lemur in Madagascar to a North American mining bee no larger than a chia seed, pollinators come in all shapes and sizes. There are thought to be as many as 350,000 described species of vertebrates and invertebrates which pollinate (Ollerton, 2017; Wardhaugh, 2015), spanning many distantly related taxonomic groups, united only by their propensity to transfer pollen between plants, facilitating their reproduction. The main groups of vertebrate pollinator are birds and bats, although some flowers are pollinated by non-flying mammals and even lizards (Carthew and Goldingay, 1997; Olesen and Valido, 2003). However, an estimated 99.5% of all pollinating species are invertebrates and of these, 99.0% belong to the ‘big four’ insect orders: Lepidoptera (butterflies and moths), Coleoptera (beetles), Hymenoptera (bees, wasps, ants and sawflies) and Diptera (true flies) (Ollerton, 2017; Wardhaugh, 2015). This thesis focuses solely on insects because they are the most important group of pollinators worldwide and because vertebrate pollination does not occur in the UK, where all fieldwork took place.

I use the terms pollinator and flower visitor interchangeably, as is commonly done in the field, but visitation does not guarantee pollination and insects do not contribute equally to the reproduction of different plants. Instead, the importance of a pollinator to a particular plant species depends on a combination of how much pollen it deposits per flower visit (linked to morphological traits like body size, shape and the prevalence of hair-like setae) and the frequency of visits (affected by local abundance and mobility) (Ballantyne et al., 2017, 2015; Földesi et al., 2020; King et al., 2013). At a global scale, bees and flies are considered to be the two insect groups with the most widespread importance as pollinators, although the contribution of moths is likely to have been underestimated due to their nocturnal activity (Ollerton, 2017; Rader et al., 2016; Walton et al., 2020).

1.2 The importance of pollinators to plants and people

It is estimated that 87.5% of the world’s flowering plant (angiosperm) species are pollinated, at least in part, by animals (Ollerton et al., 2011). The others, along with most non-flowering seed plants (gymnosperms), rely on the wind (or occasionally water) for pollen transfer and hence sexual reproduction. Wind pollination remains an effective strategy for some hugely abundant taxa, including grasses and conifers, which dominate many ecosystems (Regal, 1982). However, the transfer of pollen by an animal vector has some major differences and context-dependent advantages which have led to its great success as a strategy (Culley et al., 2002). In particular, flower-visiting animals can transport pollen directly from anther to stigma with less wasted, and can do so in windless conditions (Midgley et al., 1991).

The value of pollinators to society is immense, but challenging to quantify as so many ecosystem services depend ultimately on the pollination of flowering plants (Kremen et al., 2007; Potts et al., 2016). For example, pollinating animals may indirectly contribute towards carbon storage, flood prevention and ecotourism by facilitating sexual reproduction among rainforest trees. The role of pollinators in agriculture is more widely appreciated and its value more readily estimated. By promoting the development of fruits and seeds, pollinators improve the yields of 76% of the world's leading food crops and are essential in the production of many, such as the Brazil nut, cocoa and kiwifruit (Klein et al., 2007). Because our diets heavily comprise wind-pollinated cereals (particularly maize, rice and wheat), only a modest 5-8% of global crop production (valued at US\$235 to 577 billion per annum) can be directly attributed to animal pollination (IPBES, 2016). However, pollinators are indispensable in ensuring diverse and nutritious diets, and thus are favourable to human health, especially in the developing world (Potts et al., 2016; Smith et al., 2015).

Given the importance of insects for pollinating wild and crop plants in rural environments, it may not be apparent why urban pollinator biodiversity is valuable, except in potentially providing source populations for subsequent spread into the surrounding countryside (Gill et al., 2016; Hall et al., 2017). However, urban landscapes are heterogenous mosaics, often comprising semi-natural areas including nature reserves, which harbour populations of wild plants that require pollination (Baldock et al., 2019; Dearborn and Kark, 2010; Prendergast and Ollerton, 2021). In addition, 6% of global cropland is found in urban environments (Thebo et al., 2014), with urban agriculture particularly important in the developing world (Armar-Klemesu, 2000; Orsini et al., 2013), but food is also commonly grown in allotments or community gardens in developed countries (Breuste and Artmann, 2015; Nicholls et al., 2020). Hence urban insect communities can provide a valuable ecosystem service by pollinating crop plants (Lowenstein et al., 2014; Potter and LeBuhn, 2015). More than half the world's population now lives in an urban area, a value expected to increase to 67% by 2050 (United Nations, 2014) and already over 80% in post-industrialised countries like England (Government Office for Science, 2021). As such, urban biodiversity plays a valuable role in human wellbeing and promoting awareness of environmental issues (Dearborn and Kark, 2010; Fuller et al., 2007). Citizen science projects are a great way to engage urban residents with pollinators and at the same time, to collect valuable data to aid in their conservation (e.g. Deguines et al., 2012; Osborne et al., 2007). Finally, because urban areas are sites of extreme environmental and ecological change concentrated into small spatial and temporal scales, they can be useful as model systems in which to study the responses of species and communities to factors such as climate warming, habitat fragmentation, pollution and the spread of non-native taxa (Dearborn and Kark, 2010; Grimm et al., 2008; Harrison and Winfree, 2015).

1.3 The resources required by insect pollinators

To complete their life cycles and successfully reproduce, insect pollinators require a suite of different resources, which include sources of food and places to nest and shelter (Antoine and Forrest, 2021; Vaudo et al., 2015; Wäckers et al., 2007). The resources required vary substantially among taxa and at different life stages, with important implications for the pollinator communities supported within a particular habitat or broader landscape.

1.3.1 Floral nectar

Floral nectar, a major focus of this thesis, is an aqueous sugar solution produced by plant nectaries and secreted as an attractant, rewarding flower visitors (Heil, 2011; Roy et al., 2017). It is vital as a source of energy to power the flight muscles of insect pollinators (McCallum et al., 2013) and so is consumed by a wide variety of insects at the adult stage, including moths, butterflies, wasps, flies and bees (which also provision their larvae with some nectar) (Wäckers et al., 2007). Nectar sugars almost entirely comprise the disaccharide sucrose and its two component monosaccharides glucose and fructose (Roy et al., 2017), with the total sugar concentration (often expressed as the percentage of sugar by mass of solution) varying substantially among flowers of different species, in the range 6 to 85% (Pamminger et al., 2019). Although the principal solute is sugar, nectars also contain a variety of metabolites at lower concentrations, including amino acids, proteins, vitamins, metal ions and alkaloids, which can confer insects with nutritional and medicinal benefits (Nicolson, 2022; Richardson et al., 2015).

Nectar is costly for a plant to produce, selecting for a variety of adaptive strategies to optimise the trade-off between nectar production and pollination (Obeso, 2002; Pacini et al., 2003; Pyke et al., 1991). For example, some flowers have evolved a deep corolla tube so that their nectar is only available to a subset of relatively long-tongued pollinators, such as birds, bumblebees or moths, while others with more open structures present nectar to a much wider selection of floral visitors (Armbruster, 2017; Stang et al., 2006). An overly high degree of morphological specialisation may reduce visit frequency and render plants over-reliant on a few pollinator taxa, but a highly generalised pollination syndrome could result in a lower efficiency of conspecific pollen transfer during visits and the loss of nectar to insects which do not influence pollination (Aigner, 2001; Armbruster, 2017). Nectar chemistry is also likely to be influenced by natural selection, leading to variation in the concentration of sugars and other metabolites (González-Teuber and Heil, 2009; Nicolson, 2022; Parachnowitsch et al., 2019). For example, relatively low levels of toxic compounds in nectar may increase plant fitness by preferentially modifying pollinator behaviour and preventing spoilage by microbes (González-Teuber and Heil, 2009; Heil, 2011; Nicolson, 2022; Roy et al., 2017).

1.3.2 Pollen and other floral resources

In contrast to nectar, pollen is a powdery solid comprising grains 10 to 100 µm in diameter which readily adhere to insects and can play a role in pollinator attraction as well as plant reproduction (Hao et al., 2020; Pacini and Hesse, 2005). Pollen complements nectar as a nutritional resource, providing a diversity of proteins, lipids, vitamins and minerals necessary for healthy growth and development (Roulston and Cane, 2000). It is readily consumed by developing bee larvae (though adults conduct the necessary foraging) as well as by some beetles, hoverflies and other insects (Goulson, 1999; Wäckers et al., 2007; Weiner et al., 2010). Protein is the principal source of nutrition, comprising up to 60% of the dry weight of pollen, although the importance of lipids (up to 20% of dry weight) should not be overlooked (Campos et al., 2008; Roulston and Cane, 2000; Vaudo et al., 2020a). Pollen is a more complex nutritional resource than nectar, with the pollen of each species having a particular profile of different amino acids and lipids, which coarse metrics fail to capture. For example, some types of pollen are deficient in certain essential amino acids, highlighting the importance of insects having access to a variety of pollen sources to realise a balanced diet (Roulston and Cane, 2000). In addition to nectar and pollen, some bees visit flowers to collect oils, resins and volatile compounds, used in larval nutrition, nest construction and olfactory signalling (Buchmann, 1987; Drescher et al., 2014; Policarová et al., 2019). Other visitors to flowers may feed directly on the plant tissue or simply be using them as a site to rest or to mate.

1.3.3 Floral specialisation

The degree of floral specialisation by pollinators spans a broad spectrum from single species specialists up to super-generalists, capable of visiting hundreds or thousands of plant taxa (Armbruster, 2017). A moderate to high degree of generalisation is the norm in temperate pollination systems, with insects tending to visit a variety of plant taxa, but not all that are available (Memmott, 1999; Waser et al., 1996). Extreme examples of generalisation are provided by the western honeybee (*Apis mellifera*) and the buff-tailed bumblebee (*Bombus terrestris*), which collect nectar and pollen from a vast array of plants native to regions all over the world (Lucek et al., 2019; Potter et al., 2019; Rasmont et al., 2008). In contrast, certain moth species in the family Prodoxidae have coevolved with *Yucca* plants, with adults only visiting their flowers and larvae feeding obligately on the developing seeds following pollination (Pellmyr et al., 1996).

The range of flowers visited by an insect often depends on the floral resources being collected. For example, oligolectic solitary bees specialise on pollen from a single plant genus or family, given more closely-related pollens share more similar nutritional profiles (Roulston et al., 2000; Zu et al., 2021), but they are often less selective when nectar foraging because a wide variety of taxa provide energy-rich sugar (Falk, 2015). The range of nectar sources visited is mainly constrained by compatible morphology between flowers and insects, rather than by nutritional factors (Stang et al., 2006). In particular, the degree of size matching between nectar tube depth and proboscis length affects foraging efficiency and hence flower visitation choice (Klumpers et

al., 2019). Some of the most extreme examples of floral specialisation occur when insects visit flowers for floral oils, such as in the interaction between *Rediviva* bees and *Diascia* flowers in South Africa (Buchmann, 1987).

1.3.4 Non-floral resources

With the exception of bees, the larvae of insect pollinators feed on wide variety of non-floral resources. Most larval Lepidoptera (caterpillars) consume living plant tissue, often with a high degree of taxonomic specialisation on particular foodplants (Futuyma, 1976). Wasp larvae are typically insectivorous and many are parasitoids (Brock et al., 2021), while beetles and flies feed on various kinds of living and dead organic matter at the larval stage, including fungi, carrion, wood and faeces (Chinery, 2012). Even as flower-visiting adults, the food requirements of pollinators extend beyond floral resources. Fruit, extrafloral nectar (secreted by nectaries outside flowers) and honeydew (sugar-rich excretions from sap-sucking aphids and scale insects) can be significant non-floral sources of sugar (Requier and Leonhardt, 2020). Honeydew is so abundant in some woodlands that it can be the main component of commercially-important honeys (Requier and Leonhardt, 2020). The reliance of pollinators on floral resources varies such that some specialise almost exclusively upon them (e.g. most bees and adult hoverflies) while others merely supplement their diet with some nectar and/or pollen (e.g. many flies and beetles). Bees are unique in that they feed predominantly on floral resources as both larvae and adults.

As well as floral and non-floral sources of food, many pollinator species need places to nest and hibernate. Colonies of eusocial bees and wasps reside in nests usually underground, inside tree holes, in buildings or attached to vegetation. Locating an appropriate nest site is a prerequisite for the foundation of a colony and hence subsequent reproduction, such as in the buff-tailed bumblebee (*B. terrestris*), whose queens search for abandoned rodent burrows in spring (Inoue et al., 2008). Solitary bees and wasps also require nest sites and may construct burrows, if the soil conditions are appropriate, or use pre-existing cavities such as those in dead wood, hollow plant stems, walls and even snail shells (Antoine and Forrest, 2021; MacIvor, 2017).

1.4 Threats to insect pollinators

Insect pollinators have not escaped the widespread declines in biodiversity resulting from pervasive human activity (Butchart et al., 2010). The best evidence that pollinators are declining has come from Europe and North America (Biesmeijer et al., 2006; Cameron et al., 2011; Powney et al., 2019; Soroye et al., 2020; Thomas, 2004), although equivalent trends are likely to be found in other parts of the world if the necessary data can be collected (e.g. Morales et al., 2013; Pauw, 2007). There is a strong geographic bias in pollinator research towards Europe and North America, despite developing nations being particularly vulnerable to pollinator loss (Archer et al., 2014; IPBES, 2016).

The major threats facing pollinators and driving their declines are habitat loss, pesticide use, climate change and the spread of parasites and pathogens (Dicks et al., 2021; Goulson et al., 2015; Potts et al., 2016; Soroye et al., 2020). The principal cause underlying most habitat loss and pesticide use is intensive agriculture, which is particularly damaging to pollinators and wider biodiversity (Díaz et al., 2019; Goulson et al., 2015; Tilman et al., 2017). Landscapes dominated by modern industrial farming lack the abundant and diverse resources required by pollinators because of the prevalence of crop monocultures, the application of fertilisers and herbicides, heavy grazing by livestock and the removal of hedgerows and other remnant flower-rich patches (Baude et al., 2016; Carvell et al., 2006; Langlois et al., 2020; Pywell et al., 2005).

1.5 Insect pollinators in urban landscapes

Urbanisation is a major driver of environmental change, with towns and cities differing substantially from rural areas in their land cover, hydrology, biogeochemistry and climate (Grimm et al., 2008). Urban areas already cover around 2 to 3% of land worldwide (Liu et al., 2014), 8% of the densely-populated UK (Office for National Statistics, 2019a), and they are continuously expanding (Gao and O'Neill, 2020). Although many animal and plant species have been negatively impacted (Batáry et al., 2018; McKinney, 2008; Seto et al., 2012), responses vary greatly among taxa, with winners as well as losers in urban environments (Aronson et al., 2014; Baldock, 2020; Chace and Walsh, 2006; McKinney, 2008).

Urban green spaces, including parks, residential gardens, allotments and cemeteries, are vital habitats for pollinators, found within an inhospitable matrix comprising roads, buildings and other impervious surfaces (Baldock et al., 2019). Gardens and allotments, in particular, can be rich in floral resources and may harbour high pollinator diversity (Baldock et al., 2019; Fetridge et al., 2008; Staab et al., 2020). For example, one third of British hoverfly species and one fifth of the British bee fauna were recorded in a single suburban garden in the city of Leicester, studied intensively over a period of 30 years (Owen, 2010). Nevertheless, there is a high degree of variation among urban green spaces in their management, which affects the pollinator communities they can support (Garbuzov et al., 2015; Lange-Kabitz et al., 2021; Loram et al., 2008a; Philpott et al., 2020). Many green spaces are managed for structural simplicity, with large areas of short amenity grassland and comparatively little complex vegetation, while others are rich in floral and non-floral resources (Loram et al., 2008a; McKinney, 2008; Osborne et al., 2007). An example of the variety in green spaces is the comparison between a typical playing field, used for sport, and a patch of allotments, used for growing fruits, vegetables and ornamental flowers.

The floral composition of some urban green spaces differs markedly from that of farmland or semi-natural habitats. In particular, non-native ornamental flowering plants are predominant in gardens and allotments, leading to taxonomically diverse yet ecologically novel communities (Baldock et al., 2019, 2015; Loram et al., 2008b; Lowenstein and Minor, 2016), which often have an extended flowering season due to the presence of

exotic species and horticultural cultivars with particularly early or late flowering periods (Harrison and Winfree, 2015; Salisbury et al., 2015). Other urban green spaces, including parks and cemeteries, often more closely resemble areas of grazed pasture, so overlap in species composition much more with farmland, comprised heavily of native grassland flora (Baldock et al., 2019). As a result of variation in greenspace management and a high degree of floral diversity, we would expect urban pollinator communities to be rich in species, but to differ in composition from those in rural landscapes. Taxa with generalist foraging behaviour are likely to be particularly successful as they can profit from the floral resources provided by a wide array of non-native plants and horticultural cultivars.

Some studies have found an increased species richness (Baldock et al., 2015; Theodorou et al., 2017, 2020) or colony growth rate (Goulson et al., 2002; Samuelson et al., 2018) of bees in towns and cities compared with the farmed countryside. As such, urban environments could represent hotspots of pollinator abundance and diversity within landscapes dominated by modern industrial farming (Hall et al., 2017; Theodorou et al., 2020). However, contrasting patterns are also reported (e.g. Ahrné et al., 2009; Bates et al., 2011; Lagucki et al., 2017; Milano et al., 2019), with differences in the level of urbanisation and agricultural management intensity of comparison sites likely to affect conclusions among studies (Prendergast et al., 2022; Wenzel et al., 2020). While bees sometimes prosper in urban environments, other pollinator taxa including butterflies, beetles and true flies appear to be more sensitive to the transformational changes brought about by urbanisation and are more negatively impacted (Baldock et al., 2015; Bates et al., 2011; Deguines et al., 2012; Geslin et al., 2013; Theodorou et al., 2020). An important reason for this difference may be that bees feed on floral resources both as larvae and adults, which are common in urban green spaces (Baldock et al., 2019; Hülsmann et al., 2015), whereas other taxa require additional resources such as particular larval foodplants, which could be scarce (see section 1.3.4). The composition of urban bee communities themselves is often biased towards species with particular traits, notably cavity (versus ground) nesters, diet generalists and eusocial taxa (Cane et al., 2006; Deguines et al., 2016; Prendergast et al., 2022; Wenzel et al., 2020), although a lack of independence among traits makes interpreting these patterns challenging (Williams et al., 2010).

1.6 Conserving pollinating insects

The increasing evidence for pollinator declines, coupled with a greater appreciation of their widespread importance, has led to a focus on safeguarding pollinators (Gill et al., 2016; Potts et al., 2016). Pollinator populations are regulated by the availability in time and space of particular resources (especially nectar, pollen, nest sites and larval food), along with the timing and severity of incidental risks (such as parasites and pathogens, pesticides, predators and extreme weather events) (Roulston and Goodell, 2011). As such, measures to conserve pollinators usually focus on increasing resources, decreasing risks, or a combination of the two.

1.6.1 Conservation in the countryside

Maintaining networks of biodiverse protected areas remains a valuable strategy in conservation, but this must be in conjunction with improving the permeability of agricultural landscapes to pollinators (Dicks et al., 2016). Rural environments are often dominated by intensively managed farmland, an environment which provides few floral resources and a high exposure to agrochemicals (Goulson et al., 2015). To boost the abundance and diversity of flowering plants, farmers in many European countries are paid subsidies to sow wildflower strips around field margins, manage grasslands less intensively, increase hedgerow extent or participate in a number of other agri-environment schemes (Kleijn and Sutherland, 2003). Floral enhancements such as these often have positive effects on pollinator abundance and richness at a local scale, but responses are variable and heavily dependent on landscape context (Batáry et al., 2011; Scheper et al., 2015, 2013). Farmers can also contribute towards pollinator conservation in the countryside by reducing their reliance upon agrochemicals (herbicides, fungicides, insecticides and fertilisers), applying lower doses and adopting ecological intensification to maintain yields (Bommarco et al., 2013; Inclán et al., 2015; Potts et al., 2016).

1.6.2 Conservation in urban areas

Urban pollinator conservation tends to involve smaller-scale interventions than in the countryside, with more stakeholders involved (Baldock, 2020; Hall et al., 2017). Here, individual members of the public can play a valuable role through the management of their gardens and allotments (Baldock et al., 2019; Goddard et al., 2010), although decisions by institutions and local governments may affect larger areas of land. Floral resource enhancement usually takes the form of pollinator-friendly plantings, sown wildflower meadows and relaxed mowing regimes to promote flowering in grassland (Baldock, 2020; Hicks et al., 2016; Watson et al., 2020), where citizen science initiatives such as Plantlife's 'No Mow May' can be popular and effective (Toro and Ribbons, 2020). Artificial trap nests (often called bee hotels) are frequently used by cavity-nesting solitary bees and wasps in urban areas, although their potential to boost populations is not known, nor is the extent to which they might promote the spread of diseases (Fortel et al., 2016; MacIvor, 2017).

In general, urban pollinator communities benefit from the wildlife friendly management of green spaces, which aims to increase the extent, diversity and complexity of vegetation, while at the same time reducing the inputs of pesticides and herbicides (Ellis and Wilkinson, 2020; Majewska and Altizer, 2020; Muratet and Fontaine, 2015). A limited understanding of pollinator conservation by land managers and the lack of awareness of insect-friendly plant species remains a barrier to maximising the value of urban green spaces (Garbuzov and Ratnieks, 2014a; Lindemann-Matthies et al., 2021; Wilson et al., 2017). A paucity of knowledge can result in misunderstandings, such as the desire to keep honeybee hives to help declining wild pollinators (Egerer and Kowarik, 2020), emphasising the importance of education initiatives (Fischer et al., 2020; Wilson et al., 2017).

1.7 Knowledge gaps and thesis aims

The study of floral resources and insect pollinator populations in urban landscapes is relatively new and as such, there are a number of major gaps in our knowledge. In this thesis, I collect empirical data in the field with the goal of addressing two overarching aims, described below. Following this introductory chapter (Chapter 1), the thesis is organised into three data chapters (Chapters 2, 3 and 4) and a final discussion chapter (Chapter 5).

1.7.1 Quantifying floral resources in urban landscapes

Although the supply of floral resources has been quantified in some rural landscapes (e.g. Baude et al., 2016; Flo et al., 2018; Langlois et al., 2020; Timberlake et al., 2019), we do not have equivalent measurements for towns and cities. A study investigating changes in nectar supply at a national scale for Great Britain excluded urban areas due to a lack of underlying floral abundance data (Baude et al., 2016). Given the importance of floral resources in regulating insect pollinator populations (Roulston and Goodell, 2011), this is a major barrier to our understanding of urban pollinators and our ability to conserve them. In Chapter 2, I address this knowledge gap by quantifying the floral nectar supply of UK towns and cities, comparing it with that of rural areas in both magnitude and composition, and assessing how it is distributed among different urban land uses. In Chapter 3, I focus in detail on residential gardens (identified as the most important land use for nectar provision in Chapter 2) by measuring variation in nectar production among gardens through the year.

1.7.2 Comparing pollinator populations between urban and agricultural landscapes

A number of studies have compared the abundance and/or richness of insect pollinators between urban and agricultural sites through the visual observation or pan trapping of foragers (e.g. Baldock et al., 2015; Theodorou et al., 2020; Verboven et al., 2014). However, it is challenging to reliably compare the effective population sizes of eusocial bumblebees because they are determined by the number of nest-founding queens, rather than workers, which rarely reproduce (Darvill et al., 2004; Knight et al., 2005). In Chapter 4, I overcome this obstacle by comparing the population density of the buff-tailed bumblebee (*B. terrestris*) between UK urban and agricultural environments using molecular markers to identify separate colonies, and I subsequently link my findings back to the data on floral resources I collected in Chapters 2 and 3.

Chapter 2

Quantifying the floral nectar supply in urban and rural landscapes



The Serbian bellflower (*Campanula poscharskyana*) is native to the Dinaric Alps of Southeast Europe but has become naturalised in urban landscapes in the UK. Here, opposite the University of Bristol's Life Sciences Building, it grows in a wall which mimics the rocky environment of its home (Photo: N. Tew).

2.1 Introduction

Large-scale changes to land use and management intensity have resulted in the landscape-level depletion of floral resources, which provide food for insect pollinators (Baude et al., 2016; Carvell et al., 2006). A reduction in both the quantity and diversity of floral resources (nectar and pollen) is a major factor contributing towards the declines pollinators are experiencing, particularly in Europe and North America (Goulson et al., 2015; Roulston and Goodell, 2011). Given the key role pollinators play in the functioning of terrestrial ecosystems and their contribution to agricultural productivity (Klein et al., 2007; Ollerton et al., 2011), there is a need to quantify their food supply across entire landscapes.

Nectar supply has been quantified in some rural landscapes (Baude et al., 2016; Flo et al., 2018; Timberlake et al., 2019), but equivalent data for urban settings are lacking (but see Hicks et al. (2016) for nectar and pollen resources in urban flower meadows). This is an important knowledge gap because towns and cities are highly modified environments which are expanding rapidly worldwide (Grimm et al., 2008; Seto et al., 2012). Although urbanisation is regarded as a major threat to biodiversity (Chace and Walsh, 2006; McKinney, 2008; Seto et al., 2012), insect pollinators, particularly bees, can show a surprising degree of tolerance towards urban habitats (Baldock, 2020; Hall et al., 2017; Wenzel et al., 2020). For example, studies in the UK and Germany have found a higher species richness of bees in urban sites compared with surrounding farmland (Baldock et al., 2015; Theodorou et al., 2017, 2020), although contrasting patterns are also reported (Ahrné et al., 2009; Bates et al., 2011; Lagucki et al., 2017), probably a result of variation in urbanisation and management intensity at the study sites (Wenzel et al., 2020). The comparative success of bees in urban areas is likely to be influenced by the availability of flower-rich green spaces, such as parks and residential gardens (Baldock et al., 2019; Hülsmann et al., 2015). These habitats may be important sources of nectar and pollen due in part to the planting of a wide variety of ornamental flowering plants, some of which are attractive to insect pollinators (Garbuzov and Ratnieks, 2014b; Rollings and Goulson, 2019). This is further supported by experiments which recorded bumblebee colonies growing larger in urban and suburban habitats versus agricultural areas (Goulson et al., 2002; Samuelson et al., 2018; but see Milano et al. (2019) for a counter example).

The aim of this study is, for the first time, to quantify the nectar supply of entire urban landscapes, thereby allowing direct comparisons with rural areas, and to investigate the spatial distribution of nectar sugar within cities. Flower counts are typically used as a proxy for nectar and pollen resources (e.g. Baldock et al., 2019; Lowenstein et al., 2018; Matteson et al., 2013, but see Baude et al. (2016); Hicks et al. (2016); Timberlake et al. (2019) for exceptions), with the implicit assumption that each flower provides a similar quantity of food for foraging pollinators. However, this is a major simplification as the amount of nectar and pollen provided by individual flowers of different plant taxa can vary over orders of magnitude (Baude et al., 2016; Hicks et al., 2016). Counts may also provide an especially poor proxy for resource production in urban areas as there is a high proportion of ornamental plants, selectively bred for floral traits that are attractive to people rather than insects, which may provide less nectar and/or pollen (Corbet et al., 2001). At present, we lack a dataset

encompassing empirical values of floral resource production for a wide selection of plants commonly found in urban areas.

In this study, I measure the nectar sugar production of flowers and combine the resulting values with flower counts from two previous studies to quantify the nectar supply in UK urban and rural landscapes. I focus on nectar because it has a simpler compositional profile than pollen, making the total mass of nectar sugar more relevant as a common currency through which to compare the resource value of different land uses (Baude et al., 2016). In addition, nectar productivity data already exist for a wide variety of UK native plants (Baude et al., 2016), allowing me to build on their dataset by contributing values for many ornamental non-native taxa. Nectar production is affected by a wide variety of factors, such as the time of day, weather conditions, soil moisture and age of the flower, making it challenging to measure reliably (Comba et al., 1999b; Descamps et al., 2018; Phillips et al., 2018; Waser and Price, 2016). However, by quantifying the nectar accumulated over a one-day period for many flowers of each species, often sampled in different locations on separate days, I was able to obtain a reliable measure of the taxon-specific quantity of nectar sugar.

I asked two main research questions with the subsequent data: (1) How does the nectar supply differ between urban, farmland and nature reserve landscapes? Baldock et al. (2015) reported that pollinator abundance and richness were comparable among these three landscapes, but we do not know how they differ in floral resources. (2) How does the nectar supply differ among the separate land uses that comprise urban landscapes? Towns and cities are heterogeneous patchworks of distinct land uses that differ markedly in their value for insect pollinators (Baldock et al., 2019) and so it is important to understand their relative contributions to landscape-level nectar supply. I also examined the relationship between floral abundance and nectar sugar production to assess the strengths and weaknesses of using flower counts as a proxy for nectar resources.

2.2 Materials and methods

To quantify the nectar supply in urban and rural landscapes I combined data on floral abundance with nectar sugar production values (see Table 2.1). Floral abundance was measured in UK urban and rural areas by Baldock et al. (2019, 2015), and nectar production by Baude et al. (2016), Hicks et al. (2016), Timberlake et al. (2019), or in this study. Most published nectar sugar values correspond to UK native species, but urban landscapes contain a high proportion of non-native plants (Baldock et al., 2019; Loram et al., 2008b). Consequently, I focused my sampling of nectar in the field on the wide variety of non-native species recorded in UK towns and cities, informed by species lists associated with Baldock et al. (2019).

Table 2.1. Research questions addressed in this study. This table shows the locations of the floral abundance sampling and the data sources used to address both research questions.

Study question	Study locations	Floral abundance data source	Number of plant taxa	Nectar data sources
Q1: How does nectar supply differ between urban, farmland and nature reserve landscapes?	In/around 12 UK towns/cities	Baldock et al. 2015	206	This study (empirical) This study (modelled) Baude et al. 2016 Hicks et al. 2016
Q2: How does nectar supply differ among urban land uses?	In 4 UK towns/cities	Baldock et al. 2019	501	This study (empirical) This study (modelled) Baude et al. 2016 Hicks et al. 2016 Timberlake et al. 2019

2.2.1 Floral abundance data

To compare the nectar supply between urban, farmland and nature reserve landscapes (question 1) I used floral abundance data previously collected at 36 sites across the UK (Baldock et al., 2015). In that study, a representative site was chosen for each of the three landscape types in and around 12 towns and cities. Landscapes comprised a variety of habitats, which were sampled in proportion to their abundance at each site. Thus, urban areas included residential land (containing gardens), allotments, buildings, hard surfaces, public greenspace and woodland; farmland comprised arable fields, pasture, waste ground, field margins, hedgerows and woodland; nature reserves included woodland, grassland, heathland and wetland. To compare nectar supply among urban land uses (question 2) I used floral abundance data previously collected at 360 sites in four UK cities (Bristol, Edinburgh, Leeds and Reading) (Baldock et al., 2019). In that study, cities were divided into ten geographic regions and within each region nine land uses were surveyed: allotments, cemeteries, residential gardens (hereafter referred to as gardens), manmade surfaces (e.g. car parks and industrial estates), nature reserves, other greenspaces (e.g. amenity grassland), parks, pavements and road verges.

Floral abundance data were collected in the two studies by systematically sampling along transects and counting the number of floral units (defined as a single flower or collection of flowers following Baldock et al. (2015); see Supplementary Table 1 in Appendix 1) for each plant taxon. For the landscape comparison (question 1) floral abundance data were gathered across 100 quadrats (totalling 25 m² in aggregate) per site and each site was sampled on four separate occasions between 30 May and 19 September 2011. For the urban land use comparison (question 2) floral abundance data were gathered across 25 quadrats (totalling 25 m² in aggregate) per site and each site was sampled on three separate occasions between 15 April and 26 September (twice between 14 May and 26 September 2012 and once between 15 April and 5 September 2013). Baldock et al. (2015) recorded 206 plant taxa across urban, farmland and nature reserve sites and Baldock et al. (2019) recorded 501 plant taxa across sites in nine urban land uses. In total, 536 plant taxa were recorded in the two studies, with 171 taxa present in both.

2.2.2 Nectar sugar production data

I assigned each of the 536 plant taxa with a daily nectar sugar production value (mass of sugars produced per floral unit per 24 hours) derived either from empirical values reported in the published literature (230 taxa: Baude et al. (2016); Hicks et al. (2016); Timberlake et al. (2019)), measurements made in the field in this study (192 taxa) or predictive modelling where empirical values could not be obtained (114 taxa).

Empirical nectar values

Out of the 422 plant taxa assigned empirical values, Baldock et al. (2019, 2015) identified 64 to the level of a genus and the remaining 358 to a species, species aggregate or hybrid (hereafter referred to as species). For taxa only identified to genus level, 52 were assigned a nectar value derived from a single species in the genus and 12 were assigned a value obtained by averaging across multiple congeners. For the taxa identified to species level, 244 were assigned nectar values from the corresponding species and 114 were assigned values from a congener given that conspecific flowers were not available for sampling. This proxy method was only used if the two species shared similar floral morphologies and was deemed preferable to predictive modelling in these cases. Baude et al. (Supplementary Table 11 in 2016 paper) was the source of nectar production data for 207 taxa, Hicks et al. (S1 Table in 2016 paper) for 76 taxa and Timberlake et al. (Table S2 in 2019 paper) for 5 taxa. For 58 taxa, data from Baude et al. (2016) and Hicks et al. (2016) were combined by averaging (using a mean weighted by the number of flowers sampled) to increase the number of flowers and sampling sites contributing to the taxon-level mean nectar production value.

I measured nectar sugar production values assigned to 192 taxa in the field in March-October 2018 and February-April 2019 using the same methods as Baude et al. (2016), Hicks et al. (2016) and Timberlake et al. (2019), ensuring my values were comparable to those obtained from the published literature. Sampling locations included public and residential gardens, allotments, garden centres and public flower borders in the South of England (Table 2.2). Where possible, each taxon was sampled at two or three locations on different days to account for variation due to site, weather and plant variety (following Baude et al. (2016); see section 2.2.3). Insects were excluded from flowers to be sampled by mesh bags (pore size 1.4 mm × 1.7 mm) for 24 ± 2 hours, providing a measure of nectar accumulation over a one-day period (Fig. 2.1). Nectar was then extracted by one of two methods. Where possible, I removed nectar directly using glass microcapillaries (0.5, 1, 5, 10 and 20 µl Minicaps, Hirshmann, Eberstadt, Germany) (Fig. 2.1). Alternatively, where the direct uptake of nectar was not possible as the quantity was too small or viscous, I rinsed nectaries with 0.5-10 µl of distilled water, added with a pipette. Sugar residues were left to dissolve for one minute before the solution was removed using microcapillaries and the process repeated one further time. The concentration of the solution (C ; g of sugars per 100 g solution) was measured using a handheld refractometer modified for small volumes (Eclipse, Bellingham and Stanley, Tunbridge Wells, UK). The total mass of sugar produced (s ; µg of sugars per 24 hours) was calculated with the formula $s = 10dvC$, where v is the volume collected (µl) and d is the density of

a sucrose solution at concentration C and obtained by the formula $d = 0.0037921C + 0.0000178C^2 + 0.9988603$ (Corbet et al., 2001). I sampled 10-60 flowers for 188 of 192 taxa (2-9 for 3 taxa and 120 for 1 taxon), with a mean of 20.4 (± 0.9 SEM) flowers sampled for nectar for each plant taxon. Where possible, I sampled multiple plants and included a representative selection of flowers of different age, sex (if flowers were not hermaphroditic) and position on the plant or in the inflorescence.

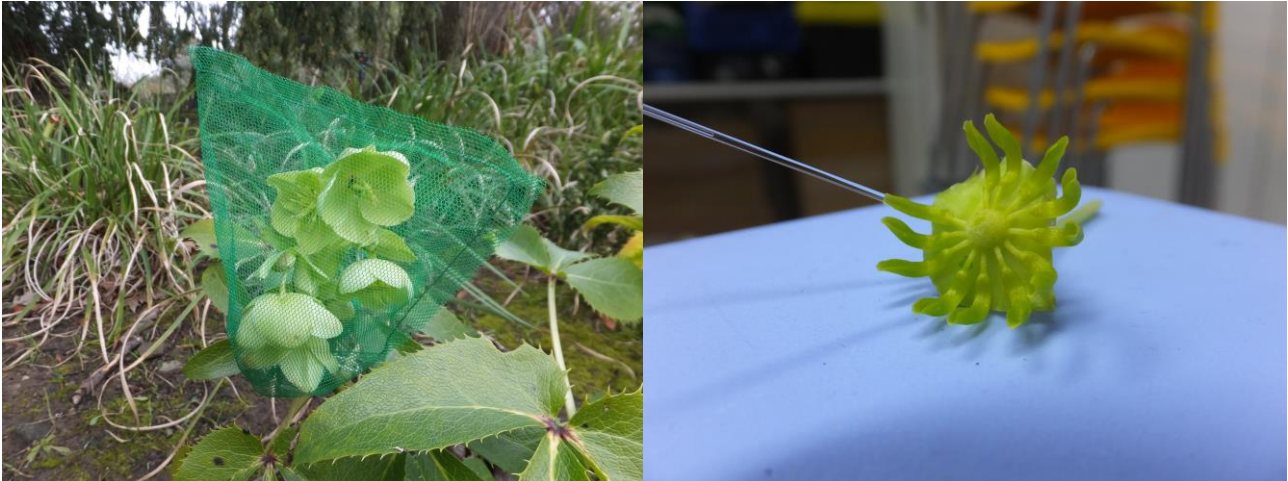


Figure 2.1. Nectar quantification methods. First, flowers were covered with a mesh bag to exclude insect visitors (left) and 24 hours later, nectar was extracted using glass microcapillaries (right). In the case of this species (*Helleborus lividus*), access to nectaries was improved by removing much of the floral structure immediately prior to extraction (right). Following this, the volume and concentration of extracted nectar were measured so that the total mass of sugars could be calculated (Photo: N. Tew).

Scaling nectar sugar from flower level to floral unit

Floral abundance data were obtained by Baldock et al. (2019, 2015) by counting floral units rather than flowers. Where the floral unit was a collection of flowers (145 taxa), nectar sugar production was scaled from flower to floral unit level by multiplying by the mean number of open flowers per floral unit. Counts of flowers per floral unit were either collected in the field in this study, obtained from Baude et al. (unpublished data) or in four cases, the floral units were counted in photographs. Nectar sugar values for Asteraceae in Hicks et al. (2016) were already given at the floral unit scale.

Table 2.2. Nectar sampling locations. The locations of sites used for sampling nectar in the field in this study.

Sampling location	Address
Ashley Down allotment	Ashgrove Avenue, Bristol (51.481 N, 2.578 W)
Brackenwood Plant and Garden Centre	Pill Road, Bristol (51.467 N, 2.662 W)
Didcot town (road verges and borders)	Didcot, Oxfordshire (51.610 N, 1.239 W)
RHS Garden Wisley	Wisley Lane, Woking, Surrey (51.314 N, 0.474 W)
Royal Fort Gardens	Tyndall Avenue, Bristol (51.458 N, 2.602 W)
Speldhurst village (a private garden)	Ferbies Road, Speldhurst, Kent (51.148 N, 0.216 E)
University of Bristol Botanic Garden	Stoke Park Road, Bristol (51.478 N, 2.626 W)
University of Bristol halls of residence	Parrys Lane, Bristol (51.478 N, 2.623 W)

Predicted nectar values

For the 114 taxa which lacked published empirical nectar sugar values, and which could not be found for sampling in the field, I estimated nectar sugar production by predictive modelling using a similar approach to Baude et al. (2016). Variation in $\log_{10}(x+1)$ nectar sugar production (μg of sugars per floral unit per 24 hours) for the empirically measured taxa was analysed using a linear model, which contained *plant family*, *floral unit type*, *flower shape* and *floral unit size* as explanatory variables (see below for a description of these traits). Prior to running this model, I excluded 96 of the original 422 taxa assigned empirical nectar sugar production values (leaving 326) due to their source nectar data being duplicated. Where multiple taxa were assigned nectar sugar production values from the same source species (e.g. both *Achillea millefolium* and *A. ptarmica* were assigned the nectar sugar production value of *A. millefolium*) I only included one of the taxa in the model to avoid artificially inflating the degrees of freedom. The estimates from this model ($N = 326$; $R^2_{\text{adj}} = 0.577$) were subsequently used to predict the nectar sugar production values of the plant taxa for which no empirical data were available (see section 2.2.3 for a validation of the approach). For the landscape comparison (question 1), modelled taxa contributed 3.9% of floral units and 1.1% of nectar sugar and for the urban land use comparison (question 2), 4.9% of floral units and 1.0% of nectar sugar. Conclusions drawn from all subsequent statistical analyses were unchanged if modelled taxa were excluded.

Plant family contained 22 classes that were either taxonomic families or higher clades (if a family was represented by four or fewer taxa in the empirical dataset then it was replaced by asterids, eudicots, monocots or rosids following Baude et al. (2016)). *Floral unit type* contained two classes that were (1) single flower or (2) collection of flowers, depending on the floral unit definition. *Flower shape* contained five classes based upon the Müller flower classification system. Flower shape definitions for most taxa were extracted using the R package ‘TR8’ (Bocci, 2015), which downloaded the trait data from the BioFlor database (Klotz et al., 2002). The five classes were: (1) open nectar (for flowers with open nectaries); (2) partly-hidden nectar (for flowers with partly-hidden nectaries); (3) hidden nectar (for flowers with completely hidden nectaries); (4) pollen, wind and trap flowers (for flowers where pollen is the major reward, flowers which are predominantly wind pollinated or flowers which trap insect pollinators rather than rewarding them with floral resources); (5) hymenopteran or lepidopteran flowers (for flowers recorded as being predominantly pollinated by

Hymenoptera or Lepidoptera). When the flower shape was not documented in the BiolFlor database, closely related and morphologically similar species were used as proxies. *Floral unit size* contained five size classes depending on the diameter of the floral unit (across the front of the floral unit, where a pollinator would land). The five classes were: (1) very small (diameter ≤ 5 mm); small ($5 \text{ mm} < \text{diameter} \leq 15$ mm); medium ($15 \text{ mm} < \text{diameter} \leq 30$ mm); large ($30 \text{ mm} < \text{diameter} \leq 60$ mm); very large: (diameter > 60 mm). Size class data were obtained from unpublished measurements in the field in this study, from Baude et al. (unpublished data) or from species descriptions in books and online resources.

Scaling nectar sugar from floral unit level to sampling site

Finally, total nectar sugar production for the area of land sampled at each site (i.e. all quadrats combined) was calculated by multiplying the floral abundance of each taxon by its corresponding value of daily nectar sugar production at the floral unit level. Although each site was sampled on four (question 1) or three (question 2) separate occasions to collect floral abundance data, there was insufficient resolution in the dataset to investigate temporal trends in nectar supply (but see Chapter 3). As a result, I pooled estimated nectar sugar production across all sampling visits to a site and divided by the number of visits to report the average daily nectar sugar production per site during the periods May-September (question 1) or April-September (question 2).

2.2.3 Data analysis and validations

All analyses were performed using R v.3.5.1 (R Core Team, 2018). Linear mixed models (LMMs) were fitted using R package ‘lme4’ (Bates et al., 2015) and diagnostic plots were inspected to validate all models against assumptions of heteroscedasticity and normality of the residuals. P-values for dependent variables were obtained from likelihood ratio tests (R function ‘drop1’) and pair-wise differences were calculated using post-hoc Tukey tests (R function ‘glht’) from R package ‘multcomp’ (Hothorn et al., 2008). Following Baldock et al. (2015), native status was determined using PLANTATT (Hill et al., 2004), with non-native taxa including both archeophytes and neophytes.

Question 1: How does nectar supply differ between urban, farmland and nature reserve landscapes?

To compare the quantity of nectar sugar produced between urban, farmland and nature reserve landscapes I analysed $\log_{10}(x+1)$ nectar sugar production per sampling site using an LMM containing landscape type as a fixed effect and national region (four regions of the UK) as a random effect to account for any geographic bias in nectar sugar production across the country. I additionally conducted this analysis separately for nectar sugar derived from native and non-native plant taxa. To investigate the strength of the correlation between floral abundance and nectar sugar production I analysed $\log_{10}(x+1)$ nectar sugar production per sampling site using a linear model (LM) containing $\log_{10}(x)$ floral abundance (number of floral units) as the only dependent variable. To compare the diversity of nectar sources between urban, farmland and nature reserve landscapes I

calculated a Shannon diversity index for each sampling site from R package ‘vegan’ (Oksanen et al., 2019) following Baude et al. (2016). The nectar source diversity index (H') was calculated as follows:

$$H' = - \sum_{i=1}^S p_i \times \ln(p_i)$$

where p_i is the proportional contribution of plant species i to nectar sugar production per sampling site and S is the total number of plant species per sampling site. Nectar source diversity was analysed using an LMM with the same fixed and random effects as for nectar sugar quantity. Conclusions were unchanged if a Simpson diversity index was calculated instead.

Question 2: How does nectar supply differ among urban land uses?

To compare the quantity of nectar sugar produced among urban land uses I analysed $\log_{10}(x+1)$ nectar sugar production per sampling site using an LMM containing land use and city as fixed effects and city region (40 regions, with ten in each city) as a random effect to account for any geographic bias (e.g. spatial autocorrelation) in nectar sugar production within cities. I additionally conducted this analysis separately for nectar sugar derived from native and non-native plant taxa. To estimate each land use’s contribution to overall nectar supply at a city scale I multiplied its median site-level nectar sugar production value (an average of sites across all four cities) by the proportion of each city that it comprises by area, with unsurveyed land uses including buildings and roads assigned a nectar production value of zero. To investigate the strength of the correlation between floral abundance and nectar sugar production I used the same approach as for Question 1. To compare the diversity of nectar sources among urban land uses, I calculated the diversity index as for Question 1 and analysed it using an LMM with the same fixed and random effects as for nectar sugar quantity.

Relationship between nectar production of plant taxa sampled in two locations

To assess the repeatability of nectar sugar measurements between locations, major axis linear regression was performed from R package ‘smart’ (Warton et al., 2012). Data were only included in this analysis for taxa measured empirically in this study in at least two locations on separate days, and where their floral unit was defined as a single flower (65 taxa). Where taxa were sampled in three locations, two locations were randomly chosen for comparison. There was a strong positive correlation between the nectar production values in the two sites ($N = 65$; $R^2 = 0.867$; Fig. 2.2), with a taxon’s nectar production in one location explaining 86.7% of the variation in its nectar production at the other location. Hence, differences in nectar sugar production within a taxon due to location, weather and plant variety were much smaller than differences in nectar sugar production among taxa.

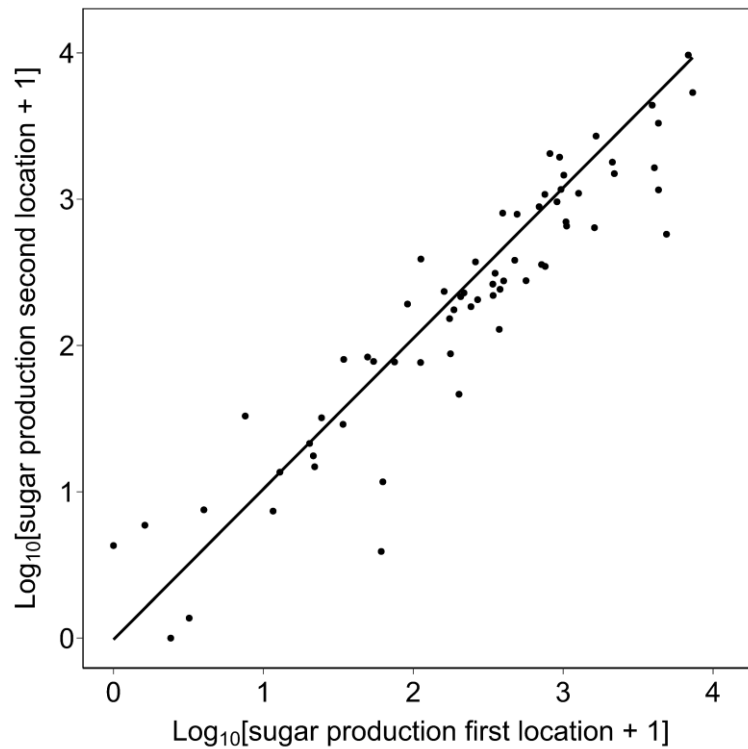


Figure 2.2. Relationship between nectar production of taxa measured in two locations. $\text{Log}_{10}(x+1)$ daily nectar sugar production of taxa (μg of sugars per flower per 24 hours) is plotted for two separate sampling locations. The fitted line from a major axis linear regression is shown.

Validation of predictive modelling approach

To check the validity of the modelling approach I used to predict the values for 114 unsurveyed taxa I adopted a repeated ‘leave-one-out’ approach on the 326 taxa for which I had empirical values of nectar sugar production. I excluded a single taxon, fitted the linear model on the remaining 325 taxa and used the estimates from this model to predict the nectar sugar production value of the excluded taxon, and then repeated this approach for all taxa. Subsequently, I applied a major axis linear regression from R packaged ‘smart’ (Warton et al., 2012) in R to assess the relationship between the $\text{log}_{10}(x+1)$ nectar sugar production (μg of sugars per floral unit per day) of predicted and empirical values for each taxon. There was a strong positive correlation between predicted and empirical values of nectar sugar production ($N = 326$; $R^2 = 0.524$; Fig. 2.3). The slope of the regression line is 0.725 (95% CI 0.652; 0.803) and y-intercept is 0.578 (95% CI 0.406; 0.749), suggesting a slight but not strong tendency for the model to underpredict nectar sugar production values.

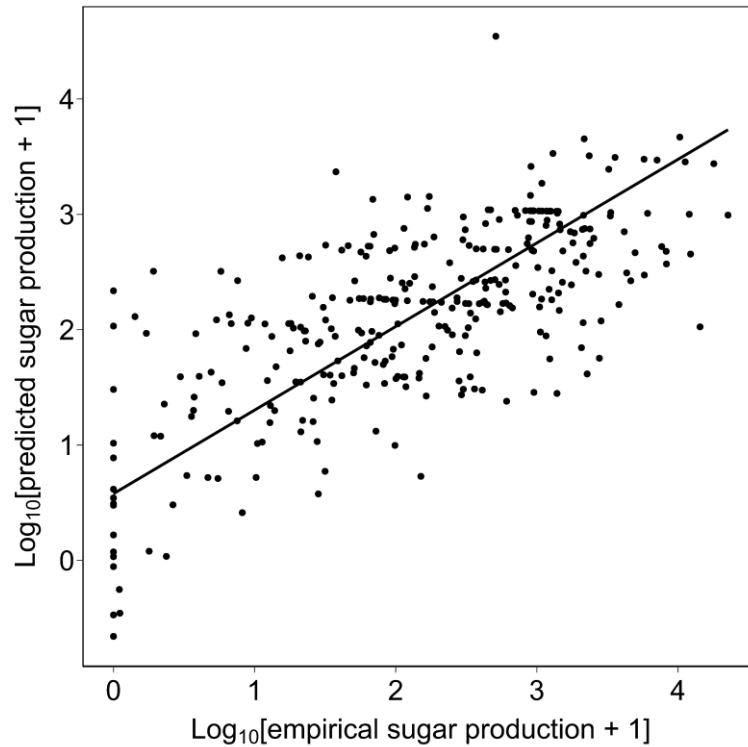


Figure 2.3. Relationship between predicted and empirical values of nectar production. Predicted and empirical values of $\log_{10}(x+1)$ daily nectar sugar production (μg of sugars per floral unit per 24 hours) are plotted for each taxon. The fitted line from a major axis linear regression is shown.

2.3 Results

2.3.1 Question 1: How does nectar supply differ between urban, farmland and nature reserve landscapes?

The quantity of nectar sugar per square metre did not differ significantly among the three landscape types (LMM: $N = 36$; $\chi^2 = 1.01$; $p = 0.60$; Fig. 2.4a), but there were differences in the composition of the plant communities underpinning nectar supply (Fig. 2.5; see Supplementary Table 2 in Appendix 1). Nectar sugar production by native taxa did not differ significantly among the three landscape types (Fig. 2.4b), but urban and farmland sites produced significantly more nectar sugar from non-native taxa than nature reserves (Fig. 2.4c; see Supplementary Table 3 in Appendix 1) and overall, non-natives comprised 65.6% of the nectar supply in urban sites, 30.0% in farmland and 0.9% in nature reserves. Nectar sugar production varied greatly among sampled sites, spanning the range $58 \mu\text{g}/\text{m}^2/\text{day}$ (a broad-leaved woodland nature reserve with few flowers recorded) to $102,698 \mu\text{g}/\text{m}^2/\text{day}$ (a heathland nature reserve dominated by *Calluna vulgaris*). The diversity of nectar sources differed significantly among the three landscapes (LMM: $N = 36$; $\chi^2 = 12.96$, $p = 0.002$), with urban sites producing nectar sugar from a significantly more diverse set of plant taxa than both farmland and nature reserves (Fig. 2.4d; see Supplementary Table 3 in Appendix 1). There was a significant positive

correlation between the quantity of nectar sugar produced and the number of floral units per site (LM: $F_{1,34} = 30.03$; $R^2 = 0.469$; $p < 0.001$; Fig. 2.7a), with floral abundance explaining 46.9% of the variation in nectar sugar production among sites.

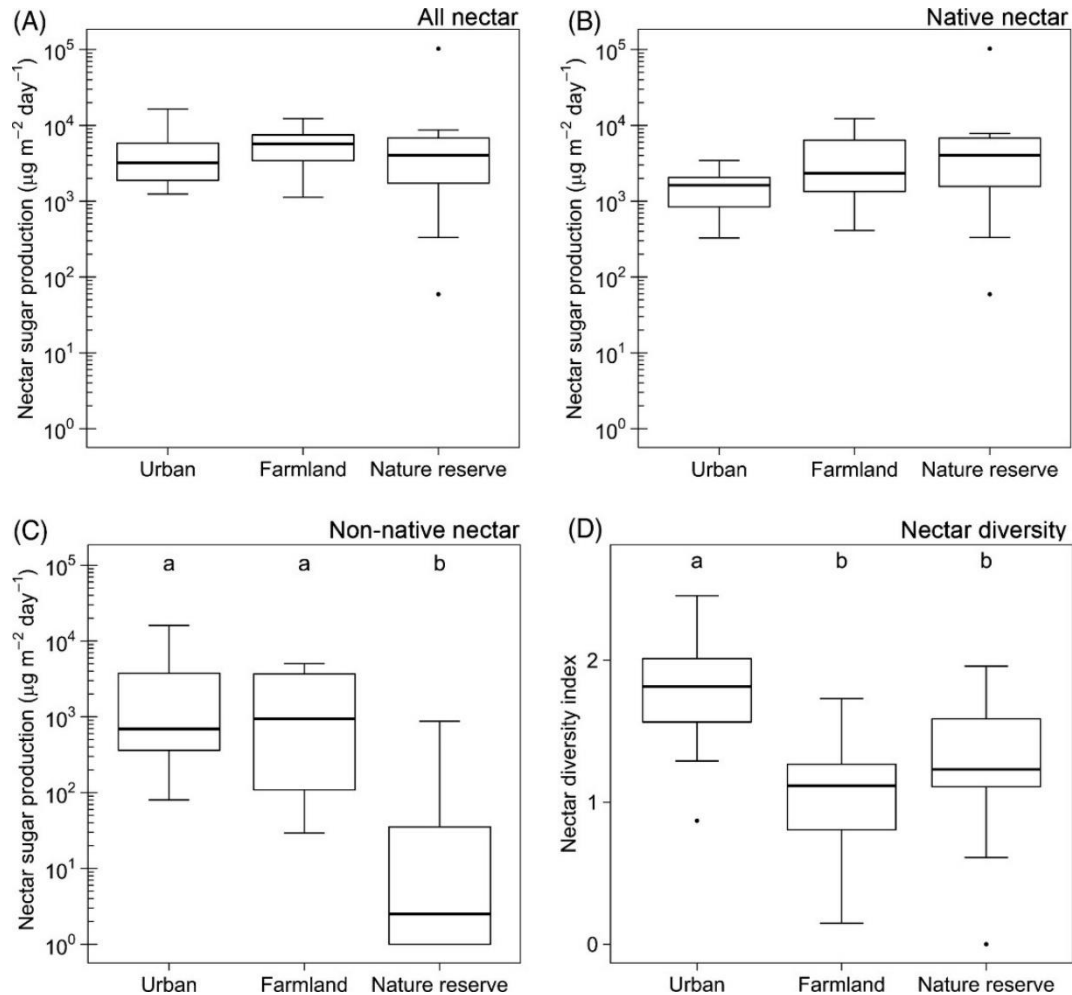


Figure 2.4. Comparison of nectar supplies among landscapes. Box and whisker plots of the mass (A-C) and diversity (D) of the nectar supply in urban, farmland and nature reserve landscapes. Daily nectar sugar production per square metre was calculated by dividing total nectar sugar production per sampling site by 100 (as 25 m^2 of land was sampled on four occasions). Data were subsequently transformed ($\log_{10}(x+1)$) for visualisation on a logarithmic y-axis and are shown for (A) all plant taxa, (B) native plant taxa and (C) non-native plant taxa. Nectar diversity index (Shannon index of nectar sources per sampling site) is shown for all taxa (D). Significantly different landscape types are indicated by different letters (Tukey multiple comparison tests). Boxes show the median, 25th and 75th percentiles; the whiskers extend to $1.5 \times$ the interquartile range; and all outliers are shown.

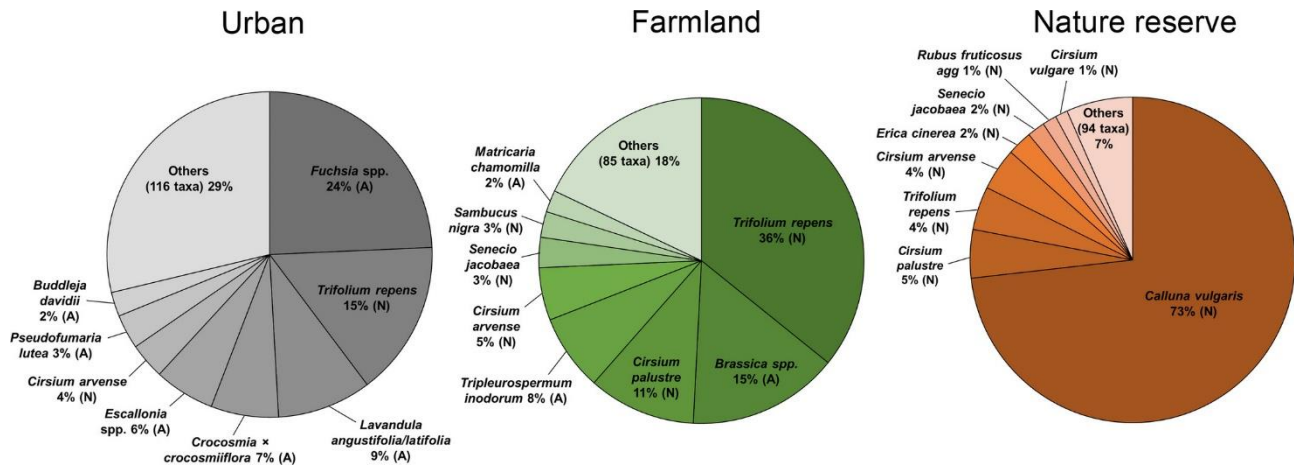


Figure 2.5. The composition of nectar supplies among landscapes. Pie charts of the contribution of flowering plant taxa to total nectar supply in urban, farmland and nature reserve landscapes. The eight taxa with the greatest contribution are shown and all other taxa are labelled as ‘Others’. The native status of each taxon is indicated by the letter ‘N’ (native) or ‘A’ (non-native alien) in parentheses. Although *Calluna vulgaris* contributed 73% of all nectar sugar in nature reserves, 96% of its production was in a single heathland site, making generalisations about its dominance in UK nature reserves unreliable.

2.3.2. Question 2: How does nectar supply differ among urban land uses?

The quantity of nectar sugar per square metre differed significantly among the nine urban land uses (LMM: $N = 360$; $\chi^2 = 269.72$; $p < 0.001$; see Supplementary Table 4 in Appendix 1), but not among the four cities (LMM: $N = 360$; $\chi^2 = 0.38$; $p = 0.95$). Gardens produced significantly more nectar sugar per square metre than all other land uses except for allotments, while pavements and manmade surfaces produced significantly less nectar per square metre than all other land uses (Fig. 2.6a). Even manmade surfaces, the lowest productivity land use, contained some nectar-rich sites (Fig. 2.6a), with flowering shrubs providing ‘hotspots’ of nectar supply. The high nectar supply in gardens and allotments was largely driven by non-native plants; nectar sugar production by native taxa did not differ significantly among any of the top seven land uses (Fig. 2.6b), while gardens and allotments produced significantly more nectar sugar from non-native taxa than all other land uses (Fig. 2.6c). Overall, non-natives comprised 69.9% of the nectar supply in allotments and 82.9% in gardens, compared with 3.8% and 4.7% in parks and other greenspaces, respectively. The principal plant taxa contributing to nectar supply in each land use are listed in Supplementary Table 5 in Appendix 1. At a city scale, gardens produced 81.1-87.6% of all nectar sugar (mean of 85.0% across the four cities), due to their high nectar sugar production per unit area and large area within cities (Table 2.3). The diversity of nectar sources differed significantly among the nine land uses (LMM: $N = 360$; $\chi^2 = 202.97$; $p < 0.001$; see Supplementary Table 4 in Appendix 1) and the four cities (LMM: $N = 360$; $\chi^2 = 18.73$; $p < 0.001$; see Supplementary Table 4 in Appendix 1), with gardens and allotments producing nectar sugar from a significantly more diverse set of plant taxa than all other land uses (Fig. 2.6d). There was a significant positive correlation between the quantity of nectar sugar produced

and the number of floral units per site (LM: $F_{1,325} = 563.99$; $R^2 = 0.634$; $p < 0.001$; Fig. 2.7b), with floral abundance explaining 63.4% of the variation in nectar sugar production among sites.

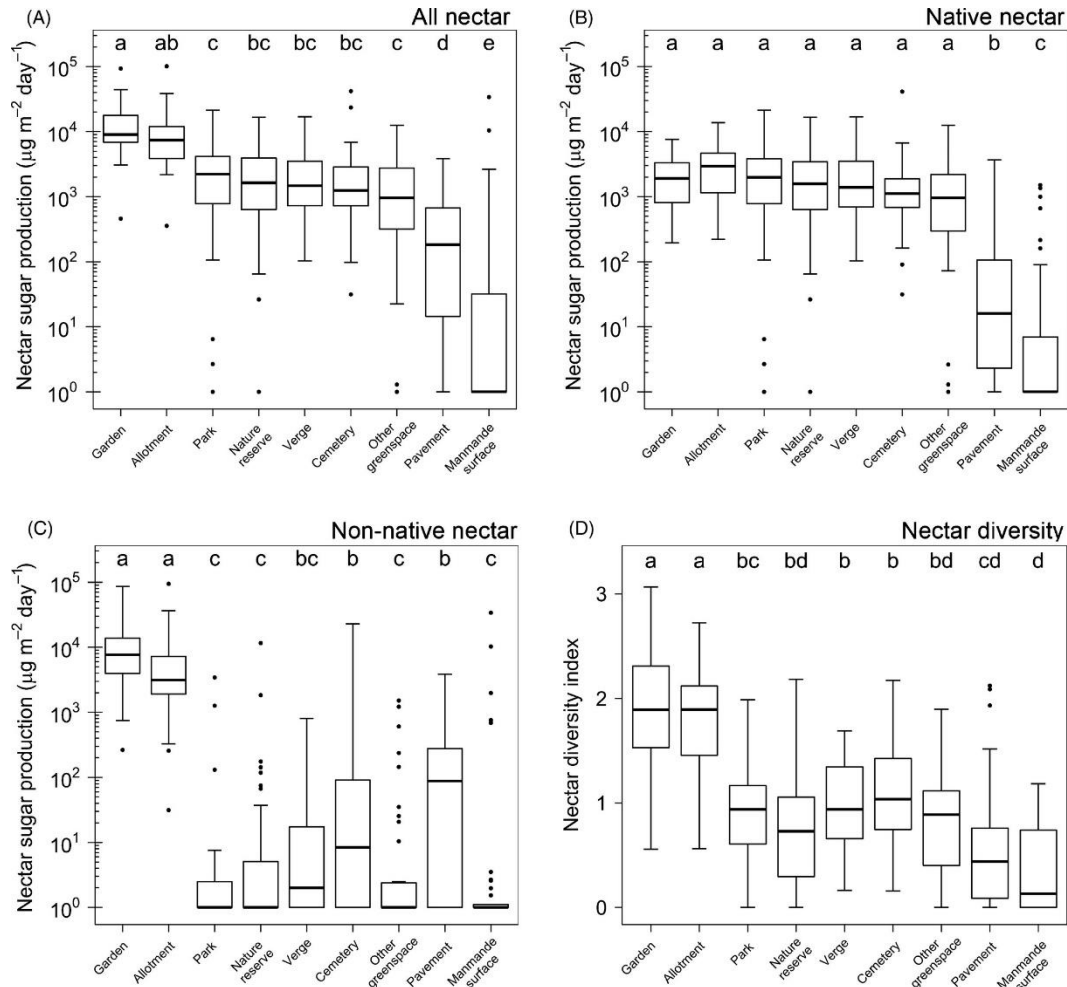


Figure 2.6. Comparison of nectar supplies among urban land uses Box and whisker plots of the mass (A–C) and diversity (D) of the nectar supply in nine urban land uses. Daily nectar sugar production per square metre was calculated by dividing total nectar sugar production per sampling site by 75 (as 25 m² of land was sampled on three occasions). Data were subsequently transformed ($\log_{10}(x+1)$) for visualisation on a logarithmic y-axis and are shown for (A) all plant taxa, (B) native plant taxa and (C) non-native plant taxa. Nectar diversity index (Shannon index of nectar sources per sampling site) is shown for all taxa (D). Significantly different landscape types are indicated by different letters (Tukey multiple comparison tests). Boxes show the median, 25th and 75th percentiles; the whiskers extend to $1.5 \times$ the interquartile range; and all outliers are shown.

Table 2.3. Nectar production of urban land uses. A comparison of urban land uses showing nectar sugar production (median and interquartile range across all sites), the percentage of city area that each land use comprises (mean and range among the four cities, from Baldock et al. (2019)) and the percentage of nectar production at a city scale that each land use contributes (mean and range among the four cities). Unsurveyed land uses including buildings and roads are not included in this table and were assigned a nectar production value of zero.

Land use	Nectar sugar production ($\mu\text{g}/\text{m}^2/\text{day}$)	Percentage of city area	Percentage of city nectar
Garden	8,988 (6,878 - 17,785)	28.8 (24.2 - 35.5)	85.0 (81.1 - 87.6)
Allotment	7,392 (3,849 - 11,997)	0.7 (0.2 - 1.0)	1.5 (0.6 - 2.1)
Park	2,235 (784 - 4,147)	4.9 (3.1 - 5.8)	3.6 (2.4 - 4.7)
Nature reserve	1,633 (631 - 3,944)	1.8 (0.08 - 3.8)	1.0 (0.4 - 2.3)
Verge	1,473 (729 - 3,498)	1.8 (1.2 - 2.2)	0.9 (0.7 - 1.1)
Cemetery	1,248 (722 - 2,845)	0.8 (0.5 - 0.9)	0.3 (0.2 - 0.4)
Other greenspace	960 (315 - 2,735)	22.5 (18.8 - 28.0)	7.3 (5.0 - 10.0)
Pavement	182 (13 - 675)	4.3 (3.8 - 5.0)	0.3 (0.2 - 0.3)
Manmade surface	0 (0 - 31)	8.2 (6.4 - 10.3)	0.0 (0.0 - 0.0)

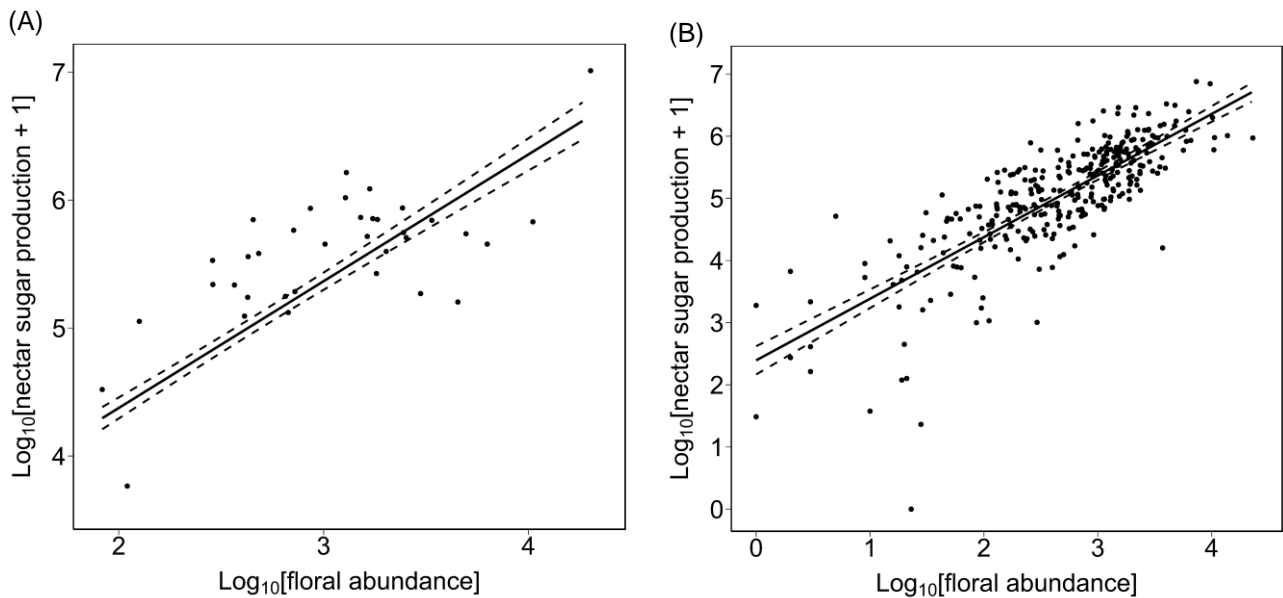


Figure 2.7. The relationship between floral abundance and nectar production. $\text{Log}_{10}(x+1)$ nectar sugar production (μg of sugars pooled across all survey visits to a sampling site) and $\text{log}_{10}(x)$ floral abundance (total floral units recorded pooled across all survey visits to a sampling site) are plotted for (A) the landscape comparison (question 1) and (B) the urban nectar comparison (question 2). The fitted line (solid) and 95% confidence intervals of the estimates (dashed) from a linear model are shown for both plots.

2.4 Discussion

I found no significant difference in the magnitude of nectar sugar production per unit area in urban, farmland and nature reserve landscapes. Urban sites had the highest nectar diversity index, providing nectar sugar from a significantly more diverse set of plant taxa than the other two landscape types. Within urban landscapes, both the magnitude and diversity of the nectar supply differed significantly among land uses. Gardens produced the most nectar sugar per unit area and provide an estimated 81-88% of nectar at the city scale. The nectar supplies in gardens and allotments were more diverse than all other land uses and were primarily contributed by non-native species. Support for using flower counts as a proxy for floral resource production was mixed: although floral abundance was significantly correlated with nectar sugar production, a large proportion of the variation remained unexplained. In what follows I first consider the limitations of my approach and then discuss my results in the context of pollinator conservation.

2.4.1 Limitations

There are four main limitations to this study. First, the food resource requirements of insect pollinators are more varied than nectar sugar alone. Some pollinators consume pollen as adults (e.g. beetles, hoverflies) and larval diets can include pollen (e.g. bees), other living plant material (e.g. butterflies and moths, hoverflies), other insects (e.g. hoverflies, wasps) and decaying organic matter (e.g. beetles, hoverflies, non-syrphid Diptera) (Vaudo et al., 2015; Ball and Morris, 2015; Wäckers et al., 2007). Nectar consumption itself is constrained by compatible morphology between plant and insect, with flower shape an important predictor of visitation among insect species (Stang et al., 2006). Although total nectar sugar is a simplistic measure of food resource availability for insect pollinators, nectar is the main energy source in the diets of adult pollinators and provides a common currency through which to compare the floral resource value of habitats (Baude et al., 2016). Second, quantifying the nectar resources provided by 536 plant taxa required some assumptions and simplifications. A single taxon with a history of cultivation can have many different varieties. For example, the *Dahlia* genus is represented by some 20,000 cultivars (Brickell, 2016). In my study, each taxon derives its nectar production value from one or a few sampled varieties. This is a necessary pragmatic simplification and I found that differences in nectar sugar production between taxa were much greater than between members of the same taxon (which were often different varieties) sampled in two locations (Fig. 2.2). Thirdly, Baldock et al. (2019, 2015) sampled floral abundance up to a height of two metres and flowers on trees, shrubs or climbers above this were not recorded. It is possible that flowers on plants more than two metres in height could produce a significant proportion of the overall nectar on some transects (Somme et al., 2016), but such plants are distributed sporadically, so recording them would require a different sampling method to that used by Baldock et al. (2019, 2015), which allowed for more representative comparisons among landscape and land use types. Large trees are more likely to be found in pavements, parks and other green spaces, compared with residential gardens, so the exclusion of flowers above two metres from the ground could lead to the proportional importance of gardens to nectar production at a city scale being overestimated. Finally, due to insufficient

resolution in the underlying floral abundance data I was unable to investigate temporal trends in nectar supply or compare landscape types at certain times of the year. In European farmland, nectar production varies greatly through the year and is particularly low in the early spring and autumn (Jachula et al., 2021; Timberlake et al., 2019). Given the wide variety of exotic species and horticultural cultivars planted in urban green spaces which flower particularly early or late, there are likely to be differences in the phenological profile of nectar supplies between landscape types, even if not in the overall quantities (see Chapter 3).

2.4.2 Implications for pollinator conservation

I did not find clear evidence that urban areas act as resource-rich refuges for insect pollinators within agriculturally dominated rural landscapes, as other authors have suggested (Hall et al., 2017; Samuelson et al., 2018). However, towns and cities contain land uses that are both very high (e.g. gardens and allotments) and very low (e.g. pavements and manmade surfaces) in nectar sugar production. My study reveals the overwhelming importance of residential gardens in providing nectar resources at a city scale. Because they produce the most nectar sugar per unit area and cover the greatest area of any urban land use (24-36% of cities), gardens supply the vast majority (81-88%) of nectar sugar produced in cities. Although the magnitude of the nectar supply in urban areas was not greater than in rural landscapes, urban nectar sugar is supplied by a more diverse plant community and not dominated by a small number of taxa, as is common in the countryside (Baude et al., 2016; Timberlake et al., 2019). A diverse array of nectar sources is likely to provide both nutritional diversity of floral rewards and morphological diversity of flowers, which are important determinants of the richness of the pollinator community that can be supported (Stang et al., 2006; Vaudo et al., 2015; Woodard and Jha, 2017). Insect pollinators capable of long-distance foraging (e.g. bumblebees) may be able to visit a combination of urban, farmland and semi-natural areas (such as nature reserves) from their nest site (Goulson et al., 2010; Osborne et al., 2008). If they are sufficiently close, urban areas have the potential to increase the diversity of floral resources in agriculturally dominated landscapes, but there remains a need to understand the extent to which different habitats complement each other by providing different floral resources.

All three sampled landscapes are complex and diverse, making broad-scale comparisons of their floral resources difficult from a relatively small area covered by quadrats, especially given the extreme variability seen in nectar production among different sites. My comparison of the three landscapes, while large scale, is a relatively broad-brush approach. In reality, urban landscapes are highly heterogeneous mosaics of different anthropogenic land uses (Baldock et al., 2019; Grimm et al., 2008), as I have discussed; farmland varies with respect to farm type and the degree of management intensity (e.g. arable vs. livestock; high vs. low intensity); and nature reserves are areas with protected status, but are not necessarily managed primarily for pollinators, and can comprise different habitats (e.g. grassland, broad-leaved woodland or heathland). While my study is a robust comparison of the three landscape types, further research into the habitats and land uses within each landscape will enable more specific comparisons to be made.

Research on pollinators in urban landscapes often attempts to explain their abundance or diversity at each sampling site with reference to the extent of nearby green spaces (e.g. Banaszak-Cibicka and Żmihorski, 2012; Sivakoff et al., 2018) or a measure of its reverse, the cover of impervious surfaces (e.g. Ahrné et al., 2009; Fortel et al., 2014). Although floral resources (or its proxy floral abundance) are sometimes measured, this is generally done at a local scale (e.g. Guenat et al., 2019; Theodorou et al., 2017). However, here I show that not all green spaces are alike with respect to their nectar supply: for example, based on median values per unit area, gardens produce four times as much nectar sugar as parks, and allotments six times as much as cemeteries (Table 2.3). Future studies should consider the quantity of floral resources around pollinator sampling sites in urban areas, rather than proxy variables such as greenspace extent and impervious surface cover, as it is floral resources which are likely to directly regulate pollinator populations (Roulston and Goodell, 2011). The nectar sugar production values of UK urban land uses, listed here (Table 2.3), represent a useful asset for researchers aiming to quantify floral resources in urban landscapes.

The high nectar sugar production in gardens and allotments was largely driven by species that are not native to the UK. Although non-native plants are often regarded as less valuable to wildlife than their native counterparts, many such as *Borago officinalis*, *Lavandula* species and *Nepeta* species, are frequently visited by UK pollinators (Baldock et al., 2019; Garbuzov and Ratnieks, 2014b; Rollings and Goulson, 2019). Temperate pollination systems tend to be fairly generalised in nature (Memmott, 1999; Waser et al., 1996), thus most flowering plants are visited by broad taxonomic groups of insects (e.g. bees, butterflies or hoverflies), rather than only a few specialist species. Consequently, a non-native plant that evolved in its natural range to attract a group of pollinators also found in the UK is likely to be visited by UK pollinators despite its origin (e.g. *Mahonia japonica* is native to Asia but attracts bumblebees in the UK; Stelzer et al., 2010). Furthermore, given the UK shares pollinator species with continental Europe, interactions between non-native plants of European origin and pollinators in the UK often represent a renewal of associations that have occurred before in evolutionary history (e.g. *Anthidium manicatum* and *Stachys byzantina*; Gallagher and Lucky, 2020). Even exotic plants that have evolved for visitation by pollinators absent from the UK can be important sources of food for UK pollinators. For example, *Fuchsia* species are commonly pollinated by hummingbirds in the Americas (González et al., 2018), but provide nectar for bumblebees, honeybees and social wasps in UK gardens (N. Tew, personal observation). Thus, there is no intrinsic reason to assume non-native plant species are less valuable to most adult flower-feeding insects than their native counterparts (Garbuzov and Ratnieks, 2014b; Majewska and Altizer, 2018; Matteson and Langellotto, 2011), although their prevalence in urban areas could drive changes in pollinator community composition (Seitz et al., 2020; Urbanowicz et al., 2020; Wenzel et al., 2020) and further research into nectar chemistry is needed to establish whether non-natives provide nectar of comparable nutritional quality (Tiedeken et al., 2017; Vaudo et al., 2015).

Urban landscapes contain land uses which differ markedly in both form and function (Dennis et al., 2018; Grimm et al., 2008) and consequently management strategies for conserving pollinators vary among land uses. In land uses that are largely paved and typically of very low nectar value, flowering shrubs can be incorporated to provide long-lived ‘hotspots’ of nectar in a relatively small space. In pavements and manmade surfaces (including car parks) I found that the non-native shrubs *Berberis* species, *Buddleja davidii* and *Ceanothus* species are responsible for positive outliers in nectar sugar production among city regions (see Supplementary Table 5 in Appendix 1). At the other end of the spectrum, gardens and allotments produce a rich and diverse nectar supply, so ensuring these land uses are retained within existing urban landscapes and integrated into new developments is a priority in urban pollinator conservation. Land uses typically covered with short-mown grass, especially parks and other greenspaces (including amenity grassland), have an intermediate value of nectar sugar production. Here, altering the frequency and timing of mowing affects floral abundance (Garbuzov et al., 2015; Johansen et al., 2019; Lerman et al., 2018) and hence nectar sugar production, mediated largely by the three native plants white clover (*Trifolium repens*), dandelion (*Taraxacum* agg.) and lawn daisy (*Bellis perennis*), which together provide 74-80% of the nectar in these land uses (see Supplementary Table 5 in Appendix 1). In addition, small patches of sown wildflowers can be incorporated into public greenspace to boost nectar supply, with native perennial mixes potentially providing 16 times as much nectar sugar per unit areas as parks and 37 times as much as other greenspaces (Hicks et al., 2016).

2.4.3 Conclusions

My results show that, per unit area, the nectar supply in UK towns and cities is comparable in magnitude to farmland and nature reserves, but differs in composition. Urban nectar is supplied by a diverse community of flowering plants, heavily comprised of non-native species. Residential gardens are the key land use underpinning nectar sugar production within urban landscapes, providing both an abundance and diversity of floral resources. Given the overwhelming importance of residential gardens, I will investigate them in more detail in Chapter 3, measuring how nectar supplies vary between gardens and through the months of the year. By quantifying the nectar supply, rather than relying on proxy variables such as greenspace cover, researchers can provide a more ecologically relevant description of the resource value of habitats and landscapes to foraging pollinators and develop evidence-based recommendations for their conservation.

Chapter 3

Spatial and temporal variation in the floral nectar supply of urban residential gardens



Residential gardens can accommodate an eclectic community of flowering plants providing an abundant supply of floral resources. Insects visiting this Bristol garden in late June can forage on *Brachyglottis* × *jubar* (from New Zealand), *Penstemon* (from North America), *Malva sylvestris* and *Silene coronaria* (both from Eurasia), among many other taxa (Photo: N. Tew).

3.1 Introduction

Flower-visiting insects including bees and hoverflies are crucial pollinators of many wild plants and agricultural crops (Klein et al., 2007; Ollerton et al., 2011). Increasing evidence for pollinator declines (e.g. Biesmeijer et al., 2006; Powney et al., 2019; Soroye et al., 2020) has led to a focus on designing and implementing strategies for conserving pollinators (Potts et al., 2016). Urban areas could play a surprisingly important role in such conservation strategies for two main reasons. First, they already cover 2-3% of the world's land (Liu et al., 2014) and are expanding (Gao and O'Neill, 2020). Second, urban green spaces can support substantial pollinator diversity (Baldock et al., 2019; Normandin et al., 2017), which may be higher than that in surrounding rural areas (Baldock et al., 2015; Theodorou et al., 2020, 2017).

Privately-owned residential gardens or yards (hereafter referred to as 'gardens') are a particularly valuable type of urban green space for insect pollinators as they are often (but not always) actively managed by gardeners to provide ornamental displays of flowering plants, which provide pollinators with food in the form of nectar and pollen. As a result, diverse pollinator communities can be found in gardens throughout the world (Baldock et al., 2019; Fetridge et al., 2008; Marín et al., 2020; Martins et al., 2017; Staab et al., 2020). Despite their small individual size, residential gardens collectively cover 16-36% of cities in different countries (Baldock et al., 2019; Colding et al., 2006; Loram et al., 2007; Mathieu et al., 2007; Ossola et al., 2021) and provide an estimated 85% of nectar sugar in urban areas in the UK (see Chapter 2). Consequently, gardens offer a unique opportunity for pollinator conservation where the combined action of many individuals can have a major impact on foraging resources at a landscape scale (Goddard et al., 2010).

Gardens vary substantially in size, shape, topography, amount of sunlight and soil type (Loram et al., 2007; Matteson and Langellotto, 2010). In addition, management by gardeners differs due to the many and diverse motivations for gardening, this being explained in part by demographic and socio-economic factors (Goddard et al., 2013; Lindemann-Matthies and Marty, 2013; Philpott et al., 2020). As a result, the abundance and composition of flowering plants is very variable among gardens, with some comprised of flower-rich borders and others dominated by short mown grass or hard surfaces (Goddard et al., 2013; Loram et al., 2008a). Consequently, the quantity of floral resources available to insect pollinators is likely to differ substantially from one garden to the next, as is the temporal pattern of resource production due to differences in flowering phenology among species. The seasonal timing of floral resources is often overlooked, but is an important factor determining the success of insect pollinators in temperate climates (Guezen and Forrest, 2021; Timberlake et al., 2021). To understand the quality of the garden habitat for foraging pollinators and identify opportunities for its enhancement we need to quantify variation in the supply of floral resources among individual gardens.

In this study I investigate for the first time how the nectar supply of residential gardens varies in space and time and use my results to develop evidence-based management recommendations for pollinator conservation in urban areas. Nectar sugar is the main energy source for adult pollinators, and is particularly important for powering their flight muscles (McCallum et al., 2013), but nectar resources have declined in rural areas due to land use change (Baude et al., 2016). I focus on three characteristics of the nectar supply in gardens. (1) *Magnitude*: I predict substantial variation in nectar sugar production among gardens and an overall peak in summer when I expect more plants to be in flower. (2) *Temporal stability*: I predict that individual gardens will vary in their seasonal patterns of nectar sugar production such that not all gardens will peak at the same time of year. However, complementarity among gardens will produce a relatively stable supply of nectar throughout the year at the scale of an urban landscape. (3) *Diversity and composition*: given gardeners can choose from a wide variety of species when planting, I predict substantial turnover in species composition among gardens.

3.2 Materials and methods

3.2.1 Selecting gardens to survey

I surveyed residential gardens in Bristol, a city of around 460,000 inhabitants (Office for National Statistics, 2019b) in Southwest England, UK, and stratified my sampling by both geographical location and neighbourhood income. Six separate regions of the city were chosen for garden surveys (Table 3.1; Fig. 3.1), with each region corresponding to an Output Area (a census reporting unit containing 101-123 households). Using an approach based upon Baldock et al. (2019), two regions were each chosen to represent areas of relatively low (band one: £19,149 and £21,215), intermediate (band two: £25,357 and £28,677) and high (band three: £41,308 and £44,992) median annual income.

I obtained permission to survey residential gardens by posting a flyer advertising the study to all properties in my chosen six regions (21-24 January 2019) and subsequently visited households to ask for access to additional gardens (04-06 February 2019) to reach a desired sample size of approximately ten gardens per region. As far as possible I tried to minimise bias in responses by visiting all properties and ensuring that residents were aware of my interest in surveying gardens of all types, irrespective of size or its perceived habitat quality for pollinators. Following this, I obtained permission to survey 59 gardens continuously from March to October, these encompassing a wide range of sizes and planting styles. Although I tried to ensure I surveyed an equal number of gardens in each income band, there were differences in the number of properties I gained permission to access (band one: 12; band two: 23; band three: 24), but this imbalance did not affect my conclusions (see section 3.3.4).

Table 3.1. Survey regions. The six regions in Bristol in which I surveyed residential gardens. Data on number of households and income for Output Areas from Baldock et al. (2019).

Region name	Output Area code	Number of households	Median household income	Income band	Number of gardens surveyed
Hanham	00HDPG0014	110	£41,307.50	3	12
Horfield	00HBPJ0003	116	£28,676.50	2	10
Knowle	00HBPL0035	123	£19,149.00	1	7
Montpelier	00HBNM0037	104	£25,357.00	2	13
Southmead	00HBPS0009	105	£21,215.00	1	5
Westbury Park	00HBPG0010	101	£44,992.00	3	12

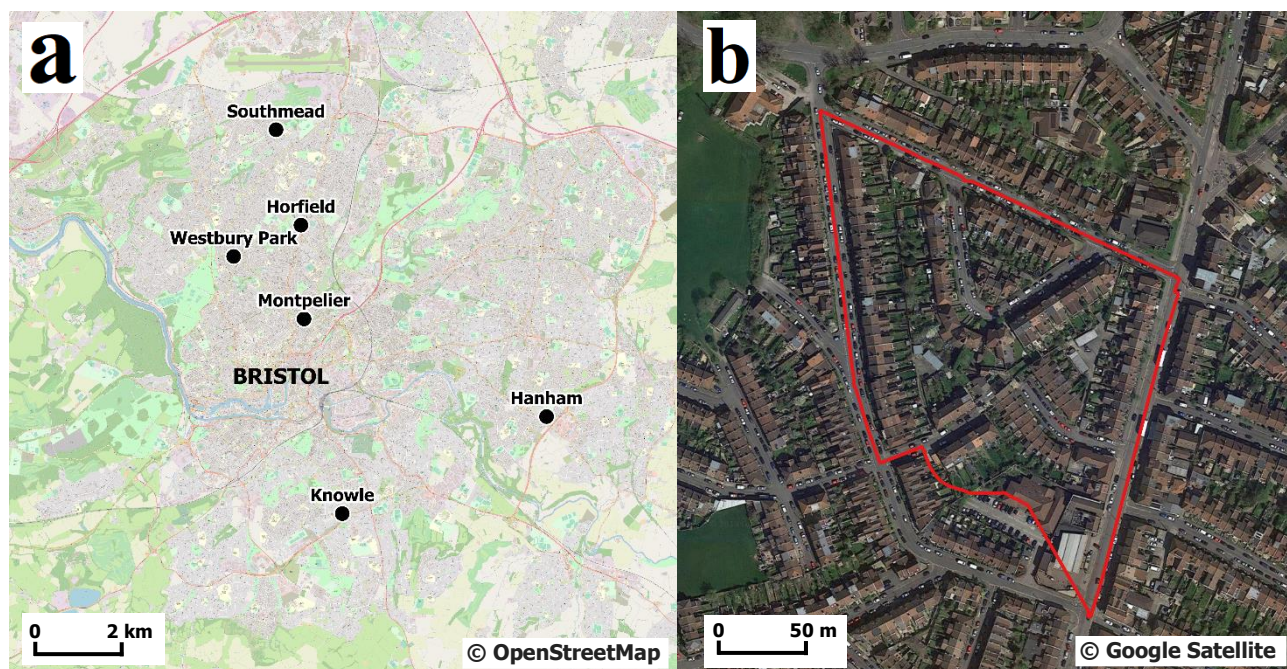


Figure 3.1. Survey regions. (a) A map showing the locations of the six regions of Bristol in which residential gardens were surveyed. (b) Example of a single Output Area (Horfield region), bounded by a red line.

3.2.2 Surveying gardens

I visited each of the 59 gardens once per calendar month between 04 March and 29 October 2019 to record floral abundance. Thus, each garden was visited eight times, with 472 garden surveys conducted. The period from March (early spring) to October (mid-autumn) covers the vast majority of the UK pollinator flight season. Although some gardens contain floral resources in late autumn and winter (November-February), pollinator activity is comparatively low at these times (Ball & Morris, 2015; Falk, 2015). I ensured gaps between visits to the same garden were close to one calendar month, with a mean gap of 30.7 days ($n=413$; range=25-42 days; 97% of gaps 25-35 days inclusive). For logistical reasons I usually visited multiple gardens in the same region on the same day, but I visited each region on two to six days spread across each month to ensure there was no systematic bias in sampling date among regions.

On the first visit I mapped each garden to measure its total area. On this and each subsequent visit I identified all plant taxa in flower as far as possible (to species, species aggregate, hybrid or genus) and counted all open floral units within the boundaries of each garden (with no height limit and including flowers on plants hanging over boundaries into gardens). I excluded grasses (Poaceae) as they offer no nectar resources. As in Chapter 2, floral units were defined as a single flower or collection of flowers (e.g. a capitulum for Asteraceae) that a pollinator can walk within but must fly between (e.g. Baldock et al., 2015; Carvalheiro et al., 2008; see Supplementary Table 6 in Appendix 2). Floral units were either counted individually in a garden using a handheld tally counter or estimated by sub-sampling and then multiplying up (e.g. for flowering shrubs and trees). For flower-rich lawns, I estimated floral units using quadrats (0.5×0.5 m) to quantify floral abundance for a fixed area, which I then scaled up to the area of the entire lawn.

3.2.3 Nectar sugar production data

The methods for assigning taxa with nectar sugar production values exactly followed those already described in Chapter 2 (section 2.2.2) and so I will only briefly summarise them here. Each of the 636 plant taxa I recorded flowering in gardens was assigned a daily nectar sugar production value (mass of sugars produced per floral unit per 24 hours) derived either from empirical values reported in the published literature (181 taxa; Baude et al. (2016); Hicks et al. (2016); Timberlake et al. (2019)), measurements I made in the field (263 taxa), or predictive modelling where empirical values could not be obtained (192 taxa).

I measured nectar sugar production values assigned to 263 taxa at field locations in Southern England as described in Chapter 2, sampling 10-52 flowers for 255 plant taxa (1-9 for 8 taxa). Also see Chapter 2 (section 2.2.3) for the relationship between nectar production of plant taxa sampled in two locations. Where the floral unit was defined as a collection of flowers (125 taxa), nectar sugar production was scaled from flower to floral unit level by multiplying by the mean number of open flowers per floral unit as described in Chapter 2. For the 192 taxa which lacked published empirical nectar sugar values, and which could not be found in sufficient

numbers for sampling in the field, I estimated nectar sugar production using a predictive modelling approach whereby I analysed variation in nectar sugar production for the empirically measured taxa using a linear model ($N = 318$; $R^2_{adj} = 0.537$) and used the model estimates to predict the nectar sugar production values for the modelled taxa. See Chapter 2 for further description (section 2.2.2) and a validation of this predictive modelling approach (section 2.2.3). Daily nectar sugar production per monthly visit was then calculated for each garden by multiplying the number of floral units of each taxon by its corresponding value of daily nectar sugar production. Taxa with empirical values of nectar sugar accounted for 91.9% of the total supply and conclusions drawn from all subsequent statistical analyses were unchanged if taxa assigned modelled nectar values were excluded.

3.2.4 Data analysis

All analyses were performed using R v.4.0.3 (R Core Team, 2020). Generalised additive mixed models (GAMMs) were fitted using R package ‘mgcv’ (Wood, 2017) and diagnostic plots (generated with R function ‘gam.check’) were inspected to validate models against assumptions of heteroscedasticity and normality of the residuals. The degree of smoothness of the regression spline (k) was selected by comparing Akaike's information criterion (AIC) among candidate models (Table 3.2 and Table 3.3).

Table 3.2. Statistical models for analysing nectar production. A comparison of candidate generalised additive mixed models for analysing nectar sugar production. The chosen model ($k=7$) is shown in bold and delta AIC shows the difference in AIC value between candidate models and this top-ranking model.

Candidate model	Degree of smoothing	AIC	Delta AIC
<code>gamm(nectar ~ s(day, fx=T, k=5) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')</code>	5	1403.66	15.12
<code>gamm(nectar ~ s(day, fx=T, k=6) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')</code>	6	1394.62	6.07
<code>gamm(nectar ~ s(day, fx=T, k=7) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')</code>	7	1388.55	0
<code>gamm(nectar ~ s(day, fx=T, k=8) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')</code>	8	1390.16	1.61
<code>gamm(nectar ~ s(day, fx=T, k=9) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')</code>	9	1388.71	0.16
<code>gamm(nectar ~ s(day, fx=T, k=10) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')</code>	10	1390.65	2.10
<code>gamm(nectar ~ s(day, fx=T, k=11) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')</code>	11	1392.02	3.48

Table 3.3. Statistical models for analysing floral richness. A comparison of candidate generalised additive mixed models for analysing plant taxon richness. The chosen model (k=3) is shown in bold and delta AIC shows the difference in AIC value between candidate models and this top-ranking model.

Candidate model	Degree of smoothing	AIC	Delta AIC
gamm(richness ~ s(day, fx=T, k=3) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')	3	133.00	0
gamm(richness ~ s(day, fx=T, k=4) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')	4	135.02	2.02
gamm(richness ~ s(day, fx=T, k=5) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')	5	133.10	0.10
gamm(richness ~ s(day, fx=T, k=6) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')	6	133.62	0.62
gamm(richness ~ s(day, fx=T, k=7) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')	7	135.62	2.62
gamm(richness ~ s(day, fx=T, k=8) + area + income, random = list(Garden_code = ~1), family = Gamma(link = log), method = 'REML')	8	137.11	4.11

Magnitude of the nectar supply through the year

To estimate 'annual' (March-October) nectar sugar production for each garden, I multiplied the mean daily nectar sugar mass for the eight survey visits by the number of days between 01 March and 31 October inclusive. To describe the non-linear trend in nectar sugar production through the sampling period I fitted a GAMM with day of the year modelled with a thin-plate regression spline. A Gamma error family with log link function gave the best fit for the data. The model also included median household income (a numeric value for each of the six sampled regions in Bristol) and garden area as fixed effects (linear fits) and the code for each garden as a random effect, this accounting for the repeated sampling of gardens (Table 3.2).

Temporal stability of the nectar supply

To investigate how the temporal stability of the garden nectar supply (i.e. consistency between months of the year) varied with the flowering plant richness of individual gardens, I regressed the coefficient of variation (standard deviation / mean) in monthly nectar sugar production onto flowering plant richness. The coefficient of variation is commonly used as a measure of instability in ecology (Doak et al., 1998), with a smaller value indicating greater stability. Next, I investigated how the total number of gardens a pollinator can visit affects the temporal stability of the overall nectar supply, using a simulation approach. I drew random combinations of gardens from the 59 I surveyed (with replacement, so gardens could be selected multiple times) to give samples of 1-100 gardens and iterated this process 1,000 times for each sample size (1-100 gardens). For each iteration I summed across gardens to give total nectar sugar per month and calculated the coefficient of variation for this aggregated supply. A pollinator flying 100 m from a central point within each of my six

surveyed regions of Bristol can visit 60 to 181 gardens (mean of 93; data from inspecting satellite imagery). Thus, 100 gardens are accessible well within the typical foraging ranges of flower-visiting insects (Greenleaf et al., 2007; Wratten et al., 2003).

Diversity and composition of the nectar supply

To describe the non-linear trend in flowering plant richness through the sampling period, I fitted a GAMM as described above (Table 3.3). I estimated beta diversity across gardens by calculating Sørensen dissimilarity and partitioning it into turnover and nestedness components, using R package ‘betapart’ (Baselga and Orme, 2012). The Sørensen dissimilarity index describes the extent to which different sites (i.e. gardens) share species (perfect similarity = 0; perfect dissimilarity = 1).

The native versus non-native status of flowering plants was determined using the online plant atlas PLANTATT (Hill et al., 2004) and plant life form was determined using Brickell (2016), with each taxon categorised as a herbaceous plant, tree, shrub or woody climber. I grouped plants into those with ‘generalised’ or ‘specialised’ flower structures according to the accessibility of the nectar provided for pollinators. Generalised flowers have an open structure with nectar accessible to all short- and long-tongued insects (e.g. *Bellis perennis*). Specialised flowers in contrast offer nectar rewards that cannot be accessed by all pollinators. In most cases this is due to a long corolla tube which requires a long tongue (e.g. *Lamium album*) and in others a physical obstacle which requires sufficient force to manipulate (e.g. *Lotus corniculatus*). Although this dichotomy is necessarily simplistic, categories were decided from a combination of corolla measurements and observations of pollinator visits.

3.3 Results

In total, I recorded over two million floral units (2,061,703) belonging to 636 plant taxa in 98 families in the 59 surveyed gardens. Garden area ranged from 31.3 m² to 407.7 m², with a mean of 156.4 m² (± 12.7 SEM) and a combined area of 0.92 ha.

3.3.1 Magnitude of the nectar supply through the year

Total annual (March-October) nectar sugar production per garden varied from 2.3 g to 1661.9 g (mean 395.5 g ± 45.2 SEM). The distribution of annual nectar supply was positively skewed, with the top 13 gardens (22%) accounting for 51% of the total nectar sugar (Fig. 3.2a). Gardens produced a mean of 3.2 g (± 2.7 SEM) of nectar sugar per square metre across the sampling period (range 0.03 g to 10.80 g). A generalised additive mixed model described a significantly non-linear trend in nectar supply through the year (GAMM: $F_{6,6} = 16.72$; $p < 0.001$), with a predicted peak of 05 July and periods of lower supply in early spring (March) and from late summer into autumn (August-October; Fig. 3.2b). There was a significant positive correlation between nectar

sugar production and median household income (GAMM: $N = 472$; $t = 2.87$; $p = 0.004$), but not between nectar sugar production and garden area (GAMM: $N = 472$; $t = 0.92$; $p = 0.358$). Together, day of the year, income and garden area explained 13.2% of the variation in nectar sugar production. The temporal pattern of nectar supply varied among individual gardens, with 22 (37%) peaking outside of May-July and at least one garden peaking in each month. The mean monthly nectar sugar production per garden varied by a factor of two across the year (from 2.2 g in July to 1.1 g in October).

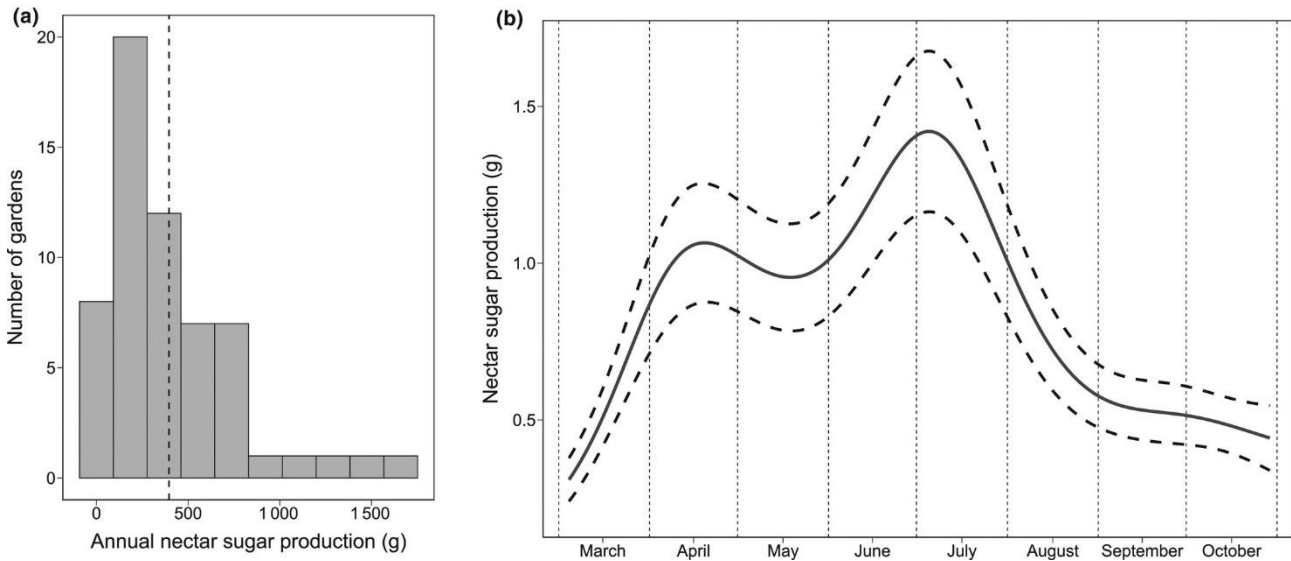


Figure 3.2. Spatial and temporal patterns in the magnitude of garden nectar supplies. (a) A histogram of annual (March-October) nectar sugar production per garden, with the mean (396 g) indicated by a dashed line. (b) Nectar sugar production per garden plotted through the sampling year, showing the prediction (using median values of household income and garden area) from a generalised additive mixed model (solid line) and boundaries one standard error above and below the prediction (dashed lines).

3.3.2 Temporal stability of the nectar supply

There was a significant negative correlation between flowering plant richness in gardens and the coefficient of variation in monthly nectar sugar production (LM: $F_{1,57} = 24.67$; $R^2 = 0.302$; $p < 0.001$; Fig. 3.3a), hence gardens with richer floras tended to have a more stable supply of nectar through the year. My simulations showed the more gardens a pollinator can visit, the more stable the overall supply of nectar through time (Fig. 3.3b). The coefficient of variation in nectar supply among months rapidly declines with an increasing number of gardens, with the mean coefficient of variation across iterations halving between one and seven gardens (Fig. 3.3b). Thus, complementarity among many gardens in residential areas smooths temporal variability in their combined nectar supply.

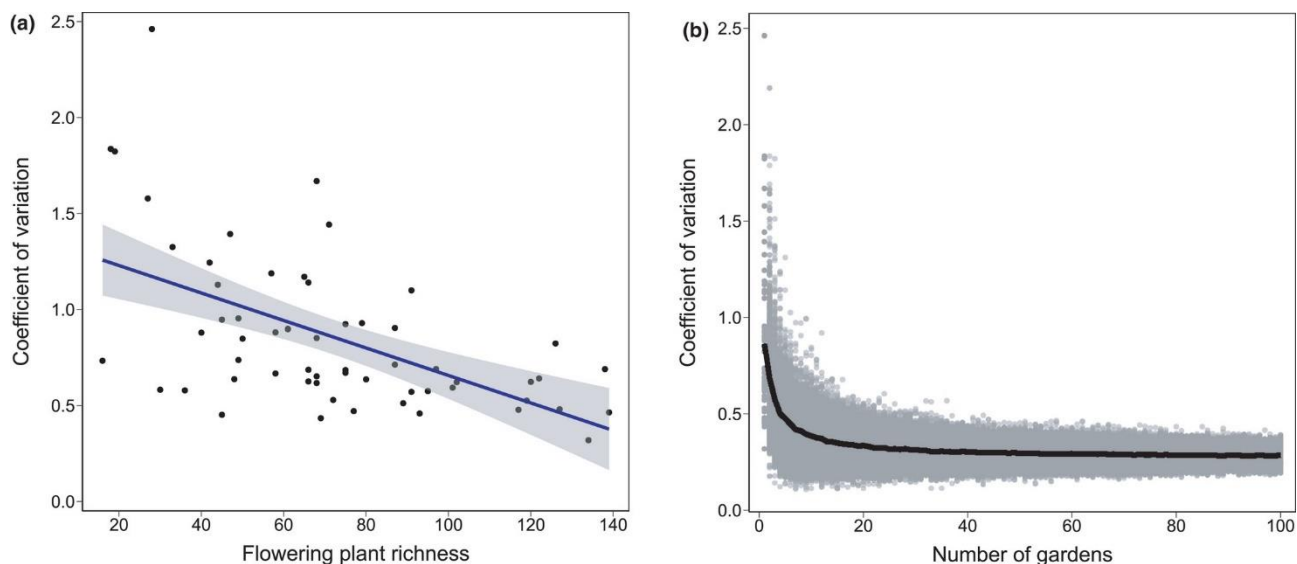


Figure 3.3. Patterns of temporal stability in garden nectar supplies. (a) The relationship between flowering plant richness and the coefficient of variation in monthly nectar sugar production (linear regression line in blue and shaded area covering one SE around the prediction). (b) The simulated relationship between the number of gardens and the coefficient of variation in their aggregated monthly nectar sugar production. Grey points represent iterations of my simulation and the mean line across iterations is shown in black.

3.3.3 Diversity and composition of the nectar supply

A generalised additive mixed model described a significantly non-linear trend in flowering plant richness through the year (GAMM: $F_{2,2} = 317.92$; $p < 0.001$), with a predicted peak of 07 July and periods of lower richness in spring (March-May) and autumn (September-October; Fig. 3.4). Neither median household income (GAMM: $N = 472$; $t = 1.58$; $p = 0.115$) nor garden area (GAMM: $N = 472$; $t = 1.92$; $p = 0.056$) correlated significantly with flowering plant richness (although the correlation for garden area was marginally not significant). The temporal pattern of flowering plant richness was relatively consistent, with 50 of the 59 gardens peaking in the summer (June-August) and none peaking in March or October. Beta diversity was very high (Sørensen dissimilarity 0.96) and driven by turnover among gardens rather than nestedness (turnover component 98%). Thus, gardens tended to share a very low proportion of their taxa and the floral composition of low richness gardens was not generally a subset of that in higher richness gardens. This was reflected in the incidence frequencies of taxa, with only 20 taxa (3.1% of the total) recorded in at least half of gardens (Table 3.4) and 203 taxa (31.9% of the total) only found in a single garden. Half of the total nectar supply was provided by 13 taxa, three quarters by 43 taxa and 95% by 154 taxa (see Supplementary Table 7 in Appendix 2).

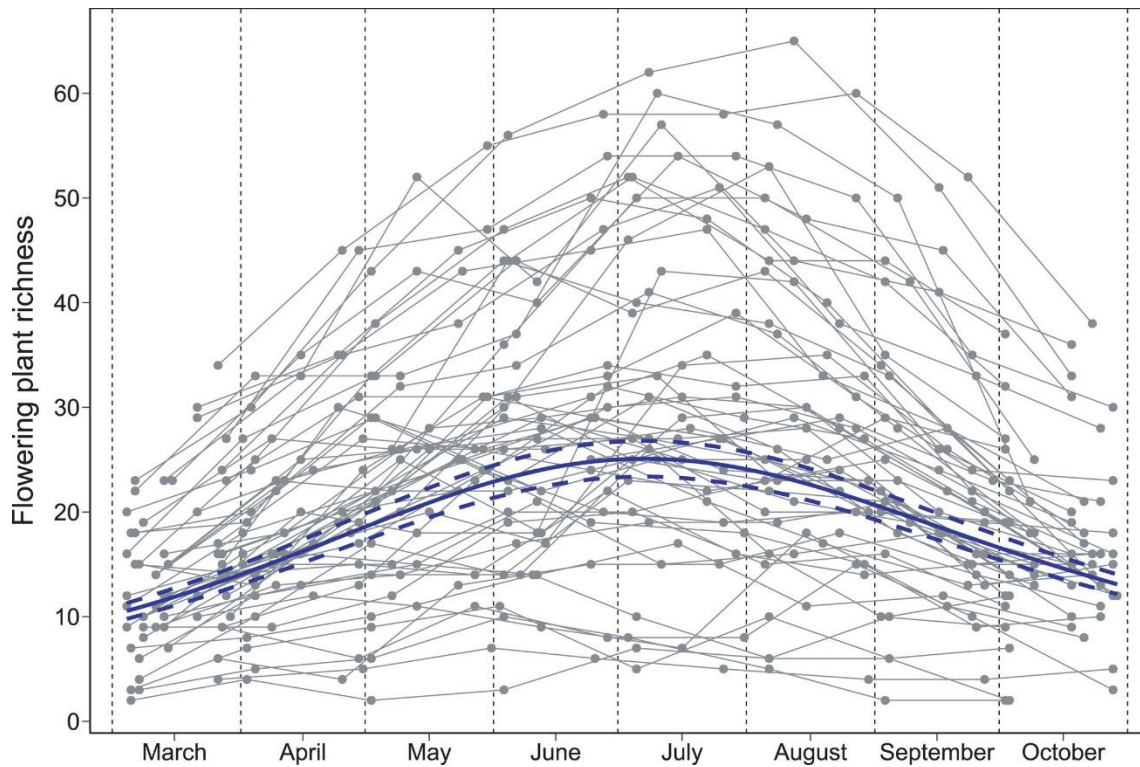


Figure 3.4. Flowering plant richness through the year. Data points for individual gardens are connected by grey lines and the prediction (using median values of household income and garden area) from a generalised additive mixed model is shown (solid blue line), along with boundaries one standard error above and below the prediction (dashed blue lines).

The composition of plant species underpinning nectar sugar production varied greatly through the year, reflecting different flowering periods among taxa (Fig. 3.5; see Supplementary Table 8 in Appendix 2). *Pieris* species provided the most nectar of any single taxon in March (31.0%) and April (26.1%) while *Fuchsia magellanica* was dominant from July to October (32.3-52.1%). Non-native taxa (77% of all taxa) contributed 90.5% of total nectar sugar production, a proportion which remained relatively consistent through the year (Fig. 3.6). Shrubs produced 57.5% of nectar (more in spring and autumn; Fig. 3.7), herbaceous plants 33.5% and the contributions of woody climbers (6.2%) and trees (2.7%) were lower. Around two thirds (66.4%) of nectar was provided by flowers with a specialised structure, with just one third (33.6%) accessible to all pollinators. This pattern changed through time, with specialised flowers providing 73.9-82.6% of nectar in July-October (Fig. 3.8).

Table 3.4. The most common flowering plants. The 20 taxa recording flowering over half of the 59 surveyed gardens. The native status of each taxon is indicated by the letter ‘N’ (native) or ‘A’ (non-native alien).

Plant taxon	Number of gardens (percentage)	Native status
<i>Euphorbia peplus</i>	53 (89.8)	A
<i>Rosa</i> spp.	50 (84.7)	A
<i>Taraxacum</i> agg.	47 (79.7)	N
<i>Epilobium ciliatum/montanum</i>	44 (74.6)	N
<i>Cardamine flexuosa/hirsuta</i>	43 (72.9)	N
<i>Geum urbanum</i>	41 (69.5)	N
<i>Narcissus</i> spp. (small flower cultivar)	40 (67.8)	A
<i>Pelargonium</i> spp.	40 (67.8)	A
<i>Geranium robertianum</i>	39 (66.1)	N
<i>Clematis</i> spp. (ornamental)	38 (64.4)	A
<i>Hyacinthoides non-scripta/hispanica</i>	37 (62.7)	N
<i>Cyclamen</i> spp.	35 (59.3)	A
<i>Fuchsia magellanica</i> /hybrid	33 (55.9)	A
<i>Cymbalaria muralis</i>	32 (54.2)	A
<i>Muscari armeniacum</i>	32 (54.2)	A
<i>Sonchus oleraceus</i>	32 (54.2)	N
<i>Circaea lutetiana</i>	31 (52.5)	N
<i>Lonicera caprifolium/japonica/periclymenum</i>	31 (52.5)	A
<i>Primula</i> spp. (<i>Polyanthus</i>)	31 (52.5)	A
<i>Senecio vulgaris</i>	30 (50.8)	N

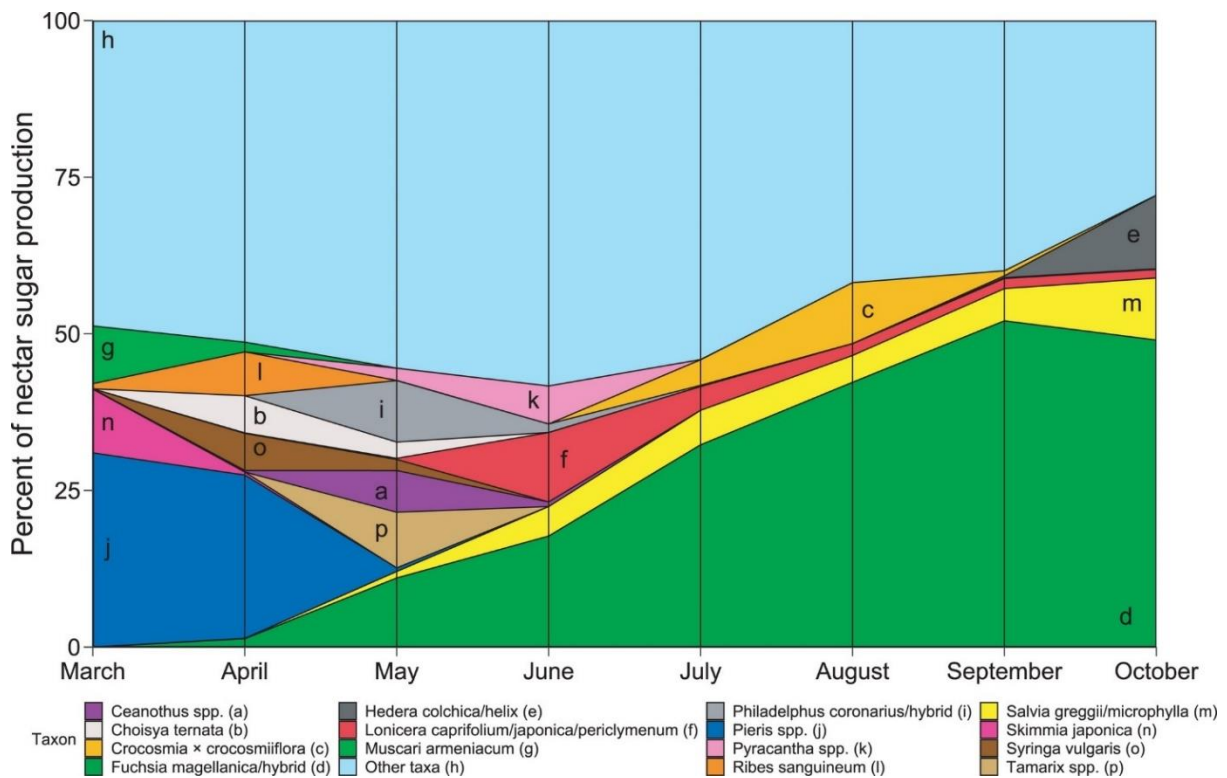


Figure 3.5. The contribution of plant taxa to monthly nectar sugar production. The percentage is indicated by the height of a coloured polygon. The 15 displayed taxa provided >5% of nectar sugar in at least one month, with the remainder included in the ‘Other taxa’ category.

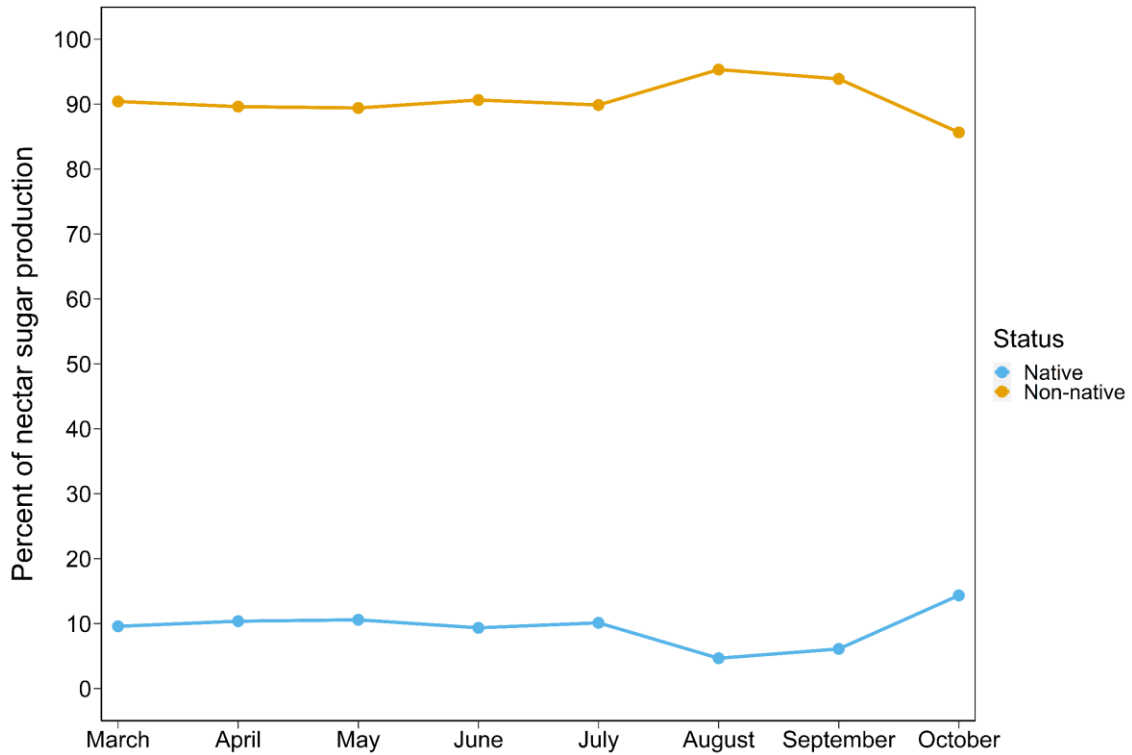


Figure 3.6. Nectar supply by native status. The percentage of the total nectar supply of all gardens in each month produced by native and non-native plant taxa.

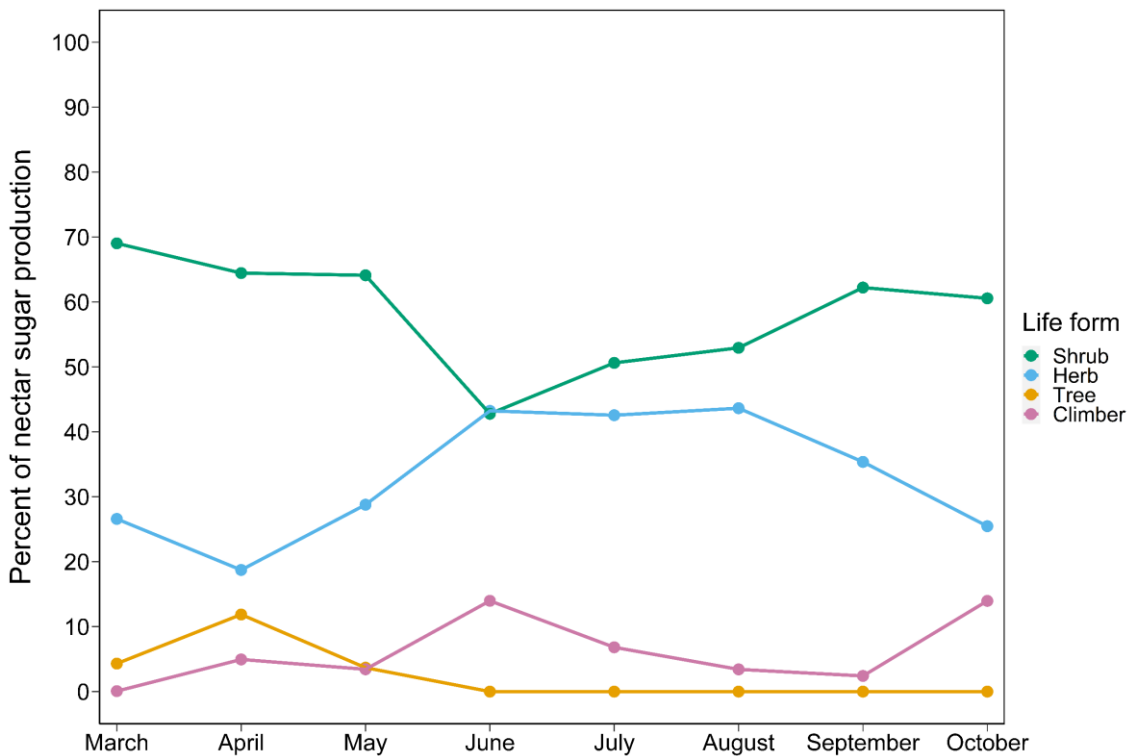


Figure 3.7. Nectar supply by plant life form. The percentage of the total nectar supply of all gardens in each month produced by shrubs, herbaceous plants (herbs), trees, and woody climbers (climbers).

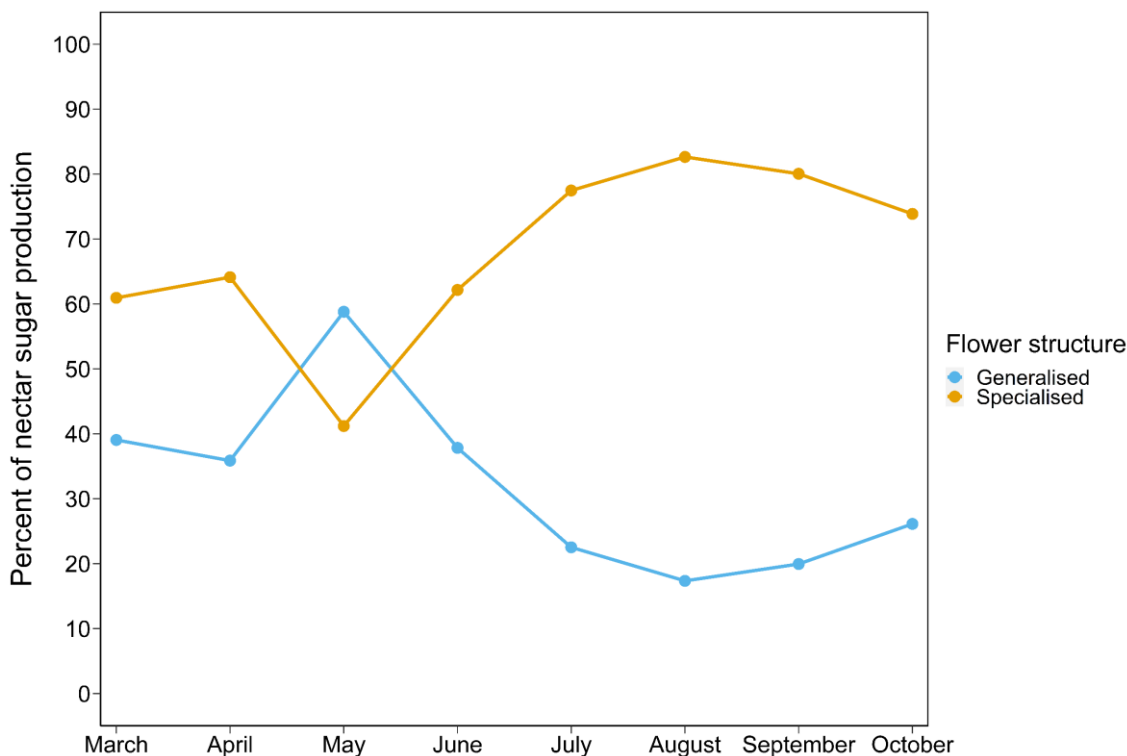


Figure 3.8. Nectar supply by flower structure. The percentage of the total nectar supply of all gardens in each month produced by flowers with a generalised or specialised structure.

3.3.4 Validation of stratified sampling method for surveying gardens

Out of the 59 gardens I obtained permission to survey, 12 were in income band one, 23 in income band two and 24 in income band three. A truly representative selection would have contained equal numbers of gardens in each income band. To test the impact of this imbalance in my sampling methods on my major conclusions, I re-ran some of my analyses on subsets of the data which contained equal numbers of gardens in each income band. For each of 20 subsets I included the 12 gardens in income band one and randomly selected 12 gardens for inclusion from each of income bands two and three, giving a balanced selection with 36 of my 59 gardens included (12 in each income band).

The results of re-running my analyses on these 20 subsets reported in Table 3.5 show that my main conclusions about spatial and temporal variation in the nectar supply of urban gardens are unaffected by the imbalance in my sampling method. In a completely balanced design, I estimate mean annual nectar sugar production to be around 6% lower, the temporal peak in nectar supply remains in early July, the effect of median household income remains significant and the effect of garden area remains non-significant.

Table 3.5. Validation of stratified sampling method. A comparison of results obtained by analysing my complete dataset (59 gardens) with results obtained by analysing 20 subsets of my data in which the number of sampled gardens in each income band was balanced.

Result being compared	Complete dataset (59 gardens)	20 subsets (36 gardens in each)
Mean annual (March-October) nectar sugar production per garden (g)	395.55	Mean: 370.47 Range: 307.18 – 417.33
Temporal peak in nectar sugar production (GAMM prediction)	05 July	Modal day: 06 July Range: 04 July – 11 July
P-value for effect of median household income on nectar sugar production	0.0043	Mean: 0.0135 Range: 0.0003 – 0.0377
P-value for effect of garden area on nectar sugar production	0.3580	Mean: 0.6774 Range: 0.3599 – 0.9470

3.4 Discussion

Garden nectar production peaked in mid-summer, but individual gardens differed markedly in both the magnitude of their nectar supply and its temporal pattern. Most of this variation was not explained by the model, indicating the importance of additional factors in determining nectar among gardens. The finding that garden size did not correlate significantly with nectar sugar production suggests that the quality of the garden habitat, driven by individual management decisions, is of primary importance. Nectar production was more stable through time in gardens with greater flowering plant richness and, at larger spatial scales temporal stability in the nectar supply rapidly emerges if pollinators forage across multiple gardens. In what follows I first consider the limitations of my work and then discuss my results in the context of urban pollinator conservation.

3.4.1. Limitations

There are three main limitations to my study of nectar supply in residential gardens. First, insect pollinators require additional resources to nectar sugar alone, which can include pollen, extrafloral nectar and honeydew, nest sites, prey items and foodplants for larvae (Wäckers et al., 2007). Given nectar sugar mass and total pollen volume both correlate with floral abundance (Hicks et al., 2016), the broad patterns I observe in nectar supply are likely to reflect those of pollen production. Currently, there is insufficient published pollen data to have included it in this study. Nevertheless, nectar sugar is a general energy source required by the vast majority of adult pollinators so it provides a common currency through which to compare the floral resource value of habitats (e.g. Baude et al., 2016; Timberlake et al., 2019). Second, I only surveyed gardens in a single city (Bristol, UK) in a single year (2019). Residential gardens cover 28% of Bristol by area (Baldock et al., 2019),

putting it within the range seen for cities worldwide (e.g. 16% in Stockholm, Sweden; Colding et al., 2006 and 36% in Dunedin, New Zealand; Mathieu et al., 2007). In addition, there was no significant difference in the nectar sugar production of urban land uses between Bristol and three other UK cities (see Chapter 2), but there is no equivalent data for non-UK cities to make comparisons. Both mean annual temperature and total rainfall for Bristol in 2019 were typical of those in the past decade (Met Office, 2020), so I expect the patterns I observed in 2019 will be representative of those in other years. While the precise shape of the seasonal nectar supply curve and the contributions of specific plant taxa will differ in other cities and years, the general findings of extreme variability and turnover among single gardens but temporal stability across multiple gardens are very likely to apply in other cities because the principle that gardens comprise many small habitat patches which differ independently in their management remains true wherever they are located. Finally, my method for obtaining permission to survey residential gardens may have introduced a degree of bias, which cannot be quantified. The requirement to gain permission before sampling private gardens necessarily precludes a completely random selection method and thus the gardens of individuals more interested in the subject of the research might have been overrepresented. If a truly representative selection of gardens included more which contained very few flowers, this would reduce my estimates for the quantity of nectar produced by an average garden, but it should not materially affect the temporal pattern, which is driven predominantly by the high-nectar gardens.

3.4.2. Nectar supply in gardens

There was substantial variation in the magnitude of nectar production among individual gardens (the scale at which management decisions are made). In my sample, the highest-nectar garden produced more than 700 times more sugar than the lowest-nectar garden during my survey period, but I found that garden size did not correlate significantly with nectar sugar production, which emphasises the importance of management decisions for nectar supply rather than total area *per se*. The highest-nectar gardens tended to be in more affluent regions (four of the top five nectar producing gardens were in income band one) and contained ornamental flower borders, while the lowest-nectar gardens were likely to be in regions of lower income (four of the bottom five in income band three) and typically lacked flower-rich borders. There was no clear negative role of hard surfaces like decking and paving in place of lawns because I observed that herbaceous plants and shrubs in pots or peripheral borders were usually the major nectar source rather than flower-rich lawns. My study shows that it is not necessary for a gardener to have a large garden to provide pollinators with a large supply of nectar because it is how they choose to garden which is most important. However, a lack of gardener knowledge of which species are nectar rich could lead to suboptimal outcomes for pollinators even where the necessary motivation exists (Lindemann-Matthies et al., 2021).

Nectar production peaked in mid-summer, when UK pollinator abundance is also highest (Balfour et al., 2018), but patterns among individual gardens were idiosyncratic with at least one garden peaking in each month from March to October. It was common for a single flowering plant taxon (often a tree or shrub) to provide the

majority of a garden's nectar sugar in a particular month, contributing to the variability in temporal patterns within and among gardens. Because each garden is managed by a single individual or group of individuals, temporal patterns of nectar supply vary among gardens in a relatively independent fashion. As a result, extreme temporal variation in nectar production tends to average out when summed across many gardens, resulting in an overall supply that is more stable through time, an example of the portfolio effect (Schindler et al., 2015). Across my 59 surveyed gardens, the mean monthly nectar sugar production only varied by a factor of two through the sampling year. This contrasts with patterns in rural farmland, where temporal peaks may be more than ten times as great as troughs in nectar supply (Timberlake et al., 2019). Because urban gardens are present at such a high density, the portfolio effect smooths temporal variability in their aggregated supply at a scale relevant to foraging pollinators. Hence, unless there are strong barriers limiting dispersal in urban areas, pollinators foraging in residential regions of towns and cities have access to a much more stable and continuous supply of nectar through the year than those in rural farmland.

The flowering plant richness of residential gardens is extremely high; I recorded 636 taxa from 98 families flowering in less than one hectare of land. This phenomenal richness (which is higher than in semi-natural habitats; e.g. Vessby et al., 2002) is driven by extreme turnover in species composition among gardens (Loram et al., 2008b). Individual gardens tend to have relatively distinct floras (only 3% of taxa were recorded in half the gardens) because gardeners have a wide variety of (native and non-native) species to choose from when planting and their active management (e.g. 'weeding') prevents plants being outcompeted (Loram et al., 2008a). The value of gardens as a habitat type is an emergent property, resulting from many small patches of land being managed independently, emphasising the importance of understanding landscape context for biodiversity conservation in urban areas (Goddard et al., 2010). Being mobile, insect pollinators have the potential to take advantage of the nectar supplied by gardens despite their patchy distribution in fragmented urban landscapes, but differences in diet, larval requirements, dispersal capability and nesting behaviour among taxa will affect the composition of pollinator communities that can be supported (Seitz et al., 2020; Wenzel et al., 2020).

3.4.3. Management recommendations

Shrubs, climbers and trees provided two-thirds of all nectar as their physical structure results in a three-dimensional arrangement of flowers, allowing a large number to be produced within a relatively small area of land. Ornamental shrubs, climbers and trees with nectar-rich flowers are therefore a space-efficient way to boost the garden nectar supply during their flowering periods. Gardens with higher flowering plant richness provide a more stable supply of nectar sugar through time, but by actively selecting nectar-rich species with complementary phenological profiles gardeners can achieve this result more efficiently with respect to cost and space (Table 3.6). An additional consideration when planting for pollinators is flower structure, which determines the accessibility of floral resources to different insects (e.g. Stang et al., 2006). From July to October 74-83% of nectar sugar was supplied by flowers that are not accessible to all pollinators (especially

Fuchsia magellanica, *Lonicera* and *Salvia* species, which have long corolla tubes), so I recommend prioritising the planting of taxa which produce relatively open flowers in late summer and autumn to ensure sufficient food for short-tongued solitary bees and Diptera (Table 3.6).

Table 3.6. Recommended plants for different seasonal periods in UK gardens. Listed plants are nectar rich, attractive to flower-visiting insects and easily acquired by gardeners. Taxa are described as native ('N') or non-native alien ('A') and as having a generalised ('G') or specialised ('S') flower structure (or including members of both categories). Gardeners should avoid invasive plants, which can escape from gardens and spread extensively in rural habitats.

Seasonal period	Recommended plants	Native status	Flower structure
Early spring (March)	<i>Helleborus</i> spp.	N or A	S
	<i>Pieris</i> spp.	A	S
	<i>Pulmonaria</i> spp.	N or A	S
	<i>Salix</i> spp. (willow)	N or A	G
	<i>Skimmia japonica</i>	A	G
Mid to late spring (April-May)	<i>Aquilegia vulgaris</i>	N	S
	<i>Ceanothus</i> spp.	A	G
	<i>Malus</i> spp. (apple)	N or A	G
	<i>Prunus avium</i> (cherry)	N	G
	<i>Ribes</i> spp. (currants)	N or A	G or S
Early to mid summer (June-July)	<i>Campanula</i> spp. (bellflower)	N or A	G
	<i>Geranium</i> spp. (cranesbill)	N or A	G or S
	<i>Lavandula</i> spp.	A	S
	<i>Lonicera periclymenum</i> (honeysuckle)	N	S
	<i>Pyracantha coccinea</i> (firethorn)	A	G
Late summer to autumn (August-October)	<i>Echinacea purpurea</i> (coneflower)	A	G
	<i>Hedera helix</i> (ivy)	N	G
	<i>Origanum vulgare</i>	N	G
	<i>Sedum</i> spp.	N or A	G
	<i>Verbena bonariensis</i>	A	S

3.4.4. Conclusions

My study demonstrates that urban residential gardens differ markedly in the magnitude and temporal pattern of nectar supply, but bigger gardens are not necessarily better for feeding pollinators. Instead, the management decisions made by individuals are particularly important, with gardeners able to control habitat quality if not quantity. By visiting multiple gardens which differ independently in plant species composition, pollinators have the potential to access a diverse and continuous supply of nectar in urban landscapes. So far, in Chapters 2 and 3, I have shown some of the ways in which nectar supplies in urban green spaces differ from those in rural areas. In Chapter 4, I will build upon these studies of pollinator food supplies by investigating how bumblebee populations differ between urbanised and farmed landscapes.

Chapter 4

Comparing buff-tailed bumblebee populations between urban and farmland landscapes



The buff-tailed bumblebee (*Bombus terrestris*) has a broad diet, allowing it to take advantage of the ornamental plants found in urban green spaces, such as this holly-leaved hellebore (*Helleborus argutifolius*) in a flower border in the University of Bristol's Royal Fort Gardens (Photo: N. Tew).

4.1 Introduction

Modern industrial agriculture is a formidable driver of biodiversity loss on a global scale, resulting in the intensive management of vast areas of land (Krebs et al., 1999; Tilman et al., 2017, 2001). Thus, semi-natural habitats such as broadleaf woodland and unimproved grassland are converted into crop monocultures and heavily grazed pasture, contributing to the ecological simplification of the landscape (Robinson and Sutherland, 2002; Stoate et al., 2001). The richness and abundance of wildlife found in intensively managed farmland is further diminished by the widespread application of herbicides, fungicides and insecticides (Geiger et al., 2010; Holzschuh et al., 2008; Tuck et al., 2014).

The scale and intensity of modern farming practices substantially impact the supply of floral resources in space and time (Carvell et al., 2006; Goulson et al., 2015; Jachula et al., 2021; Timberlake et al., 2019), which critically underpin insect pollinator populations (Roulston and Goodell, 2011; Russo et al., 2013; Woodard and Jha, 2017). For example, in the UK, where 72% of land is used for agriculture (World Bank, 2018), a period of extreme intensification between the 1930s and 1970s coincided with an estimated 32% reduction in the national supply of nectar (Baude et al., 2016). The widespread loss in both the quantity and diversity of floral resources is a major factor contributing towards pollinator declines (Baude et al., 2016; Goulson et al., 2015; Potts et al., 2010).

Urban green spaces (especially gardens) can provide a rich supply of floral resources (see Chapters 2 and 3; Baldock et al., 2019; Hülsmann et al., 2015), particularly beneficial to bees, which feed on them as both larvae and adults. The richness of bee communities in cities can be higher than in nearby farmland (Baldock et al., 2015; Theodorou et al., 2020, 2017), with urban areas potentially acting as refuges for populations within regions dominated by intensive agriculture (Hall et al., 2017). It is important to quantify the population density for bees in urbanised and farmed landscapes, in order to understand how species respond to land use change, with implications for their conservation and the pollination services they provide (Dicks et al., 2013; Dreier et al., 2014). However, it is difficult to obtain reliable measures of population density for bee species because local abundance, estimated by visual observation or pan trapping (e.g. Baldock et al., 2015; Theodorou et al., 2020; Verboven et al., 2014), is strongly influenced by the presence of flower-rich patches which draw flying insects in from an unknown distance (Berthon et al., 2021; Wood et al., 2015a). Thus, abundance may relate more to the distribution of pollinators in the landscape at a particular point in time than the size of the underlying populations (Holland et al., 2015; Wood et al., 2015a). An additional challenge exists for the eusocial bumblebees, where it is the number of colonies (and hence reproductive queens), rather than individual workers, which determines the effective population size (Darvill et al., 2004; Knight et al., 2005). Counting nests in the field is extremely labour-intensive (Kells and Goulson, 2003; Osborne et al., 2007), but instead molecular markers can be used as an indirect method to estimate colony density from the number of related individuals in the landscape, without directly locating nest sites (e.g. Darvill et al., 2004; Knight et al., 2009; Wood et al., 2015b).

In this study, I use microsatellite genotyping to compare the colony density of the buff-tailed bumblebee (*Bombus terrestris*), a widespread and commercially important crop pollinator (Dicks et al., 2015; Kleijn et al., 2015), between urban and farmland landscapes in the UK. *Bombus terrestris* is a super-generalist which forages on a wide variety of flowering plants (Rasmont et al., 2008), so can take advantage of the diverse array of native and non-native species which comprise urban flowering plant communities (Baldock et al., 2019, 2015; Lowenstein and Minor, 2016). Experimental studies conducted in the UK in summer found *B. terrestris* colonies grew faster and produced more reproductive offspring when placed into urban and suburban landscapes compared with nearby farmland (Goulson et al., 2002; Samuelson et al., 2018). Colonies in towns and cities are also able to remain active for longer periods of the year (even during winter) and produce more broods, aided by the continuous production of floral resources (Falk, 2015; Stelzer et al., 2010; see Chapter 3). As a result of these factors, I predict that urban landscapes will support a relatively high colony density of *B. terrestris*, but it is unclear whether it will exceed that of farmland, given the overall nectar supply is comparable between these landscape types (see Chapter 2).

4.2 Materials and methods

4.2.1 Study sites

The fieldwork for this study was undertaken in 2021 at 16 sites centred around eight large towns and cities (hereafter referred to collectively as cities) in Southwest UK (Bath, Bristol, Cardiff, Gloucester, Newport, Swindon, Taunton and Weston; Fig. 4.1). Eight urban sites were each paired with a nearby farmland site to minimise any geographic biases and all sites were located >5 km apart (Fig. 4.1). This distance ensures independence when sampling the bumblebee colonies, given *B. terrestris* does not forage this far from the nest (Knight et al., 2005; Redhead et al., 2016). A circle of radius 0.75 km (area 1.77 km²) was drawn around each site in QGIS v.3.4.12 and all land use mapping and bumblebee collection took place within this sampling area (following Wood et al. (2015b) and Timberlake et al. (2021)).

An urban site was located in each of the eight focal cities such that the entire circular sampling area was contained within the urban boundary. Sites were selected to represent various degrees of urbanisation, ranging from close to the city centre to those in the more peripheral suburbs. Land use for the sampling area around each urban site was obtained from the Ordnance Survey Mastermap Greenspace layer (downloaded through Digimap) and analysed in ArcMap 10.6.1 and QGIS v.3.4.12 (Fig. 4.2). The initial 17 listed land use categories were grouped into five, a ‘nature reserve’ category was added manually at one site (Swindon) and all remaining land not yet categorised (mostly buildings, roads and car parks) was labelled ‘impervious surface’ (Table 4.1). The three main land use types (covering 93-100% of each site) were impervious surface (mean 43%, range 31-61%), residential garden (mean 33%, range 20-39%) and other greenspace (mean 20%, range 12-35%) (Table 4.1), with their relative proportions similar to data reported by Baldock et al. (2019) for other UK cities.

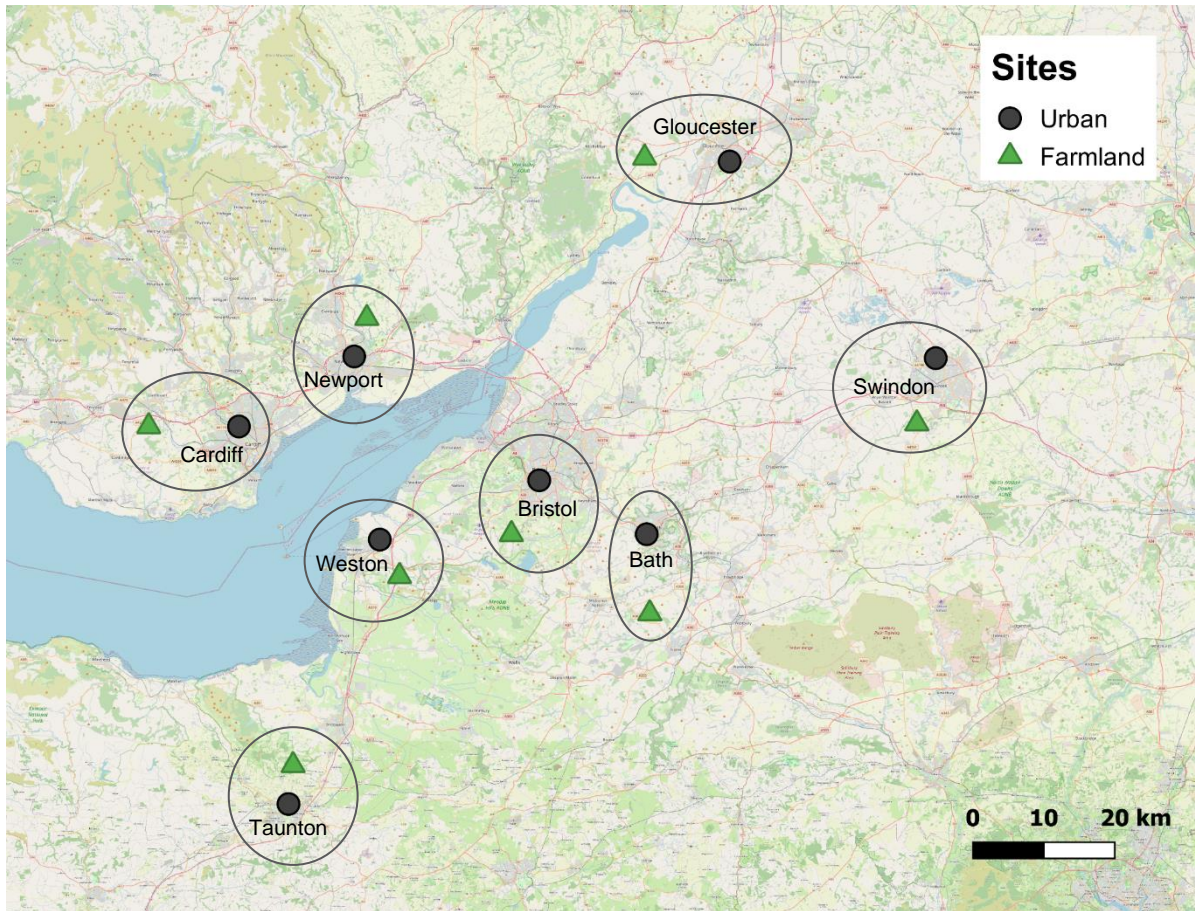


Figure 4.1. Sampling sites. The location of the 16 sampling sites in the Southwest UK. An urban site (filled dark circle) was positioned within each of the eight named cities and paired with a nearby farmland site (filled green triangle), with paired sites indicated by a grey surrounding circle.

Table 4.1. The composition of urban sampling sites. The percentage of each land use type within the sampling circle is given. The Ordnance Survey Mastermap Greenspace layer listed 17 categories, which I grouped into five: Allotment was ‘Allotments Or Community Growing Spaces’; Cemetery combined ‘Cemetery’ and ‘Religious Grounds’; Residential garden was ‘Private Garden’; Other greenspace combined ‘Amenity - Residential Or Business’, ‘Amenity - Transport’, ‘Bowling Green’, ‘Golf Course’, ‘Institutional Grounds’, ‘Land Use Changing’, ‘Natural’, ‘Other Sports Facility’, ‘Play Space’, ‘Playing Field’, ‘School Grounds’ and ‘Tennis Court’; Park was ‘Public Park Or Garden’.

Urban site	Impervious surface	Residential garden	Other greenspace	Park	Allotment	Nature reserve	Cemetery
Bath	37.95	39.36	17.20	2.85	2.36	0.00	0.30
Bristol	60.69	20.28	12.26	5.71	0.01	0.00	1.05
Cardiff	42.13	36.21	19.41	0.95	1.12	0.00	0.18
Gloucester	32.68	35.71	28.58	0.64	2.11	0.00	0.27
Newport	48.50	37.73	11.57	1.41	0.58	0.00	0.22
Swindon	30.94	29.80	34.95	0.00	0.00	4.26	0.04
Taunton	47.82	26.47	22.08	1.21	2.22	0.00	0.21
Weston	42.97	38.75	17.89	0.00	0.21	0.00	0.18
Mean	42.96	33.04	20.49	1.60	1.08	0.53	0.31

I chose farmland sites that were broadly representative of the rural landscape surrounding each of the eight focal cities by examining satellite imagery (Google Satellite) and subsequently speaking with the farmers who manage the land and gave permission to sample. Land use for the sampling area around each farmland site was manually mapped in QGIS v.3.4.12, informed by a combination of satellite imagery (Google Satellite), Land Cover Map 2015 (Rowland et al. 2017; downloaded through Digimap) and on-the-ground observations made during site visits (Fig. 4.2). The three main land use types (covering 95-99% of each site) were improved grassland (mean 65%, range 25-85%), arable cropland (mean 22%, range 0-57%) and broadleaf woodland (mean 11%, range 1-28%) (Table 4.2). No organic farms were included in the study as organic farming is relatively rare in the region and wider UK, although farmland sites varied in both the type of farming and the perceived intensity of management (Table 4.3). Farmland sites were located >3.5 km away from the edge of any town or city and only one farm site (Swindon) contained mass-flowering crops (field beans).

Table 4.2. The composition of farmland sampling sites. The percentage of each land use type within the sampling circle is given. Improved grassland included both grazed pasture and areas of ryegrass grown for silage production. Built up areas included buildings, car parks and large roads.

Farmland site	Improved grassland	Arable (cereals)	Arable (mass-flowering)	Broadleaf woodland	Built up	Water
Bath	45.03	47.19	0.00	4.58	2.90	0.29
Bristol	78.40	10.58	0.00	6.26	4.75	0.00
Cardiff	70.71	0.00	0.00	28.20	0.65	0.44
Gloucester	85.26	11.43	0.00	1.35	1.96	0.00
Newport	83.24	0.32	0.00	14.95	1.50	0.00
Swindon	25.46	45.71	11.74	15.60	1.50	0.00
Taunton	50.77	43.14	0.00	5.03	1.06	0.00
Weston	81.08	6.95	0.00	8.38	3.58	0.00
Mean	64.99	20.67	1.47	10.54	2.24	0.09

Table 4.3. A description of farmland sampling sites. This table focusses on the type of farming, perceived intensity of management and observed abundance of flowers within the farmland sampling circles.

Farmland site	Description of farmland site
Bath	Cereal crops and ryegrass fields. Some small areas of sheep and cow pasture. Intensively managed farmland with high nutrient inputs (slurry spreading) and very few flowers in fields. Some flower-rich hedgerows and small patches of woodland.
Bristol	Sheep and cow pasture with a few small areas of cereal crops. Management intensity varies with some pasture heavily grazed and other areas lightly grazed and rich in flowers. Some flower-rich hedgerows and small patches of woodland.
Cardiff	Cow pasture with small areas of sheep pasture. Management intensity intermediate with some flower-rich pasture that is not heavily grazed. Flower-rich hedgerows and ditches, and large areas of woodland.
Gloucester	Cow pasture, cereal crops and ryegrass fields. Intensively managed farmland with high nutrient inputs (slurry spreading) and generally few flowers in fields. A few flower-rich patches of fallow land, some flower-rich hedgerows and very little woodland.
Newport	Sheep pasture with small areas of cow pasture. Management intensity high with most pasture heavily grazed and very few flowers. A few flower-rich fields, some flower-rich hedgerows and large areas of woodland.
Swindon	Cereal crops, ryegrass fields and one field of broad beans (mass-flowering crop). Field margins generally wide and rich in flowers, some flower-rich hedges and patches of woodland.
Taunton	Cow pasture, cereal crops, ryegrass fields and a few small areas of horse and sheep pasture. Cow pasture is lightly grazed and is rich in flowers. Cereal and ryegrass fields are intensively managed with very few flowers. Some flower-rich hedgerows and small patches of woodland.
Weston	Cow pasture with a few small areas of sheep pasture and cereal crops. Management intensity varies with some pasture heavily grazed and other areas lightly grazed and rich in flowers. Some flower-rich hedgerows and small patches of woodland.

4.2.2 Bumblebee sampling

In late spring and summer, the abundance of *Bombus terrestris* workers is sufficiently high for sampling, as the use of molecular markers to estimate colony density requires a large number of individuals (Wood et al., 2015a). Thus, sites were visited from 25 May to 04 August 2021 and between the hours of 09:30 and 17:30, when rain was absent or falling as intermittent showers (Table 4.4). Following Timberlake et al. (2021), each site was visited on two separate days during the sampling period (site visits 28 to 43 days apart) with the aim of finding sufficient bumblebees (at least 30 following Wood et al. (2015b)) for analysis pooled across both visits. Paired sites were visited sequentially (one to five days apart) and I alternated whether the urban or farmland site in a pair was visited first (Table 4.4). Following Wood et al. (2015b), the sampling area was divided into quarters and each quarter was sampled for 1.5 to 2 hours per site visit by walking haphazardly and catching the *B. terrestris* workers encountered, taking a GPS reading (Garmin GPSMAP 62s) at each capture location. Care was taken to ensure captures were distributed evenly across sampling areas, but the patchy distribution of flower-rich habitats which attract bumblebees precluded complete coverage at some sites (Fig. 4.2). *Bombus terrestris* was distinguished from the less common white-tailed bumblebee (*Bombus lucorum*)

by the presence of a narrow band of brownish hairs at the base of the white ‘tail’ (Bees Wasps and Ants Recording Society). If a bee was captured while visiting a flower, then the plant species was identified and recorded. Bumblebees were transferred from nets to individual 15 mL plastic centrifuge tubes, kept in a cool box during fieldwork hours, and stored at -20°C on return to the laboratory at the end of each sampling day. As a proxy for body size, intertegular distance (the distance across the thorax between the wing bases) was measured in the laboratory using a digital calliper for a randomly selected 10 workers per site per visit (totalling 320 bees). Intertegular distance is highly correlated with dry body weight (Cane, 1987), which can be estimated using allometric scaling models (see section 4.2.5). Although it is possible to obtain DNA from bumblebees through non-lethal sampling methods (Holehouse et al., 2003), it was necessary to collect entire specimens for body size measurements and pollen metabarcoding (the latter not included in this thesis due to time constraints).

Table 4.4. Dates of sampling visits to sites. Paired sites were always visited sequentially (e.g. Bristol urban site then Bristol farmland site on the next available day) and I alternated whether the urban or farmland site in a pair was visited first.

City	Urban site		Farmland site	
	Visit 1	Visit 2	Visit 1	Visit 2
Bristol	25 May	29 June	26 May	25 June
Weston	01 June	30 June	27 May	01 July
Taunton	03 June	06 July	04 June	02 July
Bath	08 June	08 July	07 June	09 July
Gloucester	10 June	14 July	11 June	13 July
Newport	15 June	25 July	14 June	26 July
Cardiff	16 June	29 July	17 June	27 July
Swindon	24 June	03 August	23 June	04 August

4.2.3 Molecular methods

A tarsal sample was taken from the mid-leg of each bumblebee and stored in 100% ethanol in a 1.5 mL plastic centrifuge tube for molecular analysis. DNA was extracted from tarsi using the HotSHOT protocol (Truett et al., 2000), whereby samples were heated at 95°C for 60 minutes in 20 μl of an alkaline lysis reagent (25mM NaOH + 0.2 mM disodium EDTA; pH 12.7) after which 20 μl of a neutralising reagent (40 mM Tris-HCl; pH 4.7) was added (resultant pH 8.3). Fourteen polymorphic microsatellite loci were selected (B10, B124, B126, B96, BL03, BL06, BL11, BT10, BT18, BT26, BTERN01, BTMS0033, BTMS0045, BTMS0125) following Dreier et al. (2014), and amplified in three polymerase chain reaction (PCR) groups (multiplex sets). Two loci (BL06 and BTMS0033) failed to amplify and so were excluded from further analysis. Following Timberlake et al. (2021), PCRs were carried out in a 2 μl reaction, with 1 μl of Quiagen Mastermix, 1 μl of primer solution (at concentration 0.2 μM in a low TE buffer and 0.4 μM for primer B96) and 2 μl of dried, undiluted DNA template. Amplification included a HotstarTaq activation step for 15 minutes at 95°C , followed by 35 cycles of denaturing for 30 seconds at 94°C , annealing for 90 seconds at 57°C and extension for 60 seconds at 72°C ,

with a final extension of 45 minutes at 60°C. Microsatellite fragments were visualised on an Automated Capillary Sequencer (Applied Biosystems 3730 DNA Analyzer) in wells containing 1 µl of diluted (by factor 50) PCR product, 9 µl of formamide and 0.05 µl of a ROX 500 size standard.

Sample genotypes were determined by sizing amplified fragments using GeneMapper v5. One locus (BT26) showed highly variable and unclear peak patterns and so was excluded from subsequent analysis. At the remaining 11 loci, peak pattern was usually clear and consistent, but where there was uncertainty, the furthest peak to the right was chosen for sizing the fragment. Failed samples were repeated from either the initial extraction (6.6%), amplification (5.0%) or visualisation (7.1%) stages until complete genotypes were determined for all samples. Of 1,001 initial samples, 72 (7.2%) were identified as males due to a single peak across all loci (male bumblebees are haploid) and excluded from subsequent analysis, with 929 female (worker) samples retained. Observed and expected heterozygosity were calculated for each locus in Cervus v.3.0.7 and the assumption that loci were in Hardy-Weinberg (HW) equilibrium (i.e. allele frequencies constant through time) was tested in Genepop v.4.7.5 for a single population (Gloucester urban site) using a Markov chain of 100,000 steps (Table 4.5). To remove any confounding effects of family structure only one worker was included from each multi-individual sibship group subsequently identified. Two loci (BTERN01 and B96) deviated significantly from HW equilibrium (Table 4.5), but conclusions drawn from all subsequent statistical analyses were found to be unaffected by their inclusion, so they were retained. To estimate the rates of allele dropout (0.0-2.0%) and other genotyping errors (0.0-1.4%), 151 worker samples (16.3% of the total) were re-amplified and visualised (Table 4.5).

Table 4.5. Details of the 11 microsatellite loci used for genotyping. Observed and expected heterozygosity are indicated by HObs and HExp, respectively, and p-values for deviation from Hardy-Weinberg equilibrium were obtained using Fisher's exact test. Genotyping errors occurred when the inferred genotype of a sample was not identical when repeated. Dropout describes a partial match between a homozygous and heterozygous genotype (e.g. alleles 174/174 bp followed by 174/190 bp upon repetition) with different mismatches classified as other errors (e.g. alleles 174/182 bp followed by 174/190 bp upon repetition).

PCR group (multiplex)	Locus	Number of alleles	Range (bp)	HObs	HExp	HW P-value	Dropout rate (%)	Other errors (%)
1	B10	25	175–225	0.890	0.912	0.085	0.68	0.00
1	B126	23	152–205	0.783	0.839	0.774	0.68	0.00
1	BL11	22	141–187	0.833	0.823	0.666	1.40	1.40
1	BTMS0045	29	232–290	0.790	0.818	0.284	1.37	0.69
1	BTMS0125	15	100–128	0.887	0.900	0.213	0.00	0.68
2	B124	20	235–273	0.873	0.897	0.325	0.00	0.00
2	BT18	21	171–213	0.757	0.768	0.319	0.00	0.00
2	BTERN01	14	94–124	0.743	0.788	0.011*	1.99	0.00
3	B96	7	230–243	0.553	0.613	0.000*	0.00	0.00
3	BL03	23	127–176	0.870	0.884	0.229	0.00	0.00
3	BT10	21	137–185	0.837	0.844	0.141	0.00	0.00

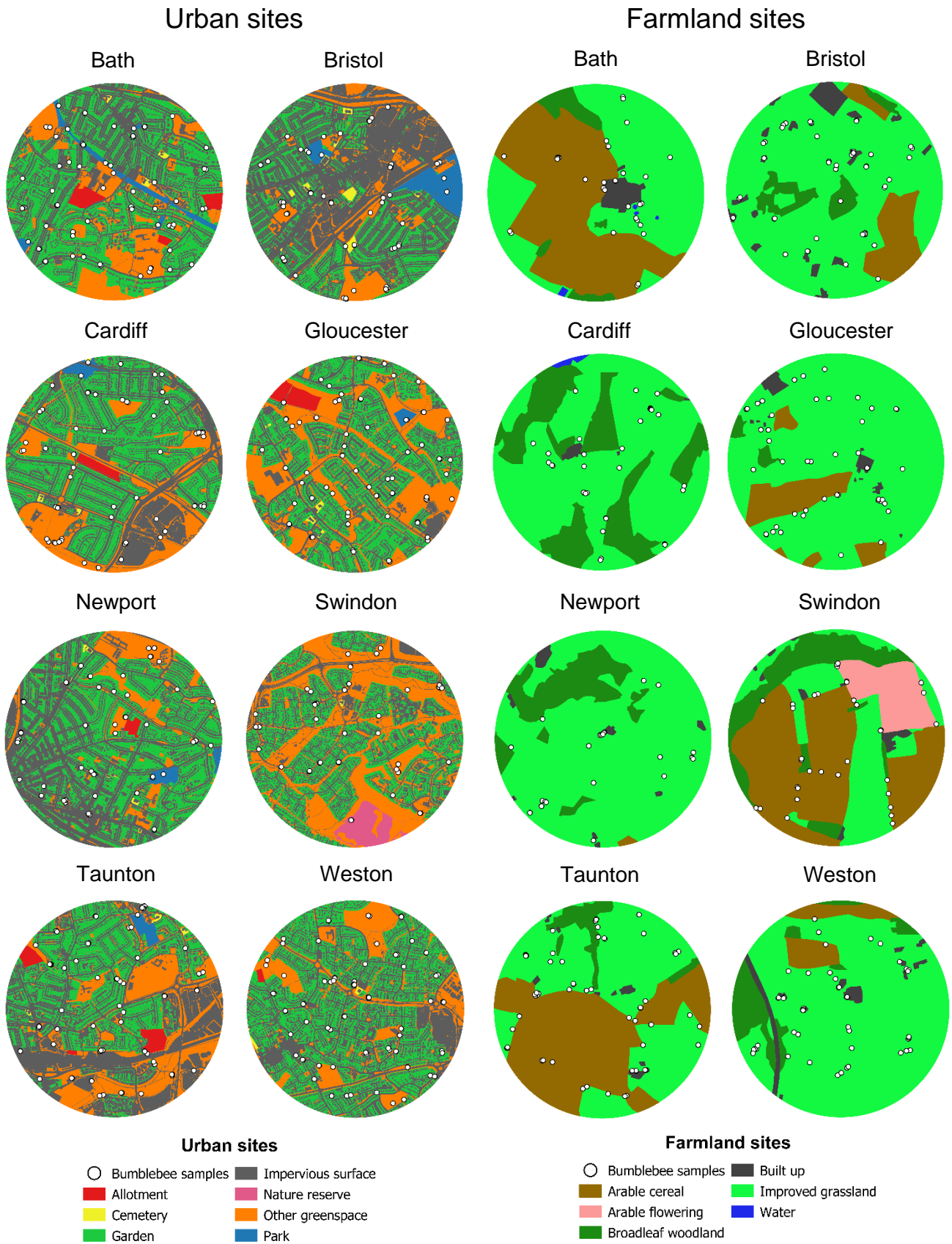


Figure 4.2. Maps of sampling areas. The 16 sampling areas (circles of radius 0.75 km) are displayed showing land use and the locations of captured bumblebees (a filled white circle for each bee).

4.2.4 Estimating colony density

Workers were assigned to colonies with Colony v2.0.6.7, a computer program which uses maximum likelihood methods to infer sibship and parentage from multi-locus genotype data (Jones and Wang, 2010). Males and females were assumed to have monogamous mating systems without inbreeding or clonal reproduction. A medium length run with five iterations and a full-likelihood method of analysis was performed and results were repeatable across runs with different random number seeds. Marker error rates (both dropout and other errors) were entered as estimated from the data (Table 4.5), but the model was also run with error rates set at 0% and 2% (dropout 0.5% and other errors 1.5%, following Wood et al. (2015b)) for comparison. This revealed slight differences in sibship assignment, but no changes to conclusions drawn from subsequent statistical analyses.

The true number of colonies present at each sampling site was estimated using the Two Innate Rate Model (TIRM) in CAPWIRE (Miller et al., 2005), a DNA-based capture-recapture model which generates a point estimate from the frequency distribution of re-sampled colonies (i.e. the number of colonies represented by one, two, three, four or five sampled bees) (Goulson et al., 2010; Wood et al., 2015b). To estimate colony density it is necessary to know the true area of sampling, as bumblebees may travel far from their nests when foraging (Knight et al., 2005). Following Wood et al., (2015b), it was assumed that *B. terrestris* workers may be foraging up to their estimate of 799 m from the nest, giving a true sampling area of 7.54 km² (circle of radius 0.75 + 0.799 km). Thus, my estimates of the number of colonies present at each sampling site obtained by CAPWIRE were divided by 7.54 to give the colony density (nests per square kilometre). While the foraging distance 799 m compares well with estimates from other studies (Knight et al., 2005; Osborne et al., 1999; Redhead et al., 2016), it is necessarily simplistic as *B. terrestris* workers sometimes forage further from their nests (Osborne et al., 2008; Walther-Hellwig and Frankl, 2000) and foraging range depends upon landscape context (Redhead et al., 2016). Choosing a different value would affect the colony density, with 500 m giving an estimate 1.5 times greater and 1200 m an estimate 1.6 times lower. For the purpose of a reliable colony density comparison between urban and farmland landscapes, the precise value is immaterial, provided it does not differ systematically between landscape types. It has been speculated that bumblebee foraging ranges may be lower in urban areas due to a high density of floral resources (Darvill et al., 2004) and this has been demonstrated in honeybees (Samuelson et al., 2022). To investigate whether foraging range differs between landscape types I measured the distance between bees from the same colony using a mean centres approach (Dreier et al., 2014; Redhead et al., 2016). Taking the mean easting and northing of worker locations from each multi-individual sibship group (i.e. colony) gave a central point for the cluster, which can be regarded simplistically as the most likely location of the nest. Colony-level foraging range was defined as the mean distance of bees from this central point, which in 54/67 cases was simply a half-way point between a pair of bees.

4.2.5 Data analysis

Data were analysed using R v4.1.2 (R Core Team, 2021) and diagnostic plots were inspected to validate models against assumptions of heteroscedasticity and normality of the residuals. Given the selection of paired study sites for sampling (see section 4.2.1), I used paired t-tests to compare sites between the two land use types, where this was possible (see section 4.3.3). I analysed the intertegular distance (a proxy for body size) of workers using a linear mixed model (LMM) from R package ‘lme4’ (Bates et al. 2015) containing landscape type as a fixed effect and city (encompassing a pair of sites) as a random effect to account for any geographic bias. Dry body weight was estimated from intertegular distance using an allometric scaling model (full taxonomic model) from R package ‘pollimetry’ (Kendall et al., 2019). To compare colony-level foraging range between landscape types I used a linear model (LM) containing landscape type as the only dependent variable and first transformed the response variable by taking the square root to ensure the model residuals were normally distributed. I tested for significant correlations between colony density and the proportional cover of major land use types using linear models. As the land use classification differed between the two landscape types (Table 4.1; Table 4.2), I analysed colony density separately for urban sites (testing for correlations with impervious surface, residential garden and other greenspace) and farmland sites (testing for correlations with improved grassland, arable cropland and broadleaf woodland).

4.3 Results

I collected 929 worker bumblebees from the 16 sites (range 27 to 80 per site), after 72 males were removed from the samples (see section 4.2.3), with significantly more workers collected from urban than farmland sites despite equal sampling effort (two-tailed paired t-test: $t(7) = 8.19$; $p < 0.001$; means: urban 71.5 ± 3.3 SEM; farmland 44.6 ± 4.2 SEM).

4.3.1 Flower visitation

Of all 929 worker bumblebees, 891 (95.9%) were collected while visiting flowers, which belonged to 98 different plant taxa. Although the number of visited plant taxa was significantly higher in urban than farmland sites (two-tailed paired t-test: $t(7) = 4.43$; $p = 0.003$; means: urban 17.6 ± 1.2 SEM; farmland 9.9 ± 1.3 SEM), this was explained in part by the fact that more bees were collected from urban sites, resulting in more flower visits recorded (547 versus 344). As such, the average number of bumblebee visits per plant taxon did not differ significantly between sites in the two landscape types (two-tailed paired t-test: $t(7) = 0.98$; $p = 0.359$). The two most visited plant taxa in both landscapes were *Trifolium repens* and *Rubus fruticosus* agg. (Table 4.6).

Table 4.6. The most visited plant taxa by bumblebees collected in urban and farmland landscapes. This table does not give a systematic comparison of the foraging diets of urban and farmland bumblebees because it is biased by the accessibility of sampling. In particular, the contributions of flowers in trees and residential gardens will have been underestimated.

Urban (547 visits)		Farmland (344 visits)	
Taxon	Percent of visits	Taxon	Percent of visits
<i>Trifolium repens</i>	22.67	<i>Trifolium repens</i>	30.52
<i>Rubus fruticosus</i> agg.	20.29	<i>Rubus fruticosus</i> agg.	22.67
<i>Hebe</i> spp.	8.59	<i>Trifolium pratense</i>	4.94
<i>Cotoneaster</i> spp.	6.94	<i>Lamium album</i>	4.65
<i>Buddleja davidii</i>	2.93	<i>Cotoneaster</i> spp.	2.91
<i>Hypericum</i> spp.	2.56	<i>Silene dioica</i>	2.91
Others (64 taxa)	36.01	Others (42 taxa)	31.40

4.3.2 Body size

Intertegular distance was significantly larger in urban bumblebees than those from farmland sites (LMM: $N = 320$; $\chi^2 = 9.18$; $p = 0.002$; means: urban $4.88 \text{ mm} \pm 0.04 \text{ SEM}$; farmland $4.73 \text{ mm} \pm 0.04 \text{ SEM}$; Fig. 4.3). Although mean intertegular distance was only 3.3% higher in urban specimens, mean dry body weight was estimated to be 7.2% higher from an allometric scaling model.

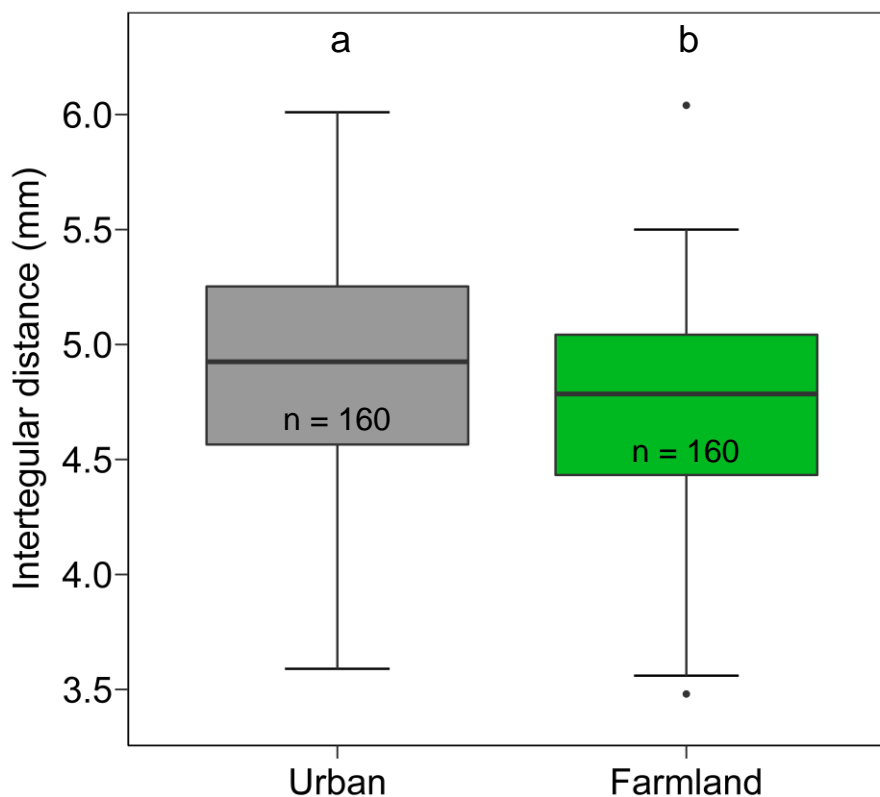


Figure 4.3. Body size for urban and farmland bumblebees. Boxes show the median, 25th and 75th percentiles; the whiskers extend to $1.5 \times$ the interquartile range; and all outliers are shown. Significantly different landscape types are indicated by different letters.

4.3.3 Colony density and foraging range

A total of 67 sibship groups containing two ($n = 54$), three ($n = 8$), four ($n = 4$) or five ($n = 1$) bumblebees were identified in the 16 sites, all assigned with a high probability of inference ($p > 0.99$). In the two sites where the fewest bumblebee samples were obtained (Cardiff farmland and Newport farmland), no multi-individual sibship groups were identified (i.e. all bees were from different colonies). Thus, colony density could not be estimated, and these two sites were excluded from further analysis (leaving 8 urban and 6 farmland sites; Table 4.7). Colony-level foraging range did not differ significantly between urban and farmland sites (LM: $t(65) = 1.138$; $p = 0.259$; urban: $n = 41$; mean = 153.3 ± 23.1 SEM; farmland: $n = 26$; mean = 186.3 ± 31.0 SEM). Consequently, it is reasonable to use the same value of maximum foraging range when estimating colony density in both landscapes.

Colony density was significantly higher in the eight urban sites than the six farmland sites (unpaired t-test: $t(11.3) = 3.57$; $p = 0.002$; Fig. 4.4), with the difference in means a factor of 2.2 (urban: 68.9 nests/km² ± 8.9 SEM; farmland: 31.2 nests/km² ± 5.7 SEM; Table 4.7). If I removed the two urban sites that were paired with the farmland sites already excluded from the analyses (Cardiff and Newport), permitting a fully paired comparison, the statistical difference between urban and farmland colony density became marginally non-significant at the five percent threshold (two-tailed paired t-test: $t(5) = 2.52$; $p = 0.053$), with the difference in means a factor of 1.9 (58.7 versus 31.2 nests/km²). There were no significant correlations between colony density and the three major land uses within urban or farmland landscapes.

Table 4.7. Bumblebee numbers and colony density estimates. Summary statistics for each site show the number of workers of *B. terrestris* genotyped and the estimated colony density. Colony density values could not be estimated for Cardiff farmland and Newport farmland sites given no multi-individual sibship groups were identified.

City	Workers genotyped		Colony density (nests/km ²)	
	Urban	Farmland	Urban	Farmland
Bath	76	39	64.1	19.6
Bristol	71	52	60.9	29.3
Cardiff	69	35	105.3	N/A
Gloucester	78	49	89.9	19.1
Newport	65	27	93.4	N/A
Swindon	53	38	30.8	23.5
Taunton	80	64	56.6	54.4
Weston	80	53	49.9	41.1
Mean	71.5	44.6	68.9	31.2

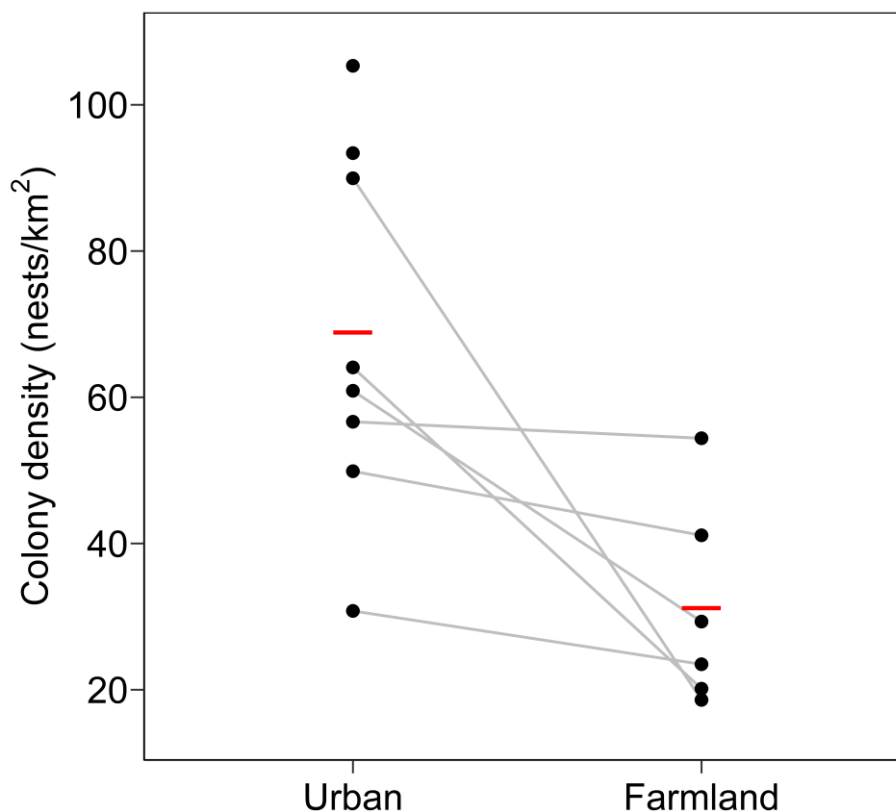


Figure 4.4. Colony density for urban and farmland bumblebees. A point is plotted for each site, with paired sites connected by a grey line and the mean across sites in each landscape type indicated by a red horizontal bar. For two urban sites (Cardiff and Newport) there was no paired farmland site.

4.4 Discussion

I found that urban areas support double the colony density of *Bombus terrestris* compared with nearby farmland, emphasising the value of towns and cities as population hotspots for this generalist pollinator. However, there was some overlap in density estimates between landscape types, indicating that some farms are comparable to some urban sites. There was no clear evidence for a difference in foraging range between urban and farmland bees, but individual workers were larger in cities. In what follows, I first consider the limitations of my work and then discuss some possible explanations for the findings of this study.

4.4.1 Limitations

There are two main limitations to this study estimating the colony density of *B. terrestris* in urban and farmland landscapes. First, eight sampling sites is a relatively low number to represent broad and variable landscape types, which was further reduced to six for farmland given the two sites with the fewest bumblebee samples had to be excluded. However, the use of molecular markers to estimate colony density requires a large number of workers to be collected at each site (Wood et al., 2015a), permitting relatively few sites to be sampled in total, with previous studies of this kind involving a similar number of sites (Darvill et al., 2004; Goulson et al.,

2010; Knight et al., 2009; Stanley et al., 2013; Timberlake et al., 2021; Wood et al., 2015b). The large disparity I found in colony density between the two landscape types meant I was able to detect a significant difference despite comparing a relatively small number of sampled sites, with the estimate for even the top farmland site still below the urban mean (Fig. 4.4). The second main limitation is that the response of *B. terrestris* to land use change cannot be assumed to represent that of all bees, or even all bumblebees. Bumblebees are eusocial (a relatively rare trait in bees), active for long periods of the year and have a varied diet (Ghisbain, 2021). Among bumblebees, *B. terrestris* is known to be especially tolerant of temperature extremes (Martinet et al., 2021; Stelzer et al., 2010) and is a particularly generalised forager (Rasmont et al., 2008), making it adept at colonising new areas (Ghisbain et al., 2021; Herbertsson et al., 2021; Inoue et al., 2008). It is possible that the findings of this study may apply to other bumblebee species, but this needs to be investigated with further empirical research as the relative success of bees in urban landscapes is species-specific and depends on a wide variety of factors (Prendergast et al., 2022).

4.4.2 The colony density of *B. terrestris* in urban and farmland landscapes

The values of colony density I report here (means of 69 and 31 nests/km² in urban and farmland sites, respectively) are in line with those previously estimated for *B. terrestris* by microsatellite genotyping at other field sites. Dicks et al. (2015) summarises five studies, three conducted in the UK (Darvill et al., 2004; Dreier et al., 2014; Knight et al., 2005), one in Ireland (Stanley et al., 2013) and one in Sweden (Huth-Schwarz et al., 2012), with results ranging from 13 to 79 nests/km² and an overall mean of 32 nests/km². Wood et al. (2015b) estimated colony density in farms in southern England using the value of maximum foraging distance I chose to make estimates (799 m), reporting a median of 88 nests/km² for farms implementing pollinator-friendly schemes and 38 nests/km² for control farms.

The most likely factor underpinning wild bee populations is the availability of food resources, although access to suitable nest sites and risks from pesticides, diseases and extreme weather conditions could all play a limiting role (Goulson et al., 2015; Inoue et al., 2008; Roulston and Goodell, 2011; Soroye et al., 2020). My estimates of colony density varied by a factor of around three in both farmland (19 to 54 nests/km²) and urban landscapes (31 to 105 nests/km²), which is likely to be due in part to some of the factors listed above. Among farmland sites I found no significant correlations between colony density and the areas of improved grassland, arable cropland or broadleaf woodland. However, observational evidence collected during fieldwork visits (Table 4.3) suggested a possible link between land management intensity and the population estimates. Farm sites estimated to have high colony densities (e.g. Taunton and Weston) contained large areas of flower-rich cow pasture that was grazed at a relatively low intensity, whereas farm sites estimated to have low colony densities (e.g. Gloucester and Bath) lacked any large areas of flower-rich habitat and instead mostly consisted of heavily fertilised monocultures of ryegrass and cereal crops (Table 4.3). It is unsurprising that colony density did not correlate with the proportion of improved grassland at the sites as this is a simplistic land use category which describes both flower-rich pasture and ryegrass monoculture (Fig. 4.5). Among urban sites I found no

significant correlations between colony density and the areas of impervious surface, residential garden or the other greenspace land use category. I expected to find a positive correlation between the area of residential garden and colony density given that gardens provide an estimated 85% of nectar sugar in UK cities (see Chapter 2) and are regularly used by *B. terrestris* for nesting (Osborne et al., 2007). It is therefore possible that neither the abundance of flowers *per se* nor the number of available nest sites currently limits urban populations. Instead, an additional factor, such as competition for food with honeybees may determine the upper bound of *B. terrestris* populations in urban landscapes (Meeus et al., 2021), but this requires further study.



Figure 4.5. A visual comparison of two fields classified as improved grassland. On the left is an area of ryegrass pasture lacking any visible flowers and typifying much of the landscape in the farm site with the lowest estimated colony density (Gloucester, with 19 nests/km²). On the right is an example of the flower-rich pasture that covers large areas of the farm site with the highest estimated colony density (Taunton, with 54 nests/km²) (Photo: N. Tew).

As predicted, the colony density of *B. terrestris* was higher in urban sites than farmland, but it was beyond the remit of this study to determine the precise reasons for this difference. Urban landscapes differ strongly from farmland in such a wide variety of characteristics that it is particularly challenging to isolate the effect any one of them has on bumblebee populations. Here, I discuss four potential reasons for the observed difference in population density, concluding that a superior food supply in urbanised versus farmed landscapes is the most likely.

(1) Superior food supply: As I show in Chapters 2 and 3, the supply of nectar in urban landscapes is more diverse in floral origin than in farmland and more stable through time, without seasonal gaps. As a super-generalist with a long flight season, *B. terrestris* may take advantage of the diverse and continuous supply of food throughout the year in urban green spaces to increase dietary nutrition and extend its breeding period, resulting in greater reproductive success (Samuelson et al., 2018; Stelzer et al., 2010; Vaudo et al., 2015). In

addition, urban areas differ strongly from farmland in the spatial distribution of foraging habitats, with a regular arrangement of small flower-rich gardens compared with large fields that can separate foraging patches by hundreds of metres (Fig. 4.2). As a result, urban bumblebees may not need to travel as far to feed as those in farmland, something demonstrated in honeybees by Samuelson et al. (2022), who found their median foraging distance was 1.5 times lower. Although I found no clear evidence that bees foraged closer to their nests in urban landscapes, this study was not designed to accurately measure foraging range, which cannot be reliably estimated from a relatively small sample of sibship groups, most of which comprised two workers. If foraging distance does differ systematically between landscape types, it is likely to further increase the difference in colony density I report here. For example, reducing the maximum foraging distance estimate for urban sites by a factor of 1.5 (from 799 m to 533 m) increases urban nest density from 2.2 to 3.2 times that of farmland.

(2) More nest sites: The National Bumblebee Nest Survey, a citizen science project in the UK, estimated the nest density of bumblebees to be more than three times as high in residential gardens than woodland (Osborne et al., 2007), but this does not necessarily mean gardens contain more sites that could be used for nesting, as populations may be limited by a different factor, such as food supply. There is no clear published evidence that nest site availability limits bumblebee populations, but this is challenging to investigate given suitable nesting habitats are also often rich in floral resources, resulting in covariation between potential limiting factors that cannot be independently assessed (Roulston and Goodell, 2011). *Bombus terrestris* nests underground, typically in abandoned rodent burrows (Falk, 2015), which are common in both urban and farmland landscapes. As a result, I expect that the overall availability of nest sites is unlikely to limit their populations or explain the difference in colony density between the two landscape types, but this cannot be demonstrated conclusively.

(3) More favourable microclimate: The heat generated and re-radiated by anthropogenic surfaces means cities are generally warmer than rural areas, termed the urban heat island effect (Rizwan et al., 2008). Milder winter temperatures can extend the flowering season of plants (Primack et al., 2009; Zipper et al., 2016), ensuring that bees have access to food for more of the year and that a higher proportion of days are warm enough to conduct foraging trips (Stelzer et al., 2010). The tolerance for high temperatures that *B. terrestris* shows (Martinet et al., 2021) may help to ensure the urban heat island effect has a net positive effect on its reproductive success. However, average temperatures in cities are usually just 1-2°C higher (Manoli et al., 2019) and *B. terrestris* can forage over a broad temperature range, spanning from 3°C (Stelzer et al., 2010) to >32°C (Kwon and Saeed, 2003). As a result, climatic factors are unlikely to explain much of the reported difference in colony density and winter-active foraging probably depends mainly on the presence of non-native shrubs with the appropriate flowering phenologies (Stelzer et al., 2010).

(4) Protection from pesticides and other toxic chemicals: Farmed landscapes are regularly treated with agrochemicals, which can have lethal and sublethal toxic effects on bees (Gill et al., 2012; Godfray et al., 2015; Woodcock et al., 2017) and have been implicated in their declines (Goulson et al., 2015; Potts et al., 2010). However, bees are also exposed to toxic chemicals in urban landscapes, where gardeners and managers of green spaces regularly use herbicides and insecticides (Lentola et al., 2017; Mahé et al., 2021; Nicholls et al., 2018; Straw et al., 2021). In addition, cities generate high concentrations of pollutants not found as abundantly in the countryside, particularly vehicle exhaust and heavy metals, which can be harmful to insects (Leonard et al., 2019; Phillips et al., 2021; Ryalls et al., 2022; Scott et al., 2022). Chemical toxicity is therefore unlikely to be a major factor explaining the higher colony density found in urban landscapes.

4.4.3 The body size of *B. terrestris* in urban and farmland landscapes

Bombus terrestris workers were larger in urban sites, a difference that was statistically significant albeit modest at 3% higher intertegular distance (estimated to scale up to a 7% greater dry body weight). These results concur with a German study by Theodorou et al. (2021), who reported 4% higher intertegular distance in *B. terrestris* workers in cities compared with rural areas. However, responses appear to be species-specific and variable between studies as Theodorou et al. (2021) found no significant difference for *Bombus lapidarius* or *Bombus pascuorum* and a Swiss study by Eggenberger et al. (2019) actually found workers of these two species were larger in rural areas. A difference in worker body size between populations could be linked to a variety of factors including local climate, habitat fragmentation, larval nutrition and foraging behaviour (Eggenberger et al., 2019; Grass et al., 2021; Theodorou et al., 2021). As discussed, cities have a warmer microclimate than the countryside, which should favour smaller urban bees that are less prone to overheating (Eggenberger et al., 2019; Theodorou et al., 2021). If habitat fragmentation was an important factor then again, urban bees should be smaller, because in farmland bees have to fly across large empty fields between foraging patches and body size correlates with foraging range (Greenleaf et al., 2007). Instead, two possible explanations for the larger body size of urban bees are that larvae have a better diet during development and/or that colonies in cities tend to recruit larger individuals to forage (Grass et al., 2021), both of which are linked to the assumption of a superior food supply in urban landscapes. A difference in forager recruitment could be due to the presence of larger flowers in urban areas, which larger workers handle more efficiently, or because a higher proportion of smaller foragers remain in the nest when it is easy to find food (Goulson et al., 2002; Grass et al., 2021).

4.4.4 Conclusions

This study demonstrates that urban landscapes provide population hotspots for *Bombus terrestris*, which nests at double the density compared with nearby farmland. A superior supply of floral resources in space and time is the most likely driver behind the observed difference, but it was beyond the remit of this study to reliably determine the factors underpinning populations. In general, urbanised and farmed landscapes differ strongly in so many variables that it is challenging for field studies such as this one to identify which factor is most important in explaining the response of a species to land use change. *Bombus terrestris* differs from other members of its genus in its dietary super-generalism, long flight season and tolerance of extreme temperatures, which make it proficient at colonising new environments. Further studies focussing on different species will help to reveal how representative my findings are for other bumblebees.

Chapter 5

Discussion



Supporting a diverse community of flower-visiting insects takes more than just floral resources. As an adult, this spotted longhorn beetle (*Rutpela maculata*) is feeding from a blooming *Pyracantha* shrub in a Bristol garden, but it required decaying wood during its larval stage (Photo: N. Tew).

5.1 Summary of research findings

The first of two main aims of this thesis was to quantify floral resources in urban landscapes. In Chapter 2, I found that urban nectar supplies in the UK are comparable in magnitude to those in farmland and nature reserves, but differ in composition, underpinned by a more diverse community of flowering plants, primarily comprising non-native species. Within urban landscapes, residential gardens and allotments were the top two land uses for the quantity and diversity of nectar supplies per unit area. However, the extensive coverage of gardens means they are overwhelmingly important overall, supplying on average 85% of a city's nectar sugar. Building on from this, I investigated UK residential gardens in more detail in Chapter 3, finding a high degree of variation in both the magnitude and seasonal timing of their nectar supplies. However, in aggregate, gardens provide a stable and continuous supply of nectar through the year because variability smooths out among many gardens which vary independently. Nectar production was not linked to garden size, but was higher in more affluent neighbourhoods, with management decisions by individual gardeners of primary importance. Overall, the garden flora was extremely rich, driven by turnover in species composition among gardens.

Having focused on insect food supplies in Chapters 2 and 3, the second main aim of the thesis was to compare pollinator populations between urban and agricultural landscapes. In Chapter 4, I found that a common and widespread generalist bumblebee (*Bombus terrestris*) nests at double the colony density in UK urban landscapes compared with nearby farmland. Individual workers were larger in cities but there was no clear evidence for a difference in foraging range between landscape types. Although it was not possible to determine the precise reasons for the observed difference in population density, a superior supply of floral resources in urbanised compared with farmed landscapes is likely to be the most important explanatory factor.

In this chapter, I first discuss what my results tell us about the supply of floral resources in urban landscapes and the consequences for pollinating insects, focussing on the quantity of nectar sugar available, flowering phenology and the composition of plant communities (section 5.2). Subsequently, I explain the outputs of my thesis and their application to conservation (section 5.3), some of the main limitations of my work and recommendations for future research (section 5.4), before ending with some concluding remarks (section 5.5).

5.2 The supply of floral resources in urban landscapes and its consequences for pollinating insects

5.2.1 The quantity of nectar sugar available

In Chapter 2, I found that the mass of nectar sugar produced per unit area did not differ significantly between urban, farmland and nature reserve landscapes, but was characterised by extreme variation among sites. Throughout conducting research for this thesis, I have become increasingly aware that nectar supplies in heavily managed landscapes are frequently typified by concentrated hotspots of production embedded within relatively barren surroundings. This is particularly true for urban areas, where a single flowering shrub could easily provide 95% of a garden's nectar in less than 5% of its area, with gardens themselves already hotspots of nectar production among roads and buildings. Such extreme variation makes broad-scale comparisons between a 'typical square metre' of urban and rural land highly simplistic. Nevertheless, the similarity between the nectar productivity values I obtained for gardens in Chapter 2 (covering Bristol, Edinburgh, Leeds and Reading) and Chapter 3 (covering Bristol) suggests sufficient land was sampled for reliable estimates.

The question of whether towns and cities have higher nectar supplies than rural landscapes has no single answer because of variation in how the countryside is managed. As I discuss in Chapter 4, differences in farming practice, including grazing intensity, herbicide use and the area of semi-natural habitat retained, greatly affect the overall supply of floral resources. As such, there will be large areas of the countryside which provide less nectar than an average city and large areas which provide more. Thus, urban areas may represent hotspots of nectar production in regions surrounded by modern industrial farming, but not in areas surrounded by more semi-natural habitat and less intensively managed land.

5.2.2 Flowering phenology and the timing of nectar production

One aspect of the urban nectar supply which does differ starkly from that in the countryside is the timing. I could not investigate this in Chapter 2 due to insufficient temporal extent and resolution in the underlying floral abundance data, but in Chapter 3, I measured nectar supply in gardens from early March to late October. A long and continuous flowering season provides floral resources throughout the life cycle of long-lived species (e.g. from March to October for the buff-tailed bumblebee, *B. terrestris*) and ensures food is available for species with shorter flight seasons when they emerge (e.g. in March for the hairy-footed flower bee, *Anthophora plumipes*, or September for the ivy bee, *Colletes hederæ*). In the European farmed countryside there is very little nectar sugar available between early October and the end of March, with few plants flowering in this period (Jachula et al., 2021; Timberlake et al., 2019). During the warmer months of the year, farmland nectar supplies are characterised by peaks and troughs rather than a smooth and stable trajectory. For example, in both the UK and Poland, nectar sugar was between seven and ten times as abundant in the April or May peak as in the June gap, before rising again by a factor of two in July (Jachula et al., 2021; Timberlake et al.,

2019). Such boom-and-bust cycles of nectar availability in the heavily simplified landscapes of modern industrial farmland result from a handful of species dominating nectar supplies, which come to largely reflect their flowering periods. For example, in the UK study, half of all nectar sugar was supplied by three species and two thirds by five species (Timberlake et al., 2019), while in the Polish study, a single mass flowering crop (*Brassica napus*) alone provided one third (Jachula et al., 2021).

The picture, however, is very different in urban landscapes, with important implications for pollinator communities (see Chapter 3). In UK residential gardens, which by my estimate in Chapter 2 produce 85% of a city's nectar, the average supply in the peak month (July) is only double that of the lowest month (October) and from April to July, nectar production varies by only a factor of 1.2. Temporal stability in the garden nectar supply emerges despite variation in the seasonal peak among individual gardens, through the portfolio effect. In short, the floral composition differs markedly from one garden to the next due to differences in planting and management choices by gardeners. With the flowering phenology varying among taxa, complementarity between gardens peaking in different months tends to smooth out peaks and troughs. This is quite unlike most farmland, where the same handful of species are likely to be in flower throughout the landscape. The greater independence of plant communities (species turnover) seen among gardens than parcels of a farmed landscape results from gardeners having a wide variety of (native and non-native) species available to plant and differing management objectives.

In March, flowers are scarce in much of the UK's farmland, with areas of scrub that harbour blackthorn (*Prunus spinosa*) and goat willow (*Salix caprea*) few and far between. But in gardens, taxa including *Pieris*, *Skimmia japonica*, *Muscari armeniacum* and *Erica carnea*, as well as varieties of *Prunus* and *Salix*, ensure an abundant nectar supply for queen bumblebees, hairy-footed flower bees, early butterflies and any other flower-visiting insects that have emerged. Similarly, by October, farmland nectar production is again low, and primarily depends on the abundance of flowering ivy (*Hedera helix*) (Garbuzov and Ratnieks, 2014c; Timberlake et al., 2019), with late-season nectar an important factor limiting some bumblebee populations (Timberlake et al., 2021). Gardens, however, still produce half as much as at their summer peak, driven especially by *Fuchsia magellanica*, varieties of *Salvia*, *Dahlia* and *Penstemon*, as well as by ivy itself. Furthermore, although less abundant and diverse, floral resources are present throughout the winter in urban landscapes. This allows *B. terrestris* to raise more broods (Falk, 2015; Stelzer et al., 2010) and could be an important factor explaining its high colony density reported in Chapter 4. The extended flowering season seen in gardens is possible because of the wide variety of exotic species and horticultural cultivars available to gardeners that have particularly early or late flowering periods (Harrison and Winfree, 2015; Salisbury et al., 2015), which could be further prolonged by the urban heat island effect (Primack et al., 2009; Zipper et al., 2016).

The phenological importance of gardens in the supply of floral resources may even spill over into farmland. In the UK and much of Europe, small towns and villages are scattered throughout the countryside, so that gardens and farmed areas are not widely separated. Both Goulson et al. (2010) and Timberlake et al. (2021) found a positive correlation between *B. terrestris* colony density in agricultural landscapes and the proportional coverage of garden within a 1 km radius, even though its maximum value was just 6%. In a manuscript in preparation with other colleagues, we show that (1) most British farmland is sufficiently close to a human settlement for bumblebees to visit both areas, (2) gardens produce the vast majority of nectar in March and October in our rural study landscapes and (3) modelling predicts that the presence of gardens can significantly increase *B. terrestris* colony density. These lines of evidence raise the intriguing possibility that gardens may buffer some insects against seasonal shortages in rural nectar supplies and that, despite covering just 2% of Great Britain by area (Office for National Statistics, 2019a), they could play a disproportionately important role in pollinator conservation at a national scale, one which is not currently supported by agri-environment schemes.

5.2.3 Diverse plant communities and novel interactions

Flowering plant communities in urban landscapes can be extremely diverse and completely unlike those found anywhere else, often comprising a unique assemblage of species, thrown together without any attention paid to their origins. A flower border in a UK park or garden might have a New Zealand *Hebe* growing between a Chinese tree peony (*Paeonia* species) and a Mexican orange blossom (*Choisya ternata*), with an understory comprising a multi-petalled cultivar of the carnation (*Dianthus caryophyllus*) from the Mediterranean region intermingled with the native British ‘weed’ groundsel (*Senecio vulgaris*). Yet many native pollinators thrive in such an environment, taking advantage of the nectar and pollen produced by flowers that their species or genus may never have visited before in its evolutionary history.



Figure 5.1. Cities are home to many novel ecological interactions. The South African plant *Agapanthus praecox* does not naturally overlap in range with bumblebees, yet here in Bristol, the garden bumblebee (*Bombus hortorum*) uses its long tongue to drink nectar from the deep flowers (Photo: N. Tew).

One potential criticism of this thesis is that my findings are primarily of relevance to generalist bees such as *B. terrestris*, whose ecology is discussed in Chapter 4. Urban plant communities may not provide the right pollen for oligolectic bees or the necessary foodplants for caterpillars and other larval insects. Alternatively, the sheer diversity of plants, akin to an ‘all you can eat buffet’, may offer something for all insects, with specialists even able to increase their diet breadth by feeding on the non-natives which have enhanced the UK’s relatively modest flora. For example, the harebell carpenter bee (*Chelostoma campanularum*), which specialises on *Campanula* pollen, visits non-native species like the peach-leaved bellflower (*Campanula persicifolia*) in gardens, while the yellow loosestrife bee (*Macropis europaea*), which visits its namesake plant (*Lysimachia vulgaris*) for pollen and floral oils, can make do with the non-native ornamental, dotted loosestrife (*Lysimachia punctata*) (Falk, 2015). Similarly, caterpillars of the elephant hawk moth (*Deilephila elpenor*) feed on South American *Fuchsia magellanica*, which belongs to the same family as their native foodplant, rosebay willowherb (*Chamaenerion angustifolium*) (Chinery, 2005), while Owen (2010) found that the East Asian shrub *Buddleja davidii* was the most widely used plant by moth caterpillars (19 species) in her Leicester garden. This is despite the fact that coevolution is particularly important for herbivorous insects, which can adapt to detoxify the chemical defences specific to plant taxa (Ehrlich and Raven, 1964; Janz, 2011; Krieger et al., 1971). If widely applicable, these examples suggest that the rich plant communities found in urban green spaces can support a wide variety of flower-visiting insects, including both generalists and specialists, despite their largely exotic origin.

For bees, although there is evidence that urbanisation is associated with a shift in community composition towards more generalists (Banaszak-Cibicka and Sikorski, 2012; Deguines et al., 2016; Wenzel et al., 2020), many oligolectic species thrive in towns and cities (Cane et al., 2006; Casanelles-Abella et al., 2022; Martins et al., 2013; Prendergast et al., 2022). A recent review found that oligolectic bees comprised on average 17% of the richness of urban communities (Prendergast et al., 2022), while towns and cities can even harbour nationally rare species (Baldock et al., 2015; Sirohi et al., 2015). Nevertheless, urban landscapes contain important areas of native vegetation (e.g. in nature reserves, brownfield sites or road verges), so the success of oligolectic and rare species does not necessarily indicate a dietary shift towards non-natives. In the case of Lepidoptera, urban landscapes appear favourable to far fewer species than the countryside (Deguines et al., 2012; Theodorou et al., 2020), which may indicate larval foodplants are lacking in sufficient abundance, despite some taxa benefiting from common garden plants (Burghardt et al., 2010).

The simple dichotomy of natives versus non-natives fails to provide a biogeographically or ecologically meaningful description of plants, yet is frequently associated with judgments on their value to wildlife (Davis et al., 2011; Lemoine and Svenning, 2022). In the above examples of the harebell carpenter bee visiting peach-leaved bellflower and the yellow loosestrife bee feeding from dotted loosestrife, we should not be surprised by this apparent dietary flexibility because these species naturally overlap in distribution in continental Europe. Being an island in Northern Europe, Great Britain contains a subset of the plants and insects found elsewhere on the continent, with very few endemics. Thus, drawing a distinction between plants native to Britain and those confined to continental Europe is somewhat arbitrary, especially as the glacial history of the region makes the current distribution of species a brief snapshot in geological and evolutionary time, heavily influenced by chance. Furthermore, given a warming climate, the spread of new plants and insects into Britain is inevitable, illustrated by the addition of species like the ivy bee and tree bumblebee to the pollinator fauna. Instead, a more meaningful distinction is between plants native to Europe and those from further afield, a similar approach to that of Salisbury et al. (2017, 2015), who distinguished between ‘near-native’ (Northern Hemisphere) and ‘exotic’ (Southern Hemisphere) species, revealing different responses by insects. Yet even this type of distinction fails to fully reflect the fact that resource specialisation is frequently at the level of a plant family or genus, rather than a single species (Abe et al., 2021; Muller, 1996), and these may have broad global distributions. Going forward, considering both the geographical and phylogenetic proximity of plants to native species would help to provide a more ecologically relevant assessment of their value to insects, while judgements should be based on measurable traits rather than purely on origins (Davis et al., 2011; Lemoine and Svenning, 2022; Schlaepfer et al., 2011). Preserving rich areas of native vegetation remains an important goal in pollinator conservation, but we must not underestimate the role of non-native plants in buffering insects against distributional shifts in their native food sources. Urban landscapes provide an excellent setting in which to study the dietary flexibility of insects, an increasingly important trait in a rapidly changing world.

5.3 Thesis outputs and applications to conservation

It is my hope that, as well as advancing our scientific understanding of floral resources and insect pollinator populations in urban landscapes, my research will have direct applications to pollinator conservation. The findings of this thesis are of relevance to a variety of stakeholder groups, including other researchers, the general public (especially those with a garden or allotment), practitioners and non-governmental organisations, local councils, landscape architects, policymakers and anyone else who directly manages or indirectly influences the management of land, particularly in urban areas. There is a widening appreciation for the importance of pollinator-friendly greenspace management, but schemes frequently lack evidence-based proposals and may be discordant with scientific studies. Thus, scientists hoping to contribute effectively to pollinator conservation need to play an active role in communicating their findings to different stakeholder groups. Through a combination of academic publications, presentations, articles in the media, radio and podcast interviews, social media promotion and other public engagement activities, I have disseminated my research findings to a wide variety of people and organisations, and will continue to do so in the future.

In Chapter 2, I describe how nectar production of flowers was quantified in the field for taxa commonly found in UK urban landscapes. In total, values were obtained for more than two hundred plant species, although not all were included in this thesis because nectar was sampled from some plants that were not recorded flowering in surveys. I aim to publish these data so that gardeners and other land managers can preferentially select nectar-rich species to plant. Furthermore, in conjunction with the Royal Horticultural Society, a funding partner of this PhD project, we aim to update recommendations of pollinator-friendly species to better reflect those shown empirically to provide abundant nectar. Although the horticultural modification of floral traits can result in a diminished or less accessible supply of resources (Comba et al., 1999a; Corbet et al., 2001), I found that many highly-modified varieties were still rich in accessible nectar and that some of the most attractive species to insects were not typical ornamental flowers, but trees and shrubs grown for ornamental foliage or hedging. In communicating pollinator-friendly management advice to the public and other stakeholders, it is important to explain that cultivars of the same species can differ markedly in their value (e.g. ‘single’ versus ‘double’ flowers), while what is attractive to a person is not necessarily attractive to a pollinator and *vice versa*. I also show that flowering shrubs can provide dense hotspots of nectar production and represent a space-efficient way to boost floral resources, while the finding that late-season nectar is predominantly derived from deep tubular flowers provides a specific evidence-based recommendation to prioritise accessible flowers during this time period (see Chapter 3). The scaled-up values of nectar sugar per unit area for different urban land uses that I report in Chapter 2 could play an important role in determining sustainable levels of urban beekeeping, which is currently done by considering total green space availability (Casanelles-Abella and Moretti, 2022; Stevenson et al., 2020), even though some green spaces are many times as rich in nectar as others. Finally, work in preparation with colleagues on the role of gardens in buffering pollinators against seasonal nectar shortages in rural landscapes, informed in a large part by my study of garden nectar supplies in Chapter 3, has the potential to influence the way gardens are valued on farms.

5.4 Limitations of this thesis and recommendations for future research

In field ecology, researchers attempt to understand a bewilderingly complex natural world with limited time, funding and other resources. As a result, studies such as mine make a variety of necessary assumptions and can never be fully comprehensive in their coverage of the subject matter. Furthermore, as research continues to advance our understanding of a relatively new topic, additional avenues for investigation become apparent. A PhD thesis is therefore valuable in both its immediate findings and its recommendations for future research. In this section, I summarise six areas in which I recommend more research take place.

5.4.1 Pollen resources

In Chapters 2 and 3, I quantify the food supply for pollinators in urban and rural areas by measuring nectar sugar, neglecting pollen, the other main floral resource. Nectar has a much simpler compositional profile than pollen, with its nutritional role primarily (although not entirely) providing energy from sugars rather than facilitating healthy growth and development through a complex assortment of proteins, lipids, vitamins and minerals (see Introduction section 1.3). This means that the total mass of nectar sugar provides a more meaningful common currency through which to describe the food supply of pollinators than does the total mass of pollen, for which insects have more specialised and relatively poorly described requirements (Vaudo et al., 2015). Nectar is also of importance to a wider set of insect taxa than pollen, with many species (e.g. the vast majority of Lepidoptera and most Diptera) only consuming nectar when visiting flowers and relatively few (e.g. some beetles) only consuming pollen.

Coarse measures of pollen quantity could be obtained for more plant species, allowing comparisons between habitat types, but to a large degree this will reflect my results for nectar sugar in Chapters 2 and 3, as nectar and pollen quantity both correlate with floral abundance (Hicks et al., 2016). However, at a species level, although many of the top nectar sources also produce a large amount of pollen (e.g. Asteraceae and Malvaceae), some high-nectar plants are low in pollen (e.g. Boraginaceae and Lamiaceae) and some low-nectar plants are high in pollen (e.g. the poppy subfamily of the Papaveraceae) (Hicks et al., 2016). Thus, quantifying pollen would allow particularly pollen-rich plants to be identified and prioritised in pollinator-friendly recommendations and plantings. Detailed descriptions of the chemical composition of pollen for an extensive array of species, combined with further research into the nutritional requirements of bee larvae, would allow us to further enhance pollinator-friendly plantings (Filipiak, 2019, 2018; McAulay et al., 2020; Vaudo et al., 2016, 2015).

5.4.2 Nectar secretion and consumption by insects

I measured the total mass of nectar sugar that flowers accumulated over a 24-hour period in the absence of insect visitation. This method has been used in previous studies (e.g. Baude et al., 2016; Hicks et al., 2016; Timberlake et al., 2019), allowing me to combine data. However, a major assumption is that flowers can completely refill with nectar just once per day. Data on refill rate following the experimental removal of nectar is available only for a relatively small number of species, but shows variation from flowers which take a few hours to refill to those taking just a matter of minutes (Castellanos et al., 2002; Stout and Goulson, 2002; Stout et al., 1998; Thomson et al., 1989). As a result, the values I obtained for nectar sugar mass could greatly underestimate the theoretical maximum sugar production by a factor which differs among plant taxa. This was a necessary simplification as I would only have been able to measure the refill rates of a small fraction of the species I sampled and that is even without considering the wide variety of factors that affect nectar secretion, such as time of day, soil moisture, temperature and the frequency of insect visitation (Comba et al., 1999b; Descamps et al., 2018; Phillips et al., 2018; Waser and Price, 2016). When scaling nectar production by many different plant species up to compare habitat types, differences in refill rate may average out, ensuring such comparisons are reliable. However, when investigating the proportional contribution of individual plant species to the overall nectar supply, differences in refill rate are important.

Future work quantifying the nectar secretion rates of more species would allow us to preferentially select those with flowers which quickly refill (e.g. some Boraginaceae; Stout and Goulson, 2002; Stout et al., 1998), thus maximising the value of pollinator-friendly recommendations and plantings. Such data are laborious to obtain by careful study, so it would be particularly beneficial if we could predict the refill rates of different taxa, at least to a coarse degree, from plant phylogeny and floral traits (as I did for nectar sugar quantity in Chapter 2). In addition, experiments comparing bagged (where insect visitation is prevented) with un-bagged (where insect visitation is permitted) flowers would help to reveal the extent to which the nectar resources of different species are consumed by pollinators. For example, I found that *Fuchsia magellanica* was the largest urban nectar source (see Chapters 2 and 3), but it exhibits some traits typical of other hummingbird-pollinated species (González et al., 2018). As a result, the frequency of visitation by insects could leave the majority of nectar unexploited, with its importance overestimated, but this is purely speculation without conducting the necessary experiments.

5.4.3 Non-floral resources

As discussed in the Introduction (see section 1.3), pollinators are also reliant on non-floral resources, which include food for larvae and places to nest and shelter. Measuring the supply of floral resources does not therefore provide a comprehensive assessment of the factors regulating urban pollinator populations (discussed for *Bombus terrestris* in Chapter 4). If a pollinator species is currently limited in distribution or abundance by an additional resource, then, all else being equal, increasing the supply of nectar and pollen will confer no

benefit. As an extreme example, although the rare pine hoverfly (*Blera fallax*) visits flowers as an adult, it is the presence of suitable rot holes in pine stumps where larvae develop that determines where it is found, rather than the supply of floral resources. In this thesis I focus on floral resources because of their widespread importance to flower-visiting insects, but acknowledge they represent a piece of a complex puzzle.

Research into the availability of non-floral resources for pollinators in urban landscapes would help us design management interventions that do more than just provide nectar- and pollen rich flowers, benefitting more taxa (Requier and Leonhardt, 2020). For example, Gaston et al. (2005) tested whether small patches of the common nettle (*Urtica dioica*) in gardens attracted egg-laying butterflies and thus could be recommended as a simple intervention to increase the biodiversity value of gardens. Although they did not find these patches to be effective (which could be because nettles are very common in cities and often present in much larger aggregations), this type of experiment could be used to answer similar questions. Citizen science projects have great promise for investigating non-floral resources for pollinators in urban landscapes because these areas contain a high density of people and access to private greenspace is restricted. One initiative could be to encourage participants to record plants consumed by caterpillars, sending in photographs to help to identify particularly important foodplants and gain a deeper understanding of dietary flexibility (see section 5.4.5). Other citizen science projects could focus on the factors influencing the use of artificial trap nests (often called bee hotels) by cavity-nesting bees or the suitability of short mown lawns for ground-nesting bees.

5.4.4 Competition with managed honeybees

There is increasing interest in the extent to which beekeeping could be harming wild pollinators through competition for food, often a result of misguided attempts by institutions and members of the public to help reverse bee declines (Egerer and Kowarik, 2020). This is particularly relevant in cities, where the density of managed hives regularly averages and often exceeds ten per square kilometre (Casanelles-Abella and Moretti, 2022; Stevenson et al., 2020) and there is already some correlational evidence for the negative effects of competition (Meeus et al., 2021; Ropars et al., 2019). In Chapter 4, I found no significant correlations between *B. terrestris* colony density and the areas major land uses, including that of residential gardens, which provide important nesting and foraging habitat. One possible explanation is that instead, competition for food with honeybees determines the upper bound of *B. terrestris* populations in urban landscapes. Assuming 40,000 honeybees to a hive (British Beekeepers Association) and 500 individuals in a *B. terrestris* nest (Bees Wasps and Ants Recording Society), a typical urban landscape of 10 hives and 69 nests (see Chapter 4) would therefore contain twelve honeybees for every buff-tailed bumblebee. Thus, a high degree of variation in hive stocking density among urban sites (e.g. from <5 to >20 per km²) could have a larger impact on floral resource availability and hence *B. terrestris* colony density than more modest differences in the area of the green spaces producing nectar and pollen. A future direction for the study presented in Chapter 4 is to obtain values of hive density for the eight urban sites I sampled to see if it correlates with *B. terrestris* colony density. Another type

of approach for addressing this research question is the experimental placement of bumblebee colonies into landscapes differing in hive density (Meeus et al., 2021), ideally controlling for differences in floral resources.

5.4.5 Novel interactions and dietary flexibility

As discussed in section 5.2.3, dietary flexibility is an important trait which could allow insects to take advantage of the diverse flowering plant communities in urban landscapes and if specialists can widen their narrow diet breadth by exploiting introduced plants, they may be more resistant to land use and climate change. This can be studied particularly effectively in gardens and other urban habitats because insects have been provided with an extensive choice of potential feeding options. Pollen metabarcoding is one promising research tool through which to assess the dietary flexibility of flower-visiting adults (Casanelles-Abella et al., 2022; Lowe et al., 2022; Potter et al., 2019; Vaudo et al., 2020b) and is especially useful for revealing nocturnal interactions (Macgregor et al., 2019). As discussed in section 5.4.3, feeding experiments and citizen science observations could be used to collect equivalent data for the foodplants used by moth and butterfly larvae. Interactions recorded in individual studies should be incorporated into extensive online databases (e.g. DoPI and HOSTS), which can be analysed to investigate diet breadth, factoring in plant phylogeny, geographic origin and various functional traits.

5.4.6 Social, political and economic barriers to pollinator-friendly management

Research into areas like nectar and pollen production and dietary specialisation may help to optimise pollinator-friendly plant selection, but much larger gains can be made by simply improving areas currently of very low value to insects. For example, no research is needed to advise gardeners that diverse flower-rich borders are better for pollinators than concrete, or to recommend that local councils include patches of trees and scrub in parks otherwise covered with short grass. It is therefore important that we understand the multitude of reasons limiting the current extent of pollinator-friendly land management. Barriers may include insufficient awareness of or motivation to address the relevant issues, a lack of the required knowledge, as well as limited time and money (Goddard et al., 2013; Lindemann-Matthies et al., 2021; Lindemann-Matthies and Marty, 2013; Philpott et al., 2020). Here, social science has a role to play in not only unravelling the drivers of individual behaviour, but also investigating the links between pollinator-friendly management and human wellbeing, with the improvement of both an important goal (Garbuzov et al., 2015; Hoyle et al., 2018; Shanahan et al., 2015).

5.5 Concluding remarks

At first glance, urban landscapes appear bleak and inhospitable environments, their grey expanses contrasting unfavourably with the leafy green countryside. Yet to a plant, a crumbling wall is not too different from a mountain ledge, while to an insect, a flower-rich garden might equate to a patch of diverse scrubland. In fact, we often forget quite how unnatural our countryside has become, where swathes of cereal crop monocultures and non-native conifer plantations blanket much of the landscape. The impact of humanity on the planet is both extreme and pervasive, so we are lucky that nature can thrive in unlikely places. I have demonstrated that urban landscapes are valuable to insect pollinators, providing a diverse and unique assemblage of flowering plants. As we head into an uncertain future marked by changes in climate, land cover and species distribution, the biodiversity in our towns and cities represents a beacon of hope, showing that wildlife can be versatile and thrive in close proximity to people.

References

- Abe, T., Volf, M., Libra, M., Kumar, R., Abe, H., Fukushima, H., Lilip, R., Salminen, J.-P., Novotny, V., Kamata, N., Murakami, M., 2021. Effects of plant traits on caterpillar communities depend on host specialisation. *Insect Conservation and Diversity* 14, 756–767. <https://doi.org/10.1111/icad.12510>
- Ahrné, K., Bengtsson, J., Elmqvist, T., 2009. Bumble Bees (*Bombus* spp) along a Gradient of Increasing Urbanization. *PLoS ONE* 4, e5574. <https://doi.org/10.1371/journal.pone.0005574>
- Aigner, P.A., 2001. Optimality modeling and fitness trade-offs: when should plants become pollinator specialists? *Oikos*, 95(1), pp.177-184.
- Antoine, C.M., Forrest, J.R.K., 2021. Nesting habitat of ground-nesting bees: a review. *Ecological Entomology* 46, 143–159. <https://doi.org/10.1111/een.12986>
- Archer, C.R., Pirk, C.W.W., Carvalheiro, L.G., Nicolson, S.W., 2014. Economic and ecological implications of geographic bias in pollinator ecology in the light of pollinator declines. *Oikos* 123, 401–407. <https://doi.org/10.1111/j.1600-0706.2013.00949.x>
- Armar-Klemesu, M., 2000. Urban agriculture and food security, nutrition and health. *Growing cities, growing food: urban agriculture on the policy agenda. A reader on urban agriculture*, pp.99-117.
- Armbruster, W.S., 2017. The specialization continuum in pollination systems: diversity of concepts and implications for ecology, evolution and conservation. *Functional Ecology* 31, 88–100. <https://doi.org/10.1111/1365-2435.12783>
- Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A., Warren, P.S., Williams, N.S.G., Cilliers, S., Clarkson, B., Dobbs, C., Dolan, R., Hedblom, M., Klotz, S., Kooijmans, J.L., Kuhn, I., MacGregor-Fors, I., McDonnell, M., Mortberg, U., Pysek, P., Siebert, S., Sushinsky, J., Werner, P., Winter, M., 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences* 281, 20133330–20133330. <https://doi.org/10.1098/rspb.2013.3330>
- Baldock, K.C., 2020. Opportunities and threats for pollinator conservation in global towns and cities. *Current Opinion in Insect Science* 38, 63–71. <https://doi.org/10.1016/j.cois.2020.01.006>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Morse, H., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Staniczenko, P.P.A., Stone, G.N., Vaughan, I.P., Memmott, J., 2019. A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature Ecology & Evolution* 1. <https://doi.org/10.1038/s41559-018-0769-y>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P., Memmott, J., 2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences* 282, 20142849–20142849. <https://doi.org/10.1098/rspb.2014.2849>
- Balfour, N.J., Ollerton, J., Castellanos, M.C., Ratnieks, F.L.W., 2018. British phenological records indicate high diversity and extinction rates among late-summer-flying pollinators. *Biological Conservation* 222, 278–283. <https://doi.org/10.1016/j.biocon.2018.04.028>
- Ball, S., Morris, R., 2015. *Britain's Hoverflies: A Field Guide*, 2nd edn. Princeton University Press.

- Ballantyne, G., Baldock, K.C.R., Rendell, L., Willmer, P.G., 2017. Pollinator importance networks illustrate the crucial value of bees in a highly speciose plant community. *Scientific Reports* 7, 8389. <https://doi.org/10.1038/s41598-017-08798-x>
- Ballantyne, G., Baldock, K.C.R., Willmer, P.G., 2015. Constructing more informative plant–pollinator networks: visitation and pollen deposition networks in a heathland plant community. *Proceedings of the Royal Society B: Biological Sciences* 282, 20151130. <https://doi.org/10.1098/rspb.2015.1130>
- Banaszak-Cibicka, W., Żmihorski, M., 2012. Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation* 16, 331–343. <https://doi.org/10.1007/s10841-011-9419-2>
- Baselga, A., Orme, C.D.L., 2012. betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution* 3, 808–812. <https://doi.org/10.1111/j.2041-210X.2012.00224.x>
- Batáry, P., Báldi, A., Kleijn, D., Tschardtke, T., 2011. Landscape-moderated biodiversity effects of agri-environmental management: a meta-analysis. *Proceedings of the Royal Society B: Biological Sciences* 278, 1894–1902. <https://doi.org/10.1098/rspb.2010.1923>
- Batáry, P., Kurucz, K., Suarez-Rubio, M., Chamberlain, D.E., 2018. Non-linearities in bird responses across urbanization gradients: A meta-analysis. *Global Change Biology* 24, 1046–1054. <https://doi.org/10.1111/gcb.13964>
- Bates, A.J., Sadler, J.P., Fairbrass, A.J., Falk, S.J., Hale, J.D., Matthews, T.J., 2011. Changing Bee and Hoverfly Pollinator Assemblages along an Urban-Rural Gradient. *PLoS ONE* 6, e23459. <https://doi.org/10.1371/journal.pone.0023459>
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software* 67. <https://doi.org/10.18637/jss.v067.i01>
- Baude, M., Kunin, W.E., Boatman, N.D., Conyers, S., Davies, N., Gillespie, M.A.K., Morton, R.D., Smart, S.M., Memmott, J., 2016. Historical nectar assessment reveals the fall and rise of floral resources in Britain. *Nature* 530, 85–88. <https://doi.org/10.1038/nature16532>
- Bees, Wasps and Ants Recording Society. *Bombus terrestris* (Linnaeus, 1758) [Online]. Available at: <https://www.bwars.com/bee/apidae/bombus-terrestris> [Accessed: 15 March 2022]
- Berthon, K., Meyer, S.T., Thomas, F., Frank, A., Weisser, W.W., Bekessy, S., 2021. Small-Scale Habitat Conditions Are More Important Than Site Context for Influencing Pollinator Visitation. *Frontiers in Ecology and Evolution* 9, 544. <https://doi.org/10.3389/fevo.2021.703311>
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel Declines in Pollinators and Insect-Pollinated Plants in Britain and the Netherlands. *Science* 313, 351–354. <https://doi.org/10.1126/science.1127863>
- Bocci, G., 2015. TR8: an R package for easily retrieving plant species traits. *Methods in Ecology and Evolution*, 6(3):347-350, <http://dx.doi.org/10.1111/2041-210X.12327>
- Bommarco, R., Kleijn, D., Potts, S.G., 2013. Ecological intensification: harnessing ecosystem services for food security. *Trends in Ecology & Evolution* 28, 230–238. <https://doi.org/10.1016/j.tree.2012.10.012>
- Breuste, J.H., Artmann, M., 2015. Allotment Gardens Contribute to Urban Ecosystem Service: Case Study Salzburg, Austria. *Journal of Urban Planning and Development* 141, A5014005. [https://doi.org/10.1061/\(ASCE\)UP.1943-5444.0000264](https://doi.org/10.1061/(ASCE)UP.1943-5444.0000264)
- Brickell, C., 2016. *RHS A-Z Encyclopedia of Garden Plants* 4th edition. Dorling Kindersley, London.

- British Beekeepers Association. Bee Facts [Online]. Available at: <https://www.bbka.org.uk/pages/faqs/category/bee-facts> [Accessed: 15 March 2022]
- Brock, R.E., Cini, A., Sumner, S., 2021. Ecosystem services provided by aculeate wasps. *Biological Reviews* 96, 1645–1675. <https://doi.org/10.1111/brv.12719>
- Buchmann, S.L., 1987. The Ecology of Oil Flowers and Their Bees. *Annual Review of Ecology and Systematics* 18, 343–369. <https://doi.org/10.1146/annurev.es.18.110187.002015>
- Burghardt, K.T., Tallamy, D.W., Philips, C., Shropshire, K.J., 2010. Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere* 1, art11. <https://doi.org/10.1890/ES10-00032.1>
- Butchart, S.H.M., Walpole, M., Collen, B., Strien, A. van, Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.-F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vié, J.-C., Watson, R., 2010. Global Biodiversity: Indicators of Recent Declines. *Science*. <https://doi.org/10.1126/science.1187512>
- Cameron, S.A., Lozier, J.D., Strange, J.P., Koch, J.B., Cordes, N., Solter, L.F., Griswold, T.L., 2011. Patterns of widespread decline in North American bumble bees. *PNAS* 108, 662–667. <https://doi.org/10.1073/pnas.1014743108>
- Campos, M.G.R., Bogdanov, S., Almeida-Muradian, L.B. de, Szczesna, T., Mancebo, Y., Frigerio, C., Ferreira, F., 2008. Pollen composition and standardisation of analytical methods. *Journal of Apicultural Research* 47, 154–161. <https://doi.org/10.1080/00218839.2008.11101443>
- Cane, J.H., 1987. Estimation of Bee Size Using Intertegular Span (Apoidea). *Journal of the Kansas Entomological Society* 60, 145–147.
- Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.H., Williams, N.M., 2006. Complex Responses Within A Desert Bee Guild (Hymenoptera: Apiformes) To Urban Habitat Fragmentation. *Ecological Applications* 16, 632–644. [https://doi.org/10.1890/1051-0761\(2006\)016\[0632:CRWADB\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2006)016[0632:CRWADB]2.0.CO;2)
- Carthew, S.M., Goldingay, R.L., 1997. Non-flying mammals as pollinators. *Trends in Ecology & Evolution* 12, 104–108. [https://doi.org/10.1016/S0169-5347\(96\)10067-7](https://doi.org/10.1016/S0169-5347(96)10067-7)
- Carvalho, L.G., Barbosa, E.R.M., Memmott, J., 2008. Pollinator networks, alien species and the conservation of rare plants: *Trinia glauca* as a case study. *Journal of Applied Ecology* 45, 1419–1427. <https://doi.org/10.1111/j.1365-2664.2008.01518.x>
- Carvell, C., Roy, D.B., Smart, S.M., Pywell, R.F., Preston, C.D., Goulson, D., 2006. Declines in forage availability for bumblebees at a national scale. *Biological Conservation* 132, 481–489. <https://doi.org/10.1016/j.biocon.2006.05.008>
- Casanelles-Abella, J., Moretti, M., 2022. Challenging the sustainability of urban beekeeping using evidence from Swiss cities. *npj Urban Sustain* 2, 1–5. <https://doi.org/10.1038/s42949-021-00046-6>

- Casanelles-Abella, J., Müller, S., Keller, A., Aleixo, C., Alós Orti, M., Chiron, F., Deguines, N., Hallikma, T., Laanisto, L., Pinho, P., Samson, R., Tryjanowski, P., Van Mensel, A., Pellissier, L., Moretti, M., 2022. How wild bees find a way in European cities: Pollen metabarcoding unravels multiple feeding strategies and their effects on distribution patterns in four wild bee species. *Journal of Applied Ecology* 59, 457–470. <https://doi.org/10.1111/1365-2664.14063>
- Castellanos, M.C., Wilson, P., Thomson, J.D., 2002. Dynamic nectar replenishment in flowers of *Penstemon* (Scrophulariaceae). *American Journal of Botany* 89, 111–118. <https://doi.org/10.3732/ajb.89.1.111>
- Chace, J.F., Walsh, J.J., 2006. Urban effects on native avifauna: a review. *Landscape and Urban Planning* 74, 46–69. <https://doi.org/10.1016/j.landurbplan.2004.08.007>
- Chinery, M., 2005. *Complete British Insects*. HarperCollins Publishers Ltd.
- Chinery, M., 2012. *Insects of Britain and Western Europe 3rd Edition*. Domino Books Ltd.
- Colding, J., Lundberg, J., Folke, C., 2006. Incorporating Green-Area User Groups in Urban Ecosystem Management. *Ambio* 35, 237–244.
- Comba, L., Corbet, S.A., Barron, A., Bird, A., Collinge, S., Miyazaki, N., Powell, M., 1999a. Garden Flowers: Insect Visits and the Floral Reward of Horticulturally-modified Variants. *Ann Bot* 83, 73–86. <https://doi.org/10.1006/anbo.1998.0798>
- Comba, L., Corbet, S.A., Hunt, L., Warren, B., 1999b. Flowers, Nectar and Insect Visits: Evaluating British Plant Species for Pollinator-friendly Gardens. *Ann Bot* 83, 369–383. <https://doi.org/10.1006/anbo.1998.0835>
- Corbet, S.A., Bee, J., Dasmahapatra, K., Gale, S., Gorrington, E., La Ferla, B., Moorhouse, T., Treveil, A., Van Bergen, Y., Vorontsova, M., 2001. Native or Exotic? Double or Single? Evaluating Plants for Pollinator-friendly Gardens. *Ann Bot* 87, 219–232. <https://doi.org/10.1006/anbo.2000.1322>
- Culley, T.M., Weller, S.G., Sakai, A.K., 2002. The evolution of wind pollination in angiosperms. *Trends in Ecology & Evolution* 17, 361–369. [https://doi.org/10.1016/S0169-5347\(02\)02540-5](https://doi.org/10.1016/S0169-5347(02)02540-5)
- Darvill, B., Knight, M.E., Goulson, D., 2004. Use of genetic markers to quantify bumblebee foraging range and nest density. *Oikos* 107, 471–478. <https://doi.org/10.1111/j.0030-1299.2004.13510.x>
- Davis, M.A., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J., Brown, J.H., Rosenzweig, M.L., Gardener, M.R., Carroll, S.P., Thompson, K., Pickett, S.T.A., Stromberg, J.C., Tredici, P.D., Suding, K.N., Ehrenfeld, J.G., Philip Grime, J., Mascaro, J., Briggs, J.C., 2011. Don't judge species on their origins. *Nature* 474, 153–154. <https://doi.org/10.1038/474153a>
- Dearborn, D.C., Kark, S., 2010. Motivations for Conserving Urban Biodiversity. *Conservation Biology* 24, 432–440. <https://doi.org/10.1111/j.1523-1739.2009.01328.x>
- Deguines, N., Julliard, R., de Flores, M., Fontaine, C., 2016. Functional homogenization of flower visitor communities with urbanization. *Ecology and Evolution* 6, 1967–1976. <https://doi.org/10.1002/ece3.2009>
- Deguines, N., Julliard, R., de Flores, M., Fontaine, C., 2012. The Whereabouts of Flower Visitors: Contrasting Land-Use Preferences Revealed by a Country-Wide Survey Based on Citizen Science. *PLoS ONE* 7, e45822. <https://doi.org/10.1371/journal.pone.0045822>

- Dennis, M., Barlow, D., Cavan, G., Cook, P.A., Gilchrist, A., Handley, J., James, P., Thompson, J., Tzoulas, K., Wheeler, C.P., Lindley, S., 2018. Mapping Urban Green Infrastructure: A Novel Landscape-Based Approach to Incorporating Land Use and Land Cover in the Mapping of Human-Dominated Systems. *Land* 7, 17. <https://doi.org/10.3390/land7010017>
- Descamps, C., Quinet, M., Baijot, A., Jacquemart, A.-L., 2018. Temperature and water stress affect plant-pollinator interactions in *Borago officinalis* (Boraginaceae). *Ecology and Evolution* 8, 3443–3456. <https://doi.org/10.1002/ece3.3914>
- Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H.M., Chan, K.M.A., Garibaldi, L.A., Ichii, K., Liu, J., Subramanian, S.M., Midgley, G.F., Miloslavich, P., Molnár, Z., Obura, D., Pfaff, A., Polasky, S., Purvis, A., Razzaque, J., Reyers, B., Chowdhury, R.R., Shin, Y.-J., Visseren-Hamakers, I., Willis, K.J., Zayas, C.N., 2019. Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science* 366. <https://doi.org/10.1126/science.aax3100>
- Dicks, L.V., Abrahams, A., Atkinson, J., Biesmeijer, J., Bourn, N., Brown, C., Brown, M.J.F., Carvell, C., Connolly, C., Cresswell, J.E., Croft, P., Darvill, B., De Zylva, P., Effingham, P., Fountain, M., Goggin, A., Harding, D., Harding, T., Hartfield, C., Heard, M.S., Heathcote, R., Heaver, D., Holland, J., Howe, M., Hughes, B., Huxley, T., Kunin, W.E., Little, J., Mason, C., Memmott, J., Osborne, J., Pankhurst, T., Paxton, R.J., Pocock, M.J.O., Potts, S.G., Power, E.F., Raine, N.E., Ranelagh, E., Roberts, S., Saunders, R., Smith, K., Smith, R.M., Sutton, P., Tilley, L.A.N., Tinsley, A., Tonhasca, A., Vanbergen, A.J., Webster, S., Wilson, A., Sutherland, W.J., 2013. Identifying key knowledge needs for evidence-based conservation of wild insect pollinators: a collaborative cross-sectoral exercise. *Insect Conservation and Diversity* 6, 435–446. <https://doi.org/10.1111/j.1752-4598.2012.00221.x>
- Dicks, L.V., Baude, M., Roberts, S.P.M., Phillips, J., Green, M., Carvell, C., 2015. How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology* 40, 22–35. <https://doi.org/10.1111/een.12226>
- Dicks, L.V., Breeze, T.D., Ngo, H.T., Senapathi, D., An, J., Aizen, M.A., Basu, P., Buchori, D., Galetto, L., Garibaldi, L.A., Gemmill-Herren, B., Howlett, B.G., Imperatriz-Fonseca, V.L., Johnson, S.D., Kovács-Hostyánszki, A., Kwon, Y.J., Lattorff, H.M.G., Lungharwo, T., Seymour, C.L., Vanbergen, A.J., Potts, S.G., 2021. A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat Ecol Evol* 5, 1453–1461. <https://doi.org/10.1038/s41559-021-01534-9>
- Dicks, L.V., Viana, B., Bommarco, R., Brosi, B., Arizmendi, M. del C., Cunningham, S.A., Galetto, L., Hill, R., Lopes, A.V., Pires, C., Taki, H., Potts, S.G., 2016. Ten policies for pollinators. *Science*. <https://doi.org/10.1126/science.aai9226>
- Digimap [Online]. Available at: <https://digimap.edina.ac.uk/> [Accessed: 15 March 2022]
- Doak, D.F., Bigger, D., Harding, E.K., Marvier, M.A., O'Malley, R.E., Thomson, D., 1998. The Statistical Inevitability of Stability-Diversity Relationships in Community Ecology. *The American Naturalist* 151, 264–276. <https://doi.org/10.1086/286117>
- DoPI: The Database of Pollinator Interactions [Online]. Available at: <https://www.dopi.org.uk/> [Accessed: 15 March 2022]
- Dreier, S., Redhead, J.W., Warren, I.A., Bourke, A.F.G., Heard, M.S., Jordan, W.C., Sumner, S., Wang, J., Carvell, C., 2014. Fine-scale spatial genetic structure of common and declining bumble bees across an agricultural landscape. *Molecular Ecology* 23, 3384–3395. <https://doi.org/10.1111/mec.12823>

- Drescher, N., Wallace, H.M., Katouli, M., Massaro, C.F., Leonhardt, S.D., 2014. Diversity matters: how bees benefit from different resin sources. *Oecologia* 176, 943–953. <https://doi.org/10.1007/s00442-014-3070-z>
- Egerer, M., Kowarik, I., 2020. Confronting the Modern Gordian Knot of Urban Beekeeping. *Trends in Ecology & Evolution* 35, 956–959. <https://doi.org/10.1016/j.tree.2020.07.012>
- Eggenberger, H., Frey, D., Pellissier, L., Ghazoul, J., Fontana, S., Moretti, M., 2019. Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. *Journal of Animal Ecology* 88, 1522–1533. <https://doi.org/10.1111/1365-2656.13051>
- Ehrlich, P.R., Raven, P.H., 1964. Butterflies and Plants: A Study in Coevolution. *Evolution* 18, 586–608. <https://doi.org/10.2307/2406212>
- Ellis, E.E., Wilkinson, T.L., 2020. Moth assemblages within urban domestic gardens respond positively to habitat complexity, but only at a scale that extends beyond the garden boundary. *Urban Ecosyst.* <https://doi.org/10.1007/s11252-020-01050-x>
- Falk, S., 2015. *Field guide to the bees of Great Britain and Ireland*. Bloomsbury Publishing Plc.
- Fetridge, E.D., Ascher, J.S., Langellotto, G.A., 2008. The Bee Fauna of Residential Gardens in a Suburb of New York City (Hymenoptera: Apoidea). *Annals of the Entomological Society of America* 101, 1067–1077. <https://doi.org/10.1603/0013-8746-101.6.1067>
- Filipiak, M., 2019. Key pollen host plants provide balanced diets for wild bee larvae: A lesson for planting flower strips and hedgerows. *Journal of Applied Ecology* 56, 1410–1418. <https://doi.org/10.1111/1365-2664.13383>
- Filipiak, M., 2018. A Better Understanding of Bee Nutritional Ecology Is Needed to Optimize Conservation Strategies for Wild Bees—The Application of Ecological Stoichiometry. *Insects* 9, 85. <https://doi.org/10.3390/insects9030085>
- Fischer, L.K., Neuenkamp, L., Lampinen, J., Tuomi, M., Alday, J.G., Bucharova, A., Cancellieri, L., Casado-Arzuaga, I., Čeplová, N., Cerveró, L., Deák, B., Eriksson, O., Fellowes, M.D.E., Manuel, B.F. de, Filibeck, G., González-Guzmán, A., Hinojosa, M.B., Kowarik, I., Lumbierres, B., Miguel, A., Pardo, R., Pons, X., Rodríguez-García, E., Schröder, R., Sperandii, M.G., Unterweger, P., Valkó, O., Vázquez, V., Klaus, V.H., 2020. Public attitudes toward biodiversity-friendly greenspace management in Europe. *Conservation Letters* 13, e12718. <https://doi.org/10.1111/conl.12718>
- Flo, V., Bosch, J., Arnan, X., Primante, C., González, A.M.M., Barril-Graells, H., Rodrigo, A., 2018. Yearly fluctuations of flower landscape in a Mediterranean scrubland: Consequences for floral resource availability. *PLOS ONE* 13, e0191268. <https://doi.org/10.1371/journal.pone.0191268>
- Földesi, R., Howlett, B.G., Grass, I., Batáry, P., 2020. Larger pollinators deposit more pollen on stigmas across multiple plant species – a meta-analysis. *Journal of Applied Ecology*. <https://doi.org/10.1111/1365-2664.13798>
- Fortel, L., Henry, M., Guilbaud, L., Guirao, A.L., Kuhlmann, M., Mouret, H., Rollin, O., Vaissière, B.E., 2014. Decreasing Abundance, Increasing Diversity and Changing Structure of the Wild Bee Community (Hymenoptera: Anthophila) along an Urbanization Gradient. *PLoS ONE* 9, e104679. <https://doi.org/10.1371/journal.pone.0104679>
- Fortel, L., Henry, M., Guilbaud, L., Mouret, H., Vaissière, B.E., 2016. Use of human-made nesting structures by wild bees in an urban environment. *Journal of Insect Conservation* 20, 239–253. <https://doi.org/10.1007/s10841-016-9857-y>

- Fuller, R.A., Irvine, K.N., Devine-Wright, P., Warren, P.H., Gaston, K.J., 2007. Psychological benefits of greenspace increase with biodiversity. *Biology Letters* 3, 390–394. <https://doi.org/10.1098/rsbl.2007.0149>
- Futuyma, D.J., 1976. Food Plant Specialization and Environmental Predictability in Lepidoptera. *The American Naturalist* 110, 285–292. <https://doi.org/10.1086/283064>
- Gallagher, S., Lucky, A., 2020. European Wool Carder Bee, Wool Carder Bee *Anthidium manicatum* (Insecta: Hymenoptera: Megachilidae). 1 2020. <https://doi.org/10.32473/edis-in1724-2019>
- Gao, J., O'Neill, B.C., 2020. Mapping global urban land for the 21st century with data-driven simulations and Shared Socioeconomic Pathways. *Nat Commun* 11, 2302. <https://doi.org/10.1038/s41467-020-15788-7>
- Garbuzov, M., Fensome, K.A., Ratnieks, F.L.W., 2015. Public approval plus more wildlife: twin benefits of reduced mowing of amenity grass in a suburban public park in Saltdean, UK. *Insect Conservation and Diversity* 8, 107–119. <https://doi.org/10.1111/icad.12085>
- Garbuzov, M., Ratnieks, F.L.W., 2014a. Listmania: The Strengths and Weaknesses of Lists of Garden Plants to Help Pollinators. *BioScience* 64, 1019–1026. <https://doi.org/10.1093/biosci/biu150>
- Garbuzov, M., Ratnieks, F.L.W., 2014b. Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Functional Ecology* 28, 364–374. <https://doi.org/10.1111/1365-2435.12178>
- Garbuzov, M., Ratnieks, F.L.W., 2014c. Ivy: an underappreciated key resource to flower-visiting insects in autumn. *Insect Conservation and Diversity* 7, 91–102. <https://doi.org/10.1111/icad.12033>
- Gaston, K.J., Smith, R.M., Thompson, K., Warren, P.H., 2005. Urban domestic gardens (II): experimental tests of methods for increasing biodiversity. *Biodivers Conserv* 14, 395. <https://doi.org/10.1007/s10531-004-6066-x>
- Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tschardtke, T., Winqvist, C., Eggers, S., Bommarco, R., Pärt, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Oñate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hänke, S., Fischer, C., Goedhart, P.W., Inchausti, P., 2010. Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology* 11, 97–105. <https://doi.org/10.1016/j.baae.2009.12.001>
- Geslin, B., Gauzens, B., Thébault, E., Dajoz, I., 2013. Plant Pollinator Networks along a Gradient of Urbanisation. *PLoS ONE* 8, e63421. <https://doi.org/10.1371/journal.pone.0063421>
- Ghisbain, G., 2021. Are Bumblebees Relevant Models for Understanding Wild Bee Decline? *Frontiers in Conservation Science* 2.
- Ghisbain, G., Gérard, M., Wood, T.J., Hines, H.M., Michez, D., 2021. Expanding insect pollinators in the Anthropocene. *Biological Reviews* 96, 2755–2770. <https://doi.org/10.1111/brv.12777>

- Gill, R.J., Baldock, K.C.R., Brown, M.J.F., Cresswell, J.E., Dicks, L.V., Fountain, M.T., Garratt, M.P.D., Gough, L.A., Heard, M.S., Holland, J.M., Ollerton, J., Stone, G.N., Tang, C.Q., Vanbergen, A.J., Vogler, A.P., Woodward, G., Arce, A.N., Boatman, N.D., Brand-Hardy, R., Breeze, T.D., Green, M., Hartfield, C.M., O'Connor, R.S., Osborne, J.L., Phillips, J., Sutton, P.B., Potts, S.G., 2016. Chapter Four - Protecting an Ecosystem Service: Approaches to Understanding and Mitigating Threats to Wild Insect Pollinators, in: Woodward, G., Bohan, D.A. (Eds.), *Advances in Ecological Research, Ecosystem Services: From Biodiversity to Society, Part 2*. Academic Press, pp. 135–206. <https://doi.org/10.1016/bs.aecr.2015.10.007>
- Gill, R.J., Ramos-Rodriguez, O., Raine, N.E., 2012. Combined pesticide exposure severely affects individual- and colony-level traits in bees. *Nature* 491, 105–108. <https://doi.org/10.1038/nature11585>
- Goddard, M.A., Dougill, A.J., Benton, T.G., 2013. Why garden for wildlife? Social and ecological drivers, motivations and barriers for biodiversity management in residential landscapes. *Ecological Economics, Sustainable Urbanisation: A resilient future* 86, 258–273. <https://doi.org/10.1016/j.ecolecon.2012.07.016>
- Goddard, M.A., Dougill, A.J., Benton, T.G., 2010. Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology & Evolution* 25, 90–98. <https://doi.org/10.1016/j.tree.2009.07.016>
- Godfray, H.C.J., Blacquière, T., Field, L.M., Hails, R.S., Potts, S.G., Raine, N.E., Vanbergen, A.J., McLean, A.R., 2015. A restatement of recent advances in the natural science evidence base concerning neonicotinoid insecticides and insect pollinators. *Proceedings of the Royal Society B: Biological Sciences* 282, 20151821. <https://doi.org/10.1098/rspb.2015.1821>
- González, C., Alvarez-Baños, A., Cuevas, E., 2018. Floral biology and pollination mechanisms of four Mexico-endemic Fuchsia species with contrasting reproductive systems. *J Plant Ecol* 11, 123–135. <https://doi.org/10.1093/jpe/rtw118>
- González-Teuber, M., Heil, M., 2009. Nectar chemistry is tailored for both attraction of mutualists and protection from exploiters. *Plant Signaling & Behavior* 4, 809–813. <https://doi.org/10.4161/psb.4.9.9393>
- Goulson, D., 1999. Foraging strategies of insects for gathering nectar and pollen, and implications for plant ecology and evolution. *Perspectives in Plant Ecology, Evolution and Systematics* 2, 185–209. <https://doi.org/10.1078/1433-8319-00070>
- Goulson, D., Hughes, W., Derwent, L., Stout, J., 2002. Colony growth of the bumblebee, *Bombus terrestris*, in improved and conventional agricultural and suburban habitats. *Oecologia* 130, 267–273. <https://doi.org/10.1007/s004420100803>
- Goulson, D., Lepais, O., O'Connor, S., Osborne, J.L., Sanderson, R.A., Cussans, J., Goffe, L., Darvill, B., 2010. Effects of land use at a landscape scale on bumblebee nest density and survival. *Journal of Applied Ecology* 47, 1207–1215. <https://doi.org/10.1111/j.1365-2664.2010.01872.x>
- Goulson, D., Nicholls, E., Botías, C., Rotheray, E.L., 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science* 347, 1255957. <https://doi.org/10.1126/science.1255957>
- Goulson, Dave, Peat, J., Stout, J.C., Tucker, J., Darvill, B., Derwent, L.C., Hughes, W.O.H., 2002. Can alloethism in workers of the bumblebee, *Bombus terrestris*, be explained in terms of foraging efficiency? *Animal Behaviour* 64, 123–130. <https://doi.org/10.1006/anbe.2002.3041>

- Government Office for Science, 2021. Trend Deck 2021: Urbanisation [Online]. Available at: <https://www.gov.uk/government/publications/trend-deck-2021-urbanisation/trend-deck-2021-urbanisation> [Accessed: 15 March 2022]
- Grass, I., Albrecht, J., Farwig, N., Jauker, F., 2021. Plant traits and landscape simplification drive intraspecific trait diversity of *Bombus terrestris* in wildflower plantings. *Basic and Applied Ecology* 57, 91–101. <https://doi.org/10.1016/j.baae.2021.10.002>
- Greenleaf, S.S., Williams, N.M., Winfree, R., Kremen, C., 2007. Bee foraging ranges and their relationship to body size. *Oecologia* 153, 589–596. <https://doi.org/10.1007/s00442-007-0752-9>
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., Briggs, J.M., 2008. Global Change and the Ecology of Cities. *Science* 319, 756–760. <https://doi.org/10.1126/science.1150195>
- Guenat, S., Kunin, W.E., Dougill, A.J., Dallimer, M., 2019. Effects of urbanisation and management practices on pollinators in tropical Africa. *Journal of Applied Ecology* 56, 214–224. <https://doi.org/10.1111/1365-2664.13270>
- Guezen, J.M., Forrest, J.R.K., 2021. Seasonality of floral resources in relation to bee activity in agroecosystems. *Ecology and Evolution* n/a. <https://doi.org/10.1002/ece3.7260>
- Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J.S., Baldock, K.C.R., Fowler, R., Frankie, G., Goulson, D., Gunnarsson, B., Hanley, M.E., Jackson, J.I., Langellotto, G., Lowenstein, D., Minor, E.S., Philpott, S.M., Potts, S.G., Sirohi, M.H., Spevak, E.M., Stone, G.N., Threlfall, C.G., 2017. The city as a refuge for insect pollinators: Insect Pollinators. *Conservation Biology* 31, 24–29. <https://doi.org/10.1111/cobi.12840>
- Hao, K., Tian, Z.-X., Wang, Z.-C., Huang, S.-Q., 2020. Pollen grain size associated with pollinator feeding strategy. *Proceedings of the Royal Society B: Biological Sciences* 287, 20201191. <https://doi.org/10.1098/rspb.2020.1191>
- Harrison, T., Winfree, R., 2015. Urban drivers of plant-pollinator interactions. *Functional Ecology* 29, 879–888. <https://doi.org/10.1111/1365-2435.12486>
- Heil, M., 2011. Nectar: generation, regulation and ecological functions. *Trends in Plant Science* 16, 191–200. <https://doi.org/10.1016/j.tplants.2011.01.003>
- Herbertsson, L., Khalaf, R., Johnson, K., Bygebjerg, R., Blomqvist, S., Persson, A.S., 2021. Long-term data shows increasing dominance of *Bombus terrestris* with climate warming. *Basic and Applied Ecology* 53, 116–123. <https://doi.org/10.1016/j.baae.2021.03.008>
- Hicks, D.M., Ouvrard, P., Baldock, K.C.R., Baude, M., Goddard, M.A., Kunin, W.E., Mitschunas, N., Memmott, J., Morse, H., Nikolitsi, M., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Sinclair, F., Westbury, D.B., Stone, G.N., 2016. Food for Pollinators: Quantifying the Nectar and Pollen Resources of Urban Flower Meadows. *PLOS ONE* 11, e0158117. <https://doi.org/10.1371/journal.pone.0158117>
- Hill, M. O., Preston, C. D., Roy, D. B., 2004. PLANTATT—Attributes of British and Irish Plants: Status, Size, Life History, Geography and Habitats (Centre for Ecology and Hydrology).
- Holehouse, K.A., Hammond, R.L., Bourke, A.F.G., 2003. Non-lethal sampling of DNA from bumble bees for conservation genetics. *Insectes Sociaux* 50, 277–285. <https://doi.org/10.1007/s00040-003-0672-6>

- Holland, J.M., Smith, B.M., Storkey, J., Lutman, P.J.W., Aebischer, N.J., 2015. Managing habitats on English farmland for insect pollinator conservation. *Biological Conservation* 182, 215–222. <https://doi.org/10.1016/j.biocon.2014.12.009>
- Holzschuh, A., Steffan-Dewenter, I., Tscharntke, T., 2008. Agricultural landscapes with organic crops support higher pollinator diversity. *Oikos* 117, 354–361. <https://doi.org/10.1111/j.2007.0030-1299.16303.x>
- HOSTS - a Database of the World's Lepidopteran Hostplants [Online]. Available at: <https://www.nhm.ac.uk/our-science/data/hostplants/search/index.dsml> [Accessed: 15 March 2022]
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous Inference in General Parametric Models. *Biometrical Journal* 50(3), 346–363.
- Hoyle, H., Norton, B., Dunnett, N., Richards, J.P., Russell, J.M., Warren, P., 2018. Plant species or flower colour diversity? Identifying the drivers of public and invertebrate response to designed annual meadows. *Landscape and Urban Planning* 180, 103–113. <https://doi.org/10.1016/j.landurbplan.2018.08.017>
- Hülsmann, M., von Wehrden, H., Klein, A.-M., Leonhardt, S.D., 2015. Plant diversity and composition compensate for negative effects of urbanization on foraging bumble bees. *Apidologie* 46, 760–770. <https://doi.org/10.1007/s13592-015-0366-x>
- Huth-Schwarz, A., Settele, J., Moritz, R.F.A., Kraus, F.B., 2012. Factors influencing *Nosema bombi* infections in natural populations of *Bombus terrestris* (Hymenoptera: Apidae). *Journal of Invertebrate Pathology* 110, 48–53. <https://doi.org/10.1016/j.jip.2012.02.003>
- Inclán, D.J., Cerretti, P., Gabriel, D., Benton, T.G., Sait, S.M., Kunin, W.E., Gillespie, M.A.K., Marini, L., 2015. Organic farming enhances parasitoid diversity at the local and landscape scales. *Journal of Applied Ecology* 52, 1102–1109. <https://doi.org/10.1111/1365-2664.12457>
- Inoue, M.N., Yokoyama, J., Washitani, I., 2008. Displacement of Japanese native bumblebees by the recently introduced *Bombus terrestris* (L.) (Hymenoptera: Apidae). *J Insect Conserv* 12, 135–146. <https://doi.org/10.1007/s10841-007-9071-z>
- IPBES, 2016. The assessment report of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on pollinators, pollination and food production. S.G. Potts, V. L. Imperatriz-Fonseca, and H. T. Ngo (eds). Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, Bonn, Germany. 552 pages. <https://doi.org/10.5281/zenodo.3402856>
- Jachula, J., Denisow, B., Wrzesień, M., 2021. Habitat heterogeneity helps to mitigate pollinator nectar sugar deficit and discontinuity in an agricultural landscape. *Sci Total Environ* 782, 146909. <https://doi.org/10.1016/j.scitotenv.2021.146909>
- Janz, N., 2011. Ehrlich and Raven Revisited: Mechanisms Underlying Codiversification of Plants and Enemies. *Annual Review of Ecology, Evolution, and Systematics* 42, 71–89. <https://doi.org/10.1146/annurev-ecolsys-102710-145024>
- Johansen, L., Westin, A., Wehn, S., Iuga, A., Ivascu, C.M., Kallioniemi, E., Lennartsson, T., 2019. Traditional semi-natural grassland management with heterogeneous mowing times enhances flower resources for pollinators in agricultural landscapes. *Global Ecology and Conservation* 18, e00619. <https://doi.org/10.1016/j.gecco.2019.e00619>

- Jones, O.R., Wang, J., 2010. COLONY: a program for parentage and sibship inference from multilocus genotype data. *Molecular Ecology Resources* 10, 551–555. <https://doi.org/10.1111/j.1755-0998.2009.02787.x>
- Kells, A.R., Goulson, D., 2003. Preferred nesting sites of bumblebee queens (Hymenoptera: Apidae) in agroecosystems in the UK. *Biological Conservation* 109, 165–174. [https://doi.org/10.1016/S0006-3207\(02\)00131-3](https://doi.org/10.1016/S0006-3207(02)00131-3)
- Kendall, L.K., Rader, R., Gagic, V., Cariveau, D.P., Albrecht, M., Baldock, K.C.R., Freitas, B.M., Hall, M., Holzschuh, A., Molina, F.P., Morten, J.M., Pereira, J.S., Portman, Z.M., Roberts, S.P.M., Rodriguez, J., Russo, L., Sutter, L., Vereecken, N.J., Bartomeus, I., 2019. Pollinator size and its consequences: Robust estimates of body size in pollinating insects. *Ecology and Evolution* 9, 1702–1714. <https://doi.org/10.1002/ece3.4835>
- King, C., Ballantyne, G., Willmer, P.G., 2013. Why flower visitation is a poor proxy for pollination: measuring single-visit pollen deposition, with implications for pollination networks and conservation. *Methods in Ecology and Evolution* 4, 811–818. <https://doi.org/10.1111/2041-210X.12074>
- Kleijn, D., Sutherland, W.J., 2003. How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40, 947–969. <https://doi.org/10.1111/j.1365-2664.2003.00868.x>
- Kleijn, D., Winfree, R., Bartomeus, I., Carvalheiro, L.G., Henry, M., Isaacs, R., Klein, A.-M., Kremen, C., M'Gonigle, L.K., Rader, R., Ricketts, T.H., Williams, N.M., Lee Adamson, N., Ascher, J.S., Báldi, A., Batáry, P., Benjamin, F., Biesmeijer, J.C., Blitzer, E.J., Bommarco, R., Brand, M.R., Bretagnolle, V., Button, L., Cariveau, D.P., Chifflet, R., Colville, J.F., Danforth, B.N., Elle, E., Garratt, M.P.D., Herzog, F., Holzschuh, A., Howlett, B.G., Jauker, F., Jha, S., Knop, E., Krewenka, K.M., Le Féon, V., Mandelik, Y., May, E.A., Park, M.G., Pisanty, G., Reemer, M., Riedinger, V., Rollin, O., Rundlöf, M., Sardiñas, H.S., Scheper, J., Sciligo, A.R., Smith, H.G., Steffan-Dewenter, I., Thorp, R., Tscharrntke, T., Verhulst, J., Viana, B.F., Vaissière, B.E., Veldtman, R., Ward, K.L., Westphal, C., Potts, S.G., 2015. Delivery of crop pollination services is an insufficient argument for wild pollinator conservation. *Nature Communications* 6, 7414. <https://doi.org/10.1038/ncomms8414>
- Klein Alexandra-Maria, Vaissière Bernard E, Cane James H, Steffan-Dewenter Ingolf, Cunningham Saul A, Kremen Claire, Tscharrntke Teja, 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences* 274, 303–313. <https://doi.org/10.1098/rspb.2006.3721>
- Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. <http://www2.ufz.de/biolflor/index.jsp>
- Klumpers, S.G.T., Stang, M., Klinkhamer, P.G.L., 2019. Foraging efficiency and size matching in a plant–pollinator community: the importance of sugar content and tongue length. *Ecology Letters* 22, 469–479. <https://doi.org/10.1111/ele.13204>
- Knight, M.E., Martin, A.P., Bishop, S., Osborne, J.L., Hale, R.J., Sanderson, R.A., Goulson, D., 2005. An interspecific comparison of foraging range and nest density of four bumblebee (*Bombus*) species. *Molecular Ecology* 14, 1811–1820. <https://doi.org/10.1111/j.1365-294X.2005.02540.x>
- Knight, M.E., Osborne, J.L., Sanderson, R.A., Hale, R.J., Martin, A.P., Goulson, D., 2009. Bumblebee nest density and the scale of available forage in arable landscapes. *Insect Conservation and Diversity* 2, 116–124. <https://doi.org/10.1111/j.1752-4598.2009.00049.x>

- Krebs, J.R., Wilson, J.D., Bradbury, R.B., Siriwardena, G.M., 1999. The second Silent Spring? *Nature* 400, 611–612. <https://doi.org/10.1038/23127>
- Kremen, C., Williams, N.M., Aizen, M.A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Packer, L., Potts, S.G., Roulston, T., Steffan-Dewenter, I., Vázquez, D.P., Winfree, R., Adams, L., Crone, E.E., Greenleaf, S.S., Keitt, T.H., Klein, A.-M., Regetz, J., Ricketts, T.H., 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. *Ecology Letters* 10, 299–314. <https://doi.org/10.1111/j.1461-0248.2007.01018.x>
- Krieger, R.I., Feeny, P.P., Wilkinson, C.F., 1971. Detoxication Enzymes in the Guts of Caterpillars: An Evolutionary Answer to Plant Defenses? *Science* 172, 579–581. <https://doi.org/10.1126/science.172.3983.579>
- Kwon, Y.J., Saeed, S., 2003. Effect of temperature on the foraging activity of *Bombus terrestris* L. (Hymenoptera: Apidae) on greenhouse hot pepper (*Capsicum annuum* L.). *Appl. Entomol. Zool.* 38, 275–280. <https://doi.org/10.1303/aez.2003.275>
- Lagucki, E., Burdine, J.D., McCluney, K.E., 2017. Urbanization alters communities of flying arthropods in parks and gardens of a medium-sized city. *PeerJ* 5, e3620. <https://doi.org/10.7717/peerj.3620>
- Lange-Kabitz, C., Reich, M., Zoch, A., 2021. Extensively managed or abandoned urban green spaces and their habitat potential for butterflies. *Basic and Applied Ecology* 54, 85–97. <https://doi.org/10.1016/j.baae.2021.04.012>
- Langlois, A., Jacquemart, A.-L., Piqueray, J., 2020. Contribution of Extensive Farming Practices to the Supply of Floral Resources for Pollinators. *Insects* 11, 818. <https://doi.org/10.3390/insects11110818>
- Lemoine, R.T., Svenning, J.-C., 2022. Nativeness is not binary—a graduated terminology for native and non-native species in the Anthropocene. *Restoration Ecology* n/a, e13636. <https://doi.org/10.1111/rec.13636>
- Lentola, A., David, A., Abdul-Sada, A., Tapparo, A., Goulson, D., Hill, E.M., 2017. Ornamental plants on sale to the public are a significant source of pesticide residues with implications for the health of pollinating insects. *Environmental Pollution* 228, 297–304. <https://doi.org/10.1016/j.envpol.2017.03.084>
- Leonard, R.J., Vergoz, V., Proschogo, N., McArthur, C., Hochuli, D.F., 2019. Petrol exhaust pollution impairs honey bee learning and memory. *Oikos* 128, 264–273. <https://doi.org/10.1111/oik.05405>
- Lerman, S.B., Contosta, A.R., Milam, J., Bang, C., 2018. To mow or to mow less: Lawn mowing frequency affects bee abundance and diversity in suburban yards. *Biological Conservation* 221, 160–174. <https://doi.org/10.1016/j.biocon.2018.01.025>
- Lindemann-Matthies, P., Marty, T., 2013. Does ecological gardening increase species richness and aesthetic quality of a garden? *Biological Conservation* 159, 37–44. <https://doi.org/10.1016/j.biocon.2012.12.011>
- Lindemann-Matthies, P., Mulyk, L., Remmele, M., 2021. Garden plants for wild bees – Laypersons’ assessment of their suitability and opinions on gardening approaches. *Urban Forestry & Urban Greening* 62, 127181. <https://doi.org/10.1016/j.ufug.2021.127181>
- Liu, Z., He, C., Zhou, Y., Wu, J., 2014. How much of the world’s land has been urbanized, really? A hierarchical framework for avoiding confusion. *Landscape Ecol* 29, 763–771. <https://doi.org/10.1007/s10980-014-0034-y>

- Loram, A., Thompson, K., Warren, P.H., Gaston, K.J., 2008b. Urban domestic gardens (XII): The richness and composition of the flora in five UK cities. *Journal of Vegetation Science* 19, 321–330. <https://doi.org/10.3170/2008-8-18373>
- Loram, A., Tratalos, J., Warren, P.H., Gaston, K.J., 2007. Urban domestic gardens (X): the extent & structure of the resource in five major cities. *Landscape Ecol* 22, 601–615. <https://doi.org/10.1007/s10980-006-9051-9>
- Loram, A., Warren, P.H., Gaston, K.J., 2008a. Urban Domestic Gardens (XIV): The Characteristics of Gardens in Five Cities. *Environmental Management* 42, 361. <https://doi.org/10.1007/s00267-008-9097-3>
- Lowe, A., Jones, L., Brennan, G., Creer, S., de Vere, N., 2022. Seasonal progression and differences in major floral resource use by bees and hoverflies in a diverse horticultural and agricultural landscape revealed by DNA metabarcoding. *Journal of Applied Ecology* n/a. <https://doi.org/10.1111/1365-2664.14144>
- Lowenstein, D.M., Matteson, K.C., Minor, E.S., 2018. Evaluating the dependence of urban pollinators on ornamental, non-native, and ‘weedy’ floral resources. *Urban Ecosyst*. <https://doi.org/10.1007/s11252-018-0817-z>
- Lowenstein, D.M., Matteson, K.C., Xiao, I., Silva, A.M., Minor, E.S., 2014. Humans, bees, and pollination services in the city: the case of Chicago, IL (USA). *Biodiversity and Conservation* 23, 2857–2874. <https://doi.org/10.1007/s10531-014-0752-0>
- Lowenstein, D.M., Minor, E.S., 2016. Diversity in flowering plants and their characteristics: integrating humans as a driver of urban floral resources. *Urban Ecosystems* 19, 1735–1748. <https://doi.org/10.1007/s11252-016-0563-z>
- Lucek, K., Galli, A., Gurten, S., Hohmann, N., Maccagni, A., Patsiou, T., Willi, Y., 2019. Metabarcoding of honey to assess differences in plant-pollinator interactions between urban and non-urban sites. *Apidologie* 50, 317–329. <https://doi.org/10.1007/s13592-019-00646-3>
- Macgregor, C.J., Kitson, J.J.N., Fox, R., Hahn, C., Lunt, D.H., Pocock, M.J.O., Evans, D.M., 2019. Construction, validation, and application of nocturnal pollen transport networks in an agro-ecosystem: a comparison using light microscopy and DNA metabarcoding: Constructing nocturnal pollination networks. *Ecological Entomology* 44, 17–29. <https://doi.org/10.1111/een.12674>
- MacIvor, J.S., 2017. Cavity-nest boxes for solitary bees: a century of design and research. *Apidologie* 48, 311–327. <https://doi.org/10.1007/s13592-016-0477-z>
- Mahé, C., Jumarie, C., Boily, M., 2021. The countryside or the city: Which environment is better for the honeybee? *Environmental Research* 195, 110784. <https://doi.org/10.1016/j.envres.2021.110784>
- Majewska, A., Altizer, S., 2018. Planting gardens to support insect pollinators. *Conservation Biology* 0. <https://doi.org/10.1111/cobi.13271>
- Majewska, A.A., Altizer, S., 2020. Planting gardens to support insect pollinators. *Conservation Biology* 34, 15–25. <https://doi.org/10.1111/cobi.13271>
- Manoli, G., Fatichi, S., Schläpfer, M., Yu, K., Crowther, T.W., Meili, N., Burlando, P., Katul, G.G., Bou-Zeid, E., 2019. Magnitude of urban heat islands largely explained by climate and population. *Nature* 573, 55–60. <https://doi.org/10.1038/s41586-019-1512-9>

- Marín, L., Martínez-Sánchez, M.E., Sagot, P., Navarrete, D., Morales, H., 2020. Floral visitors in urban gardens and natural areas: Diversity and interaction networks in a neotropical urban landscape. *Basic and Applied Ecology* 43, 3–15. <https://doi.org/10.1016/j.baae.2019.10.003>
- Martinet, B., Dellicour, S., Ghisbain, G., Przybyla, K., Zambra, E., Lecocq, T., Boustani, M., Baghirov, R., Michez, D., Rasmont, P., 2021. Global effects of extreme temperatures on wild bumblebees. *Conservation Biology* 35, 1507–1518. <https://doi.org/10.1111/cobi.13685>
- Martins, A.C., Gonçalves, R.B., Melo, G.A.R., 2013. Changes in wild bee fauna of a grassland in Brazil reveal negative effects associated with growing urbanization during the last 40 years. *Zoologia (Curitiba)* 30, 157–176. <https://doi.org/10.1590/S1984-46702013000200006>
- Martins, K.T., Gonzalez, A., Lechowicz, M.J., 2017. Patterns of pollinator turnover and increasing diversity associated with urban habitats. *Urban Ecosystems* 20, 1359–1371. <https://doi.org/10.1007/s11252-017-0688-8>
- Mathieu, R., Freeman, C., Aryal, J., 2007. Mapping private gardens in urban areas using object-oriented techniques and very high-resolution satellite imagery. *Landscape and Urban Planning* 81, 179–192. <https://doi.org/10.1016/j.landurbplan.2006.11.009>
- Matteson, K.C., Grace, J.B., Minor, E.S., 2013. Direct and indirect effects of land use on floral resources and flower-visiting insects across an urban landscape. *Oikos* 122, 682–694. <https://doi.org/10.1111/j.1600-0706.2012.20229.x>
- Matteson, K.C., Langellotto, G.A., 2011. Small scale additions of native plants fail to increase beneficial insect richness in urban gardens: Native plant additions in urban gardens. *Insect Conservation and Diversity* 4, 89–98. <https://doi.org/10.1111/j.1752-4598.2010.00103.x>
- Matteson, K.C., Langellotto, G.A., 2010. Determinates of inner city butterfly and bee species richness. *Urban Ecosystems* 13, 333–347. <https://doi.org/10.1007/s11252-010-0122-y>
- McAulay, M.K., Killingsworth, S.Z., Forrest, J.R.K., 2020. Understanding pollen specialization in mason bees: a case study of six species. *Oecologia*. <https://doi.org/10.1007/s00442-020-04786-7>
- McCallum, K.P., McDougall, F.O., Seymour, R.S., 2013. A review of the energetics of pollination biology. *J Comp Physiol B* 183, 867–876. <https://doi.org/10.1007/s00360-013-0760-5>
- McKinney, M.L., 2008. Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosyst* 11, 161–176. <https://doi.org/10.1007/s11252-007-0045-4>
- Meeus, I., Parmentier, L., Pisman, M., de Graaf, D.C., Smaghe, G., 2021. Reduced nest development of reared *Bombus terrestris* within apiary dense human-modified landscapes. *Sci Rep* 11, 3755. <https://doi.org/10.1038/s41598-021-82540-6>
- Memmott, J., 1999. The structure of a plant-pollinator food web. *Ecology Letters* 2, 276–280. <https://doi.org/10.1046/j.1461-0248.1999.00087.x>
- Met Office, 2020. UK and regional series [Online]. Available at: <https://www.metoffice.gov.uk/research/climate/maps-and-data/uk-and-regional-series> [Accessed 21 January 2021]
- Midgley, J.J., Bond, W.J., Jarzembowski, E.A., Grubb, P.J., Chaloner, W.G., Harper, J.L., Lawton, J.H., 1991. How important is biotic pollination and dispersal to the success of the angiosperms? *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 333, 209–215. <https://doi.org/10.1098/rstb.1991.0069>

- Milano, N.J., Iverson, A.L., Nault, B.A., McArt, S.H., 2019. Comparative survival and fitness of bumble bee colonies in natural, suburban, and agricultural landscapes. *Agriculture, Ecosystems & Environment* 284, 106594. <https://doi.org/10.1016/j.agee.2019.106594>
- Miller, C.R., Joyce, P., Waits, L.P., 2005. A new method for estimating the size of small populations from genetic mark-recapture data: GENETIC MARK-RECAPTURE ESTIMATION. *Molecular Ecology* 14, 1991–2005. <https://doi.org/10.1111/j.1365-294X.2005.02577.x>
- Morales, C.L., Arbetman, M.P., Cameron, S.A., Aizen, M.A., 2013. Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment* 11, 529–534. <https://doi.org/10.1890/120321>
- Muller, A., 1996. Host-Plant Specialization in Western Palearctic Anthidine Bees (Hymenoptera: Apoidea: Megachilidae). *Ecological Monographs* 66, 235–257. <https://doi.org/10.2307/2963476>
- Muratet, A., Fontaine, B., 2015. Contrasting impacts of pesticides on butterflies and bumblebees in private gardens in France. *Biological Conservation* 182, 148–154. <https://doi.org/10.1016/j.biocon.2014.11.045>
- Nicholls, E., Botías, C., Rotheray, E.L., Whitehorn, P., David, A., Fowler, R., David, T., Feltham, H., Swain, J.L., Wells, P., Hill, E.M., Osborne, J.L., Goulson, D., 2018. Monitoring Neonicotinoid Exposure for Bees in Rural and Peri-urban Areas of the U.K. during the Transition from Pre- to Post-moratorium. *Environmental Science & Technology* 52, 9391–9402. <https://doi.org/10.1021/acs.est.7b06573>
- Nicholls, E., Ely, A., Birkin, L., Basu, P., Goulson, D., 2020. The contribution of small-scale food production in urban areas to the sustainable development goals: a review and case study. *Sustain Sci* 15, 1585–1599. <https://doi.org/10.1007/s11625-020-00792-z>
- Nicolson, S.W., 2022. Sweet solutions: nectar chemistry and quality. *Philosophical Transactions of the Royal Society B*, 377(1853), p.20210163.
- Normandin, É., Vereecken, N.J., Buddle, C.M., Fournier, V., 2017. Taxonomic and functional trait diversity of wild bees in different urban settings. *PeerJ* 5, e3051. <https://doi.org/10.7717/peerj.3051>
- Obeso, J.R., 2002. The costs of reproduction in plants. *New phytologist*, 155(3), pp.321-348.
- Office for National Statistics, 2019a. UK natural capital: urban accounts [Online]. Available at: <https://www.ons.gov.uk/economy/environmentalaccounts/bulletins/uknaturalcapital/urbanaccounts> [Accessed: 15 March 2022]
- Office for National Statistics, 2019b. Estimates of the population for the UK, England and Wales, Scotland and Northern Ireland [Online]. Available at: <https://www.ons.gov.uk/peoplepopulationandcommunity/populationandmigration/populationestimates/datasets/populationestimatesforukenglandandwalesscotlandandnorthernireland> [Accessed: 19 January 2021]
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., 2019. *vegan: Community Ecology Package*. R package version 2.5-6. <https://CRAN.R-project.org/package=vegan>
- Olesen, J.M., Valido, A., 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends in Ecology & Evolution* 18, 177–181. [https://doi.org/10.1016/S0169-5347\(03\)00004-1](https://doi.org/10.1016/S0169-5347(03)00004-1)

- Ollerton, J., 2017. Pollinator Diversity: Distribution, Ecological Function, and Conservation. *Annual Review of Ecology, Evolution, and Systematics* 48, 353–376. <https://doi.org/10.1146/annurev-ecolsys-110316-022919>
- Ollerton, J., Winfree, R., Tarrant, S., 2011. How many flowering plants are pollinated by animals? *Oikos* 120, 321–326. <https://doi.org/10.1111/j.1600-0706.2010.18644.x>
- Orsini, F., Kahane, R., Nono-Womdim, R., Gianquinto, G., 2013. Urban agriculture in the developing world: a review. *Agron. Sustain. Dev.* 33, 695–720. <https://doi.org/10.1007/s13593-013-0143-z>
- Osborne, J.L., Clark, S.J., Morris, R.J., Williams, I.H., Riley, J.R., Smith, A.D., Reynolds, D.R., Edwards, A.S., 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. *Journal of Applied Ecology* 36, 519–533. <https://doi.org/10.1046/j.1365-2664.1999.00428.x>
- Osborne, J.L., Martin, A.P., Carreck, N.L., Swain, J.L., Knight, M.E., Goulson, D., Hale, R.J., Sanderson, R.A., 2008. Bumblebee flight distances in relation to the forage landscape. *Journal of Animal Ecology* 77, 406–415. <https://doi.org/10.1111/j.1365-2656.2007.01333.x>
- Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J., Sanderson, R.A., 2007. Quantifying and comparing bumblebee nest densities in gardens and countryside habitats: Bumblebee nest survey in gardens and countryside. *Journal of Applied Ecology* 45, 784–792. <https://doi.org/10.1111/j.1365-2664.2007.01359.x>
- Ossola, A., Jenerette, G.D., McGrath, A., Chow, W., Hughes, L., Leishman, M.R., 2021. Small vegetated patches greatly reduce urban surface temperature during a summer heatwave in Adelaide, Australia. *Landscape and Urban Planning* 209, 104046. <https://doi.org/10.1016/j.landurbplan.2021.104046>
- Owen, J., 2010. *Wildlife of a garden: a thirty-year study*. The Royal Horticultural Society.
- Pacini, E., Hesse, M., 2005. Pollenkitt – its composition, forms and functions. *Flora - Morphology, Distribution, Functional Ecology of Plants* 200, 399–415. <https://doi.org/10.1016/j.flora.2005.02.006>
- Pacini, E.N.M.V.J., Nepi, M. and Vesprini, J.L., 2003. Nectar biodiversity: a short review. *Plant Systematics and Evolution*, 238(1), pp.7-21.
- Pamminger, T., Becker, R., Himmelreich, S., Schneider, C.W., Bergtold, M., 2019. The nectar report: quantitative review of nectar sugar concentrations offered by bee visited flowers in agricultural and non-agricultural landscapes. *PeerJ* 7, e6329. <https://doi.org/10.7717/peerj.6329>
- Parachnowitsch, A.L., Manson, J.S. and Sletvold, N., 2019. Evolutionary ecology of nectar. *Annals of Botany*, 123(2), pp.247-261.
- Pauw, A., 2007. Collapse of a Pollination Web in Small Conservation Areas. *Ecology* 88, 1759–1769. <https://doi.org/10.1890/06-1383.1>
- Pellmyr, O., Thompson, J.N., Brown, J.M., Harrison, R.G., 1996. Evolution of Pollination and Mutualism in the Yucca Moth Lineage. *The American Naturalist* 148, 827–847. <https://doi.org/10.1086/285958>
- Phillips, B.B., Bullock, J.M., Gaston, K.J., Hudson-Edwards, K.A., Bamford, M., Cruse, D., Dicks, L.V., Falagan, C., Wallace, C., Osborne, J.L., 2021. Impacts of multiple pollutants on pollinator activity in road verges. *Journal of Applied Ecology* 58, 1017–1029. <https://doi.org/10.1111/1365-2664.13844>
- Phillips, B.B., Shaw, R.F., Holland, M.J., Fry, E.L., Bardgett, R.D., Bullock, J.M., Osborne, J.L., 2018. Drought reduces floral resources for pollinators. *Global Change Biology* 24, 3226–3235. <https://doi.org/10.1111/gcb.14130>

- Philpott, S., Egerer, M., Bichier, P., Cohen, H., Cohen, R., Liere, H., Jha, S., Lin, B., 2020. Gardener demographics, experience, and motivations drive differences in plant species richness and composition in urban gardens. *Ecology and Society* 25. <https://doi.org/10.5751/ES-11666-250408>
- Policarová, J., Cardinal, S., Martins, A.C., Straka, J., 2019. The role of floral oils in the evolution of apid bees (Hymenoptera: Apidae). *Biological Journal of the Linnean Society* 128, 486–497. <https://doi.org/10.1093/biolinnean/blz099>
- Potter, A., LeBuhn, G., 2015. Pollination service to urban agriculture in San Francisco, CA. *Urban Ecosystems* 18, 885–893. <https://doi.org/10.1007/s11252-015-0435-y>
- Potter, C., Vere, N. de, Jones, L.E., Ford, C.R., Hegarty, M.J., Hodder, K.H., Diaz, A., Franklin, E.L., 2019. Pollen metabarcoding reveals broad and species-specific resource use by urban bees. *PeerJ* 7, e5999. <https://doi.org/10.7717/peerj.5999>
- Potts, S.G., Biesmeijer, J.C., Kremen, C., Neumann, P., Schweiger, O., Kunin, W.E., 2010. Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution* 25, 345–353. <https://doi.org/10.1016/j.tree.2010.01.007>
- Potts, S.G., Imperatriz-Fonseca, V., Ngo, H.T., Aizen, M.A., Biesmeijer, J.C., Breeze, T.D., Dicks, L.V., Garibaldi, L.A., Hill, R., Settele, J., Vanbergen, A.J., 2016. Safeguarding pollinators and their values to human well-being. *Nature* 540, 220–229. <https://doi.org/10.1038/nature20588>
- Powney, G.D., Carvell, C., Edwards, M., Morris, R.K.A., Roy, H.E., Woodcock, B.A., Isaac, N.J.B., 2019. Widespread losses of pollinating insects in Britain. *Nature Communications* 10, 1018. <https://doi.org/10.1038/s41467-019-08974-9>
- Prendergast, K.S., Dixon, K.W., Bateman, P.W., 2022. A global review of determinants of native bee assemblages in urbanised landscapes. *Insect Conservation and Diversity* n/a. <https://doi.org/10.1111/icad.12569>
- Prendergast, K.S., Ollerton, J., 2021. Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens. *Urban Ecosyst.* <https://doi.org/10.1007/s11252-020-01089-w>
- Primack, R.B., Higuchi, H., Miller-Rushing, A.J., 2009. The impact of climate change on cherry trees and other species in Japan. *Biological Conservation, The Conservation and Management of Biodiversity in Japan* 142, 1943–1949. <https://doi.org/10.1016/j.biocon.2009.03.016>
- Pyke, G.H., 1991. What does it cost a plant to produce floral nectar? *Nature*, 350(6313), pp.58-59.
- Pywell, R.F., Warman, E.A., Carvell, C., Sparks, T.H., Dicks, L.V., Bennett, D., Wright, A., Critchley, C.N.R., Sherwood, A., 2005. Providing foraging resources for bumblebees in intensively farmed landscapes. *Biological Conservation* 121, 479–494. <https://doi.org/10.1016/j.biocon.2004.05.020>
- R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- R Core Team, 2021. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.

- Rader, R., Bartomeus, I., Garibaldi, L.A., Garratt, M.P.D., Howlett, B.G., Winfree, R., Cunningham, S.A., Mayfield, M.M., Arthur, A.D., Andersson, G.K.S., Bommarco, R., Brittain, C., Carvalheiro, L.G., Chacoff, N.P., Entling, M.H., Foully, B., Freitas, B.M., Gemmill-Herren, B., Ghazoul, J., Griffin, S.R., Gross, C.L., Herbertsson, L., Herzog, F., Hipólito, J., Jaggar, S., Jauker, F., Klein, A.-M., Kleijn, D., Krishnan, S., Lemos, C.Q., Lindström, S.A.M., Mandelik, Y., Monteiro, V.M., Nelson, W., Nilsson, L., Pattimore, D.E., Pereira, N. de O., Pisanty, G., Potts, S.G., Reemer, M., Rundlöf, M., Sheffield, C.S., Scheper, J., Schüepp, C., Smith, H.G., Stanley, D.A., Stout, J.C., Szentgyörgyi, H., Taki, H., Vergara, C.H., Viana, B.F., Woyciechowski, M., 2016. Non-bee insects are important contributors to global crop pollination. *PNAS* 113, 146–151. <https://doi.org/10.1073/pnas.1517092112>
- Rasmont, P., Coppee, A., Michez, D., De Meulemeester, T., 2008. An overview of the *Bombus terrestris* (L. 1758) subspecies (Hymenoptera: Apidae). *Annales de la Société entomologique de France (N.S.)* 44, 243–250. <https://doi.org/10.1080/00379271.2008.10697559>
- Redhead, J.W., Dreier, S., Bourke, A.F.G., Heard, M.S., Jordan, W.C., Sumner, S., Wang, J., Carvell, C., 2016. Effects of habitat composition and landscape structure on worker foraging distances of five bumble bee species. *Ecological Applications* 26, 726–739. <https://doi.org/10.1890/15-0546>
- Regal, P.J., 1982. Pollination by Wind and Animals: Ecology of Geographic Patterns. *Annual Review of Ecology and Systematics* 13, 497–524. <https://doi.org/10.1146/annurev.es.13.110182.002433>
- Requier, F., Leonhardt, S.D., 2020. Beyond flowers: including non-floral resources in bee conservation schemes. *J Insect Conserv* 24, 5–16. <https://doi.org/10.1007/s10841-019-00206-1>
- Richardson, L.L., Adler, L.S., Leonard, A.S., Andicoechea, J., Regan, K.H., Anthony, W.E., Manson, J.S., Irwin, R.E., 2015. Secondary metabolites in floral nectar reduce parasite infections in bumblebees. *Proceedings of the Royal Society B: Biological Sciences* 282, 20142471. <https://doi.org/10.1098/rspb.2014.2471>
- Rizwan, A.M., Dennis, L.Y.C., Liu, C., 2008. A review on the generation, determination and mitigation of Urban Heat Island. *Journal of Environmental Sciences* 20, 120–128. [https://doi.org/10.1016/S1001-0742\(08\)60019-4](https://doi.org/10.1016/S1001-0742(08)60019-4)
- Robinson, R.A., Sutherland, W.J., 2002. Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39, 157–176. <https://doi.org/10.1046/j.1365-2664.2002.00695.x>
- Rollings, R., Goulson, D., 2019. Quantifying the attractiveness of garden flowers for pollinators. *J Insect Conserv*. <https://doi.org/10.1007/s10841-019-00177-3>
- Ropars, L., Dajoz, I., Fontaine, C., Muratet, A., Geslin, B., 2019. Wild pollinator activity negatively related to honey bee colony densities in urban context. *PLoS ONE* 14, e0222316. <https://doi.org/10.1371/journal.pone.0222316>
- Roulston, T.H., Cane, J.H., 2000. Pollen nutritional content and digestibility for animals 23.
- Roulston, T.H., Cane, J.H., Buchmann, S.L., 2000. What Governs Protein Content of Pollen: Pollinator Preferences, Pollen–Pistil Interactions, or Phylogeny? *Ecological Monographs* 70, 617–643. [https://doi.org/10.1890/0012-9615\(2000\)070](https://doi.org/10.1890/0012-9615(2000)070)
- Roulston, T.H., Goodell, K., 2011. The Role of Resources and Risks in Regulating Wild Bee Populations. *Annual Review of Entomology* 56, 293–312. <https://doi.org/10.1146/annurev-ento-120709-144802>
- Rowland, C.S. Morton, R.D. Carrasco, L. McShane, G.; O’Neil, A.W. Wood, C.M., 2017. Land Cover Map 2015 (vector, GB). NERC Environmental Information Data Centre. <https://doi.org/10.5285/6c6c9203-7333-4d96-88ab-78925e7a4e73>

- Roy, R., Schmitt, A.J., Thomas, J.B., Carter, C.J., 2017. Review: Nectar biology: From molecules to ecosystems. *Plant Science* 262, 148–164. <https://doi.org/10.1016/j.plantsci.2017.04.012>
- Russo, L., DeBarros, N., Yang, S., Shea, K., Mortensen, D., 2013. Supporting crop pollinators with floral resources: network-based phenological matching. *Ecology and Evolution* 3, 3125–3140. <https://doi.org/10.1002/ece3.703>
- Ryalls, J.M.W., Langford, B., Mullinger, N.J., Bromfield, L.M., Nemitz, E., Pfrang, C., Girling, R.D., 2022. Anthropogenic air pollutants reduce insect-mediated pollination services. *Environmental Pollution* 297, 118847. <https://doi.org/10.1016/j.envpol.2022.118847>
- Salisbury, A., Al-Beidh, S., Armitage, J., Bird, S., Bostock, H., Platoni, A., Tatchell, M., Thompson, K., Perry, J., 2017. Enhancing gardens as habitats for plant-associated invertebrates: should we plant native or exotic species? *Biodiversity and Conservation* 26, 2657–2673. <https://doi.org/10.1007/s10531-017-1377-x>
- Salisbury, A., Armitage, J., Bostock, H., Perry, J., Tatchell, M., Thompson, K., 2015. EDITOR'S CHOICE: Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species? *Journal of Applied Ecology* 52, 1156–1164. <https://doi.org/10.1111/1365-2664.12499>
- Samuelson, A.E., Gill Richard J., Brown Mark J. F., Leadbeater Ellouise, 2018. Lower bumblebee colony reproductive success in agricultural compared with urban environments. *Proceedings of the Royal Society B: Biological Sciences* 285, 20180807. <https://doi.org/10.1098/rspb.2018.0807>
- Samuelson, A.E., Schürch, R., Leadbeater, E., 2022. Dancing bees evaluate central urban forage resources as superior to agricultural land. *Journal of Applied Ecology* 59, 79–88. <https://doi.org/10.1111/1365-2664.14011>
- Scheper, J., Bommarco, R., Holzschuh, A., Potts, S.G., Riedinger, V., Roberts, S.P.M., Rundlöf, M., Smith, H.G., Steffan-Dewenter, I., Wickens, J.B., Wickens, V.J., Kleijn, D., 2015. Local and landscape-level floral resources explain effects of wildflower strips on wild bees across four European countries. *Journal of Applied Ecology* 52, 1165–1175. <https://doi.org/10.1111/1365-2664.12479>
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S.G., Rundlöf, M., Smith, H.G., Kleijn, D., 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. *Ecology Letters* 16, 912–920. <https://doi.org/10.1111/ele.12128>
- Schindler, D.E., Armstrong, J.B., Reed, T.E., 2015. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* 13, 257–263. <https://doi.org/10.1890/140275>
- Schlaepfer, M.A., Sax, D.F., Olden, J.D., 2011. The Potential Conservation Value of Non-Native Species. *Conservation Biology* 25, 428–437. <https://doi.org/10.1111/j.1523-1739.2010.01646.x>
- Scott, S.B., Sivakoff, F.S., Gardiner, M.M., 2022. Exposure to urban heavy metal contamination diminishes bumble bee colony growth. *Urban Ecosyst.* <https://doi.org/10.1007/s11252-022-01206-x>
- Seitz, N., vanEngelsdorp, D., Leonhardt, S.D., 2020. Are native and non-native pollinator friendly plants equally valuable for native wild bee communities? *Ecology and Evolution* 10, 12838–12850. <https://doi.org/10.1002/ece3.6826>
- Seto, K.C., Güneralp, B., Hutyra, L.R., 2012. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *PNAS* 109, 16083–16088. <https://doi.org/10.1073/pnas.1211658109>

- Shanahan, D.F., Fuller, R.A., Bush, R., Lin, B.B., Gaston, K.J., 2015. The Health Benefits of Urban Nature: How Much Do We Need? *BioScience* 65, 476–485. <https://doi.org/10.1093/biosci/biv032>
- Sirohi, M.H., Jackson, J., Edwards, M., Ollerton, J., 2015. Diversity and abundance of solitary and primitively eusocial bees in an urban centre: a case study from Northampton (England). *Journal of Insect Conservation* 19, 487–500. <https://doi.org/10.1007/s10841-015-9769-2>
- Sivakoff, F.S., Prajzner, S.P., Gardiner, M.M., 2018. Unique Bee Communities within Vacant Lots and Urban Farms Result from Variation in Surrounding Urbanization Intensity. *Sustainability* 10, 1926. <https://doi.org/10.3390/su10061926>
- Smith, M.R., Singh, G.M., Mozaffarian, D., Myers, S.S., 2015. Effects of decreases of animal pollinators on human nutrition and global health: a modelling analysis. *The Lancet* 386, 1964–1972. [https://doi.org/10.1016/S0140-6736\(15\)61085-6](https://doi.org/10.1016/S0140-6736(15)61085-6)
- Somme, L., Moquet, L., Quinet, M., Vanderplanck, M., Michez, D., Lognay, G., Jacquemart, A.-L., 2016. Food in a row: urban trees offer valuable floral resources to pollinating insects. *Urban Ecosyst* 19, 1149–1161. <https://doi.org/10.1007/s11252-016-0555-z>
- Soroye, P., Newbold, T., Kerr, J., 2020. Climate change contributes to widespread declines among bumble bees across continents. *Science* 367, 685–688. <https://doi.org/10.1126/science.aax8591>
- Staab, M., Pereira-Peixoto, M.H., Klein, A.-M., 2020. Exotic garden plants partly substitute for native plants as resources for pollinators when native plants become seasonally scarce. *Oecologia*. <https://doi.org/10.1007/s00442-020-04785-8>
- Stang, M., Klinkhamer, P.G.L., Meijden, E.V.D., 2006. Size constraints and flower abundance determine the number of interactions in a plant–flower visitor web. *Oikos* 112, 111–121. <https://doi.org/10.1111/j.0030-1299.2006.14199.x>
- Stanley, D.A., Knight, M.E., Stout, J.C., 2013. Ecological Variation in Response to Mass-Flowering Oilseed Rape and Surrounding Landscape Composition by Members of a Cryptic Bumblebee Complex. *PLOS ONE* 8, e65516. <https://doi.org/10.1371/journal.pone.0065516>
- Stelzer, R.J., Chittka, L., Carlton, M., Ings, T.C., 2010. Winter Active Bumblebees (*Bombus terrestris*) Achieve High Foraging Rates in Urban Britain. *PLoS One* 5. <https://doi.org/10.1371/journal.pone.0009559>
- Stevenson, P.C., Bidartondo, M.I., Blackhall-Miles, R., Cavagnaro, T.R., Cooper, A., Geslin, B., Koch, H., Lee, M.A., Moat, J., O’Hanlon, R., Sjöman, H., Sofu, A., Stara, K., Suz, L.M., 2020. The state of the world’s urban ecosystems: What can we learn from trees, fungi, and bees? *PLANTS, PEOPLE, PLANET* 2, 482–498. <https://doi.org/10.1002/ppp3.10143>
- Stoate, C., Boatman, N.D., Borralho, R.J., Carvalho, C.R., Snoo, G.R. de, Eden, P., 2001. Ecological impacts of arable intensification in Europe. *Journal of Environmental Management* 63, 337–365. <https://doi.org/10.1006/jema.2001.0473>
- Stout, J., Goulson, D., 2002. The influence of nectar secretion rates on the responses of bumblebees (*Bombus* spp.) to previously visited flowers. *Behavioral Ecology and Sociobiology* 52, 239–246. <https://doi.org/10.1007/s00265-002-0510-2>
- Stout, J.C., Goulson, D., Allen, J.A., 1998. Repellent scent-marking of flowers by a guild of foraging bumblebees (*Bombus* spp.). *Behav Ecol Sociobiol* 43, 317–326. <https://doi.org/10.1007/s002650050497>

- Straw, E.A., Carpentier, E.N., Brown, M.J.F., 2021. Roundup causes high levels of mortality following contact exposure in bumble bees. *Journal of Applied Ecology* 58, 1167–1176. <https://doi.org/10.1111/1365-2664.13867>
- Tew, N.E., Baldock, K.C.R., Vaughan, I.P., Bird, S., Memmott, J., 2022. Turnover in floral composition explains species diversity and temporal stability in the nectar supply of urban residential gardens. *Journal of Applied Ecology* n/a. <https://doi.org/10.1111/1365-2664.14094>
- Tew, N.E., Memmott, J., Vaughan, I.P., Bird, S., Stone, G.N., Potts, S.G. and Baldock, K.C., 2021. Quantifying nectar production by flowering plants in urban and rural landscapes. *Journal of Ecology*, 109(4), pp.1747-1757.
- Thebo, A.L., Drechsel, P., Lambin, E.F., 2014. Global assessment of urban and peri-urban agriculture: irrigated and rainfed croplands. *Environ. Res. Lett.* 9, 114002. <https://doi.org/10.1088/1748-9326/9/11/114002>
- Theodorou, P., Albig, K., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T.E., Paxton, R.J., 2017. The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. *Functional Ecology* 31, 838–847. <https://doi.org/10.1111/1365-2435.12803>
- Theodorou, P., Baltz, L.M., Paxton, R.J., Soro, A., 2021. Urbanization is associated with shifts in bumblebee body size, with cascading effects on pollination. *Evolutionary Applications* 14, 53–68. <https://doi.org/10.1111/eva.13087>
- Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I., Wubet, T., Murray, T.E., Paxton, R.J., 2020a. Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nat Commun* 11, 576. <https://doi.org/10.1038/s41467-020-14496-6>
- Thomas, J.A., 2004. Comparative Losses of British Butterflies, Birds, and Plants and the Global Extinction Crisis. *Science* 303, 1879–1881. <https://doi.org/10.1126/science.1095046>
- Thomson, J.D., McKenna, M.A., Cruzan, M.B., 1989. Temporal Patterns of Nectar and Pollen Production in *Aralia Hispida*: Implications for Reproductive Success. *Ecology* 70, 1061–1068. <https://doi.org/10.2307/1941375>
- Tiedeken, E.J., Egan, P.A., Stevenson, P.C., Wright, G.A., Brown, M.J.F., Power, E.F., Farrell, I., Matthews, S.M., Stout, J.C., 2017. Nectar chemistry modulates the impact of an invasive plant on native pollinators. *Functional Ecology* 885–893. <https://doi.org/10.1111/1365-2435.12588> @10.1111/(ISSN)1365-2435.Plantpollinatorinteractions
- Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S., Packer, C., 2017. Future threats to biodiversity and pathways to their prevention. *Nature* 546, 73–81. <https://doi.org/10.1038/nature22900>
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W.H., Simberloff, D., Swackhamer, D., 2001. Forecasting Agriculturally Driven Global Environmental Change. *Science*. <https://doi.org/10.1126/science.1057544>
- Timberlake, T.P., Vaughan, I.P., Baude, M., Memmott, J., 2021. Bumblebee colony density on farmland is influenced by late-summer nectar supply and garden cover. *Journal of Applied Ecology* 58, 1006–1016. <https://doi.org/10.1111/1365-2664.13826>
- Timberlake, T.P., Vaughan, I.P., Memmott, J., 2019. Phenology of farmland floral resources reveals seasonal gaps in nectar availability for bumblebees. *Journal of Applied Ecology*. <https://doi.org/10.1111/1365-2664.13403>

- Toro, I.D., Ribbons, R.R., 2020. No Mow May lawns have higher pollinator richness and abundances: An engaged community provides floral resources for pollinators. *PeerJ* 8, e10021. <https://doi.org/10.7717/peerj.10021>
- Truett, G.E., Heeger, P., Mynatt, R.L., Truett, A.A., Walker, J.A., Warman, M.L., 2000. Preparation of PCR-Quality Mouse Genomic DNA with Hot Sodium Hydroxide and Tris (HotSHOT). *BioTechniques* 29, 52–54. <https://doi.org/10.2144/00291bm09>
- Tuck, S.L., Winqvist, C., Mota, F., Ahnström, J., Turnbull, L.A., Bengtsson, J., 2014. Land-use intensity and the effects of organic farming on biodiversity: a hierarchical meta-analysis. *Journal of Applied Ecology* 51, 746–755. <https://doi.org/10.1111/1365-2664.12219>
- United Nations, Department of Economic and Social Affairs, Population Division, 2014. *World Urbanization Prospects: The 2014 Revision, Highlights (ST/ESA/SER.A/352)*.
- Urbanowicz, C., Muñoz, P.A., McArt, S.H., 2020. Honey bees and wild pollinators differ in their preference for and use of introduced floral resources. *Ecology and Evolution* n/a. <https://doi.org/10.1002/ece3.6417>
- Vaudo, A.D., Biddinger, D.J., Sickel, W., Keller, A., López-Urbe, M.M., 2020b. Introduced bees (*Osmia cornifrons*) collect pollen from both coevolved and novel host-plant species within their family-level phylogenetic preferences. *Royal Society Open Science* 7, 200225. <https://doi.org/10.1098/rsos.200225>
- Vaudo, A.D., Patch, H.M., Mortensen, D.A., Tooker, J.F., Grozinger, C.M., 2016. Macronutrient ratios in pollen shape bumble bee (*Bombus impatiens*) foraging strategies and floral preferences. *PNAS* 113, E4035–E4042. <https://doi.org/10.1073/pnas.1606101113>
- Vaudo, A.D., Tooker, J.F., Grozinger, C.M., Patch, H.M., 2015. Bee nutrition and floral resource restoration. *Current Opinion in Insect Science, Social Insects * Vectors and Medical and Veterinary Entomology* 10, 133–141. <https://doi.org/10.1016/j.cois.2015.05.008>
- Vaudo, A.D., Tooker, J.F., Patch, H.M., Biddinger, D.J., Coccia, M., Crone, M.K., Fiely, M., Francis, J.S., Hines, H.M., Hodges, M., Jackson, S.W., Michez, D., Mu, J., Russo, L., Safari, M., Treanore, E.D., Vanderplanck, M., Yip, E., Leonard, A.S., Grozinger, C.M., 2020a. Pollen Protein: Lipid Macronutrient Ratios May Guide Broad Patterns of Bee Species Floral Preferences. *Insects* 11, 132. <https://doi.org/10.3390/insects11020132>
- Verboven, H.A.F., Uyttenbroeck, R., Brys, R., Hermy, M., 2014. Different responses of bees and hoverflies to land use in an urban–rural gradient show the importance of the nature of the rural land use. *Landscape and Urban Planning* 126, 31–41. <https://doi.org/10.1016/j.landurbplan.2014.02.017>
- Vessby, K., Söderström, B., Glimskär, A., Svensson, B., 2002. Species-Richness Correlations of Six Different Taxa in Swedish Seminatural Grasslands. *Conservation Biology* 16, 430–439. <https://doi.org/10.1046/j.1523-1739.2002.00198.x>
- Wäckers, F.L., Romeis, J., van Rijn, P., 2007. Nectar and Pollen Feeding by Insect Herbivores and Implications for Multitrophic Interactions. *Annual Review of Entomology* 52, 301–323. <https://doi.org/10.1146/annurev.ento.52.110405.091352>
- Walther-Hellwig, K., Frankl, R., 2000. Foraging habitats and foraging distances of bumblebees, *Bombus* spp. (Hym., Apidae), in an agricultural landscape. *Journal of Applied Entomology* 124, 299–306. <https://doi.org/10.1046/j.1439-0418.2000.00484.x>

- Walton, R.E., Sayer, C.D., Bennion, H., Axmacher, J.C., 2020. Nocturnal pollinators strongly contribute to pollen transport of wild flowers in an agricultural landscape. *Biology Letters* 16, 20190877. <https://doi.org/10.1098/rsbl.2019.0877>
- Wardhaugh, C.W., 2015. How many species of arthropods visit flowers? *Arthropod-Plant Interactions* 9, 547–565. <https://doi.org/10.1007/s11829-015-9398-4>
- Warton, D.I., Duursma, R.A., Falster, D.S., Taskinen, S., 2012. smatr 3—an R package for estimation and inference about allometric lines. *Methods in Ecology and Evolution*, 3(2), pp.257-259.
- Waser, N.M., Chittka, L., Price, M.V., Williams, N.M., Ollerton, J., 1996. Generalization in Pollination Systems, and Why it Matters. *Ecology* 77, 1043–1060. <https://doi.org/10.2307/2265575>
- Waser, N.M., Price, M.V., 2016. Drought, pollen and nectar availability, and pollination success. *Ecology* 97, 1400–1409. <https://doi.org/10.1890/15-1423.1>
- Watson, C.J., Carignan-Guillemette, L., Turcotte, C., Maire, V., Proulx, R., 2020. Ecological and economic benefits of low-intensity urban lawn management. *Journal of Applied Ecology* 57, 436–446. <https://doi.org/10.1111/1365-2664.13542>
- Weiner, C.N., Hilpert, A., Werner, M., Linsenmair, K.E., Blüthgen, N., 2010. Pollen amino acids and flower specialisation in solitary bees. *Apidologie* 41, 476–487. <https://doi.org/10.1051/apido/2009083>
- Wenzel, A., Grass, I., Belavadi, V.V., Tschardt, T., 2020. How urbanization is driving pollinator diversity and pollination – A systematic review. *Biological Conservation* 241, 108321. <https://doi.org/10.1016/j.biocon.2019.108321>
- Williams, N.M., Crone, E.E., Roulston, T.H., Minckley, R.L., Packer, L., Potts, S.G., 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation, Conserving complexity: Global change and community-scale interactions* 143, 2280–2291. <https://doi.org/10.1016/j.biocon.2010.03.024>
- Wilson, J.S., Forister, M.L., Carril, O.M., 2017. Interest exceeds understanding in public support of bee conservation. *Frontiers in Ecology and the Environment* 15, 460–466. <https://doi.org/10.1002/fee.1531>
- Wood, S.N., 2017. *Generalized Additive Models: An Introduction with R* (2nd edition). Chapman and Hall/CRC
- Wood, T. J., Holland, J.M., Goulson, D., 2015a. A comparison of techniques for assessing farmland bumblebee populations. *Oecologia* 177, 1093–1102. <https://doi.org/10.1007/s00442-015-3255-0>
- Wood, Thomas J., Holland, J.M., Hughes, W.O.H., Goulson, D., 2015b. Targeted agri-environment schemes significantly improve the population size of common farmland bumblebee species. *Molecular Ecology* 24, 1668–1680. <https://doi.org/10.1111/mec.13144>
- Woodard, S.H., Jha, S., 2017. Wild bee nutritional ecology: predicting pollinator population dynamics, movement, and services from floral resources. *Current Opinion in Insect Science* 21, 83–90. <https://doi.org/10.1016/j.cois.2017.05.011>
- Woodcock, B.A., Bullock, J.M., Shore, R.F., Heard, M.S., Pereira, M.G., Redhead, J., Ridding, L., Dean, H., Sleep, D., Henrys, P., Peyton, J., Hulmes, S., Hulmes, L., Sároszpataki, M., Saure, C., Edwards, M., Genersch, E., Knäbe, S., Pywell, R.F., 2017. Country-specific effects of neonicotinoid pesticides on honey bees and wild bees. *Science*. <https://doi.org/10.1126/science.aaa1190>

- World Bank, 2018. Agricultural land (% of land area). [Online]. Available at:
https://data.worldbank.org/indicator/AG.LND.AGRI.ZS?most_recent_value_desc=true
[Accessed: 15 March 2022]
- Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R., Tylianakis, J.M., 2003. Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia* 134, 605–611. <https://doi.org/10.1007/s00442-002-1128-9>
- Zipper, S.C., Schatz, J., Singh, A., Kucharik, C.J., Townsend, P.A., Loheide, S.P., 2016. Urban heat island impacts on plant phenology: intra-urban variability and response to land cover. *Environ. Res. Lett.* 11, 054023. <https://doi.org/10.1088/1748-9326/11/5/054023>
- Zu, P., Koch, H., Schwery, O., Pironon, S., Phillips, C., Ondo, I., Farrell, I.W., Nes, W.D., Moore, E., Wright, G.A., Farman, D.I., Stevenson, P.C., 2021. Pollen sterols are associated with phylogeny and environment but not with pollinator guilds. *New Phytologist* 230, 1169–1184. <https://doi.org/10.1111/nph.17227>

Appendix 1: Supplementary information for Chapter 2

Supplementary Table 1. The definition of a floral unit for all plant taxa in this study.

Floral unit definition	Plant taxa
Single flower	<i>Acer</i> spp, <i>Alstroemeria</i> spp., all Amaryllidaceae, all Asparagaceae, <i>Atriplex</i> spp., <i>Begonia</i> spp., <i>Berberis</i> spp., all Boraginaceae, all Brassicaceae (apart from <i>Lobularia maritima</i>), <i>Camellia japonica</i> , all Campanulaceae, all Caprifoliaceae (apart from <i>Sambucus nigra</i>), all Caryophyllaceae, <i>Chenopodium</i> spp., all Cistaceae, all Convolvulaceae, all Crassulaceae, all Cucurbitaceae, <i>Cuphea ignea</i> , <i>Cyclamen hederifolium</i> , <i>Dactylorhiza</i> spp., <i>Dorotheanthus bellidiformis</i> , all Ericaceae (apart from <i>Calluna vulgaris</i>), <i>Escallonia</i> spp., <i>Euonymus japonica</i> , all Fabaceae (apart from <i>Medicago</i> spp. and <i>Trifolium</i> spp.), <i>Francoa sonchifolia</i> , all Geraniaceae, <i>Hedera helix</i> , <i>Hemerocallis</i> spp., <i>Houttuynia cordata</i> , all Hydrangeaceae, <i>Hypericum</i> spp., <i>Ilex aquifolium</i> , <i>Impatiens</i> spp., all Iridaceae, all Lamiaceae (apart from <i>Lavandula</i> spp.), all Liliaceae, <i>Linum catharticum</i> , <i>Limnanthes douglasii</i> , all Malvaceae, <i>Mercurialis perennis</i> , all Montiaceae, <i>Narthecium ossifragum</i> , all Oleaceae, all Onagraceae, all Orobanchaceae, <i>Oxalis</i> spp., <i>Pachysandra terminalis</i> , all Papaveraceae, <i>Passiflora caerulea</i> , <i>Plantago</i> spp., all Plumbaginaceae, all Polemoniaceae, <i>Polygala serpyllifolia</i> , all Polygonaceae (apart from <i>Persicaria bistorta</i>), all Primulaceae, all Ranunculaceae, <i>Reseda lutea</i> , <i>Ribes</i> spp., all Rosaceae (apart from <i>Spiraea</i> spp.), all Rubiaceae, all Rutaceae, all Saxifragaceae, all Scrophulariaceae (apart from <i>Buddleja davidii</i> and <i>Veronica</i> spp. subgenus <i>Pseudoveronica</i>), all Solanaceae, <i>Tamus communis</i> , <i>Tropaeolum majus</i> , all Verbenaceae, <i>Vinca</i> spp., <i>Viola</i> spp.
Part of panicle	<i>Spiraea</i> spp.
Secondary umbel	All Apiaceae
Single branch of capitula	<i>Solidago canadensis</i> , <i>Solidago gigantea</i>
Single capitulum	All Asteraceae (apart from <i>Solidago canadensis</i> and <i>Solidago gigantea</i>), all Dipsacaceae
Single catkin	<i>Salix</i> spp.
Single compound cyme	<i>Centranthus ruber</i>
Single corymb	<i>Cornus</i> spp., <i>Lobularia maritima</i> , <i>Sambucus nigra</i>
Single cyme	<i>Euphorbia</i> spp.
Single panicle	<i>Buddleja davidii</i>
Single raceme	<i>Calluna vulgaris</i> , <i>Medicago</i> spp., <i>Persicaria bistorta</i> , <i>Trifolium</i> spp., <i>Veronica</i> spp. subgenus <i>Pseudoveronica</i>
Single spadix	<i>Zantedeschia aethiopica</i>
Single spike	<i>Lavandula</i> spp.
Single thyrses	<i>Ceanothus</i> spp.

Supplementary Table 2. The ten taxa with the greatest contribution to nectar sugar production in each landscape are shown and all other taxa are labelled as ‘Others’. The native status of each taxon is indicated by the letter ‘N’ (native) or ‘A’ (non-native alien). Some taxa with a high nectar sugar contribution were only recorded flowering in one or a few quadrats, making generalisations about their nectar sugar production in different UK landscapes unreliable from the data presented below.

Plant taxon	Native status	% of total nectar sugar	Landscape
<i>Fuchsia</i> spp.	A	24.3	Urban
<i>Trifolium repens</i>	N	15.5	Urban
<i>Lavandula angustifolia/latifolia</i> and hybrid	A	9.4	Urban
<i>Crocosmia</i> × <i>crocosmiiflora</i>	A	6.7	Urban
<i>Escallonia</i> spp.	A	6.0	Urban
<i>Cirsium arvense</i>	N	3.6	Urban
<i>Pseudofumaria lutea</i>	A	3.4	Urban
<i>Buddleja davidii</i>	A	2.4	Urban
<i>Chamerion angustifolium</i>	N	2.2	Urban
<i>Rubus fruticosus</i> agg.	N	1.8	Urban
Others (114 taxa)		24.8	Urban
<i>Trifolium repens</i>	N	35.8	Farmland
<i>Brassica</i> spp.	A	15.0	Farmland
<i>Cirsium palustre</i>	N	10.7	Farmland
<i>Tripleurospermum inodorum</i>	A	7.6	Farmland
<i>Cirsium arvense</i>	N	5.2	Farmland
<i>Senecio jacobaea</i>	N	3.0	Farmland
<i>Sambucus nigra</i>	N	2.6	Farmland
<i>Matricaria chamomilla</i>	A	2.2	Farmland
<i>Cirsium vulgare</i>	N	2.0	Farmland
<i>Impatiens glandulifera</i>	A	1.7	Farmland
Others (83 taxa)		14.2	Farmland
<i>Calluna vulgaris</i>	N	73.2	Nature reserve
<i>Cirsium palustre</i>	N	4.8	Nature reserve
<i>Trifolium repens</i>	N	4.3	Nature reserve
<i>Cirsium arvense</i>	N	4.2	Nature reserve
<i>Erica cinerea</i>	N	2.5	Nature reserve
<i>Senecio jacobaea</i>	N	1.8	Nature reserve
<i>Rubus fruticosus</i> agg	N	1.4	Nature reserve
<i>Cirsium vulgare</i>	N	1.2	Nature reserve
<i>Centaurea nigra</i>	N	1.0	Nature reserve
<i>Trifolium pratense</i>	N	0.7	Nature reserve
Others (92 taxa)		4.9	Nature reserve

Supplementary Table 3. Results of linear mixed models for the comparison of landscape types (question 1). Significance of fixed effects is shown and p-values from Tukey post hoc tests are given for all significant ($p < 0.05$) comparisons. Farm: farmland landscapes; NR: nature reserve landscapes.

Response variable and sample size	Effect of landscape type (df = 2)	Comparison	Tukey post hoc tests
All nectar sugar (mass) N = 36	$\chi^2 = 1.01$, $p = 0.60$	NA	NA
Native nectar sugar (mass) N = 36	$\chi^2 = 2.84$, $p = 0.24$	NA	NA
Non-native nectar sugar (mass) N = 36	$\chi^2 = 28.29$, $p < 0.001$	Farm > NR Urban > NR	$p < 0.001$ $p < 0.001$
Nectar source diversity N = 36	$\chi^2 = 12.96$, $p = 0.002$	Urban > Farm Urban > NR	$p < 0.001$ $p = 0.013$

Supplementary Table 4. Results of linear mixed models for the comparison of urban land uses (question 2). Significance of fixed effects is shown and p-values from Tukey post hoc tests are given for all significant ($p < 0.05$) comparisons. Alt: allotments; Cem: cemeteries; Gdn: gardens; MMS: manmade surfaces; NR: nature reserves; OGS: other green spaces; Par: parks; Pav: pavements; Ver: road verges.

Response variable and sample size	Effect of land use type (df = 8)	Comparison	Tukey post hoc tests	Effect of city (df = 3)	Comparison	Tukey post hoc tests
All nectar sugar (mass) N = 360	$\chi^2 = 269.72$ $p < 0.001$	Alt > MMS Alt > OGS Alt > Par Alt > Pav Cem > MMS Cem > Pav Gdn > Cem Gdn > MMS Gdn > NR Gdn > OGS Gdn > Par Gdn > Pav Gdn > Ver NR > MMS NR > Pav OGS > MMS OGS > Pav Par > MMS Par > Pav Pav > MMS Ver > MMS Ver > Pav	$p < 0.001$ $p < 0.001$ $p = 0.044$ $p < 0.001$ $p < 0.001$ $p < 0.001$ $p = 0.020$ $p < 0.001$ $p = 0.007$ $p < 0.001$ $p = 0.005$ $p < 0.001$ $p = 0.028$ $p < 0.001$ $p < 0.001$ $p < 0.001$ $p = 0.006$ $p < 0.001$ $p < 0.001$ $p < 0.001$ $p < 0.001$ $p < 0.001$ $p < 0.001$	$\chi^2 = 0.38$ $p = 0.95$	NA	NA

Native nectar sugar (mass) N = 360	$\chi^2 = 313.78$ p < 0.001	Alt > MMS	p < 0.001	$\chi^2 = 0.42$ p = 0.94	NA	NA
		Alt > Pav	p < 0.001			
		Cem > MMS	p < 0.001			
		Cem > Pav	p < 0.001			
		Gdn > MMS	p < 0.001			
		Gdn > Pav	p < 0.001			
		NR > MMS	p < 0.001			
		NR > Pav	p < 0.001			
		OGS > MMS	p < 0.001			
		OGS > Pav	p < 0.001			
		Par > MMS	p < 0.001			
		Par > Pav	p < 0.001			
		Pav > MMS	p < 0.001			
		Ver > MMS	p < 0.001			
		Ver > Pav	p < 0.001			
Non-native nectar sugar (mass) N = 360	$\chi^2 = 298.36$ p < 0.001	Alt > Cem	p < 0.001	$\chi^2 = 4.82$ p = 0.19	NA	NA
		Alt > MMS	p < 0.001			
		Alt > NR	p < 0.001			
		Alt > OGS	p < 0.001			
		Alt > Par	p < 0.001			
		Alt > Pav	p < 0.001			
		Alt > Ver	p < 0.001			
		Cem > MMS	p = 0.002			
		Cem > NR	p = 0.010			
		Cem > OGS	p = 0.037			
		Cem > Par	p = 0.004			
		Gdn > Cem	p < 0.001			
		Gdn > MMS	p < 0.001			
		Gdn > NR	p < 0.001			
		Gdn > OGS	p < 0.001			
		Gdn > Par	p < 0.001			
		Gdn > Pav	p < 0.001			
		Gdn > Ver	p < 0.001			
		Pav > MMS	p < 0.001			
		Pav > NR	p < 0.001			
Pav > OGS	p < 0.001					
Pav > Par	p < 0.001					
Nectar source diversity N = 360	$\chi^2 = 202.97$ p < 0.001	Alt > Cem	p < 0.001	$\chi^2 = 18.73$ p < 0.001	Bristol >	
		Alt > MMS	p < 0.001		Leeds	p = 0.012
		Alt > NR	p < 0.001		Reading >	
		Alt > OGS	p < 0.001		Edinburgh	p = 0.020
		Alt > Par	p < 0.001		Reading >	
		Alt > Pav	p < 0.001		Leeds	p < 0.001
		Alt > Ver	p < 0.001			
		Cem > MMS	p < 0.001			
		Cem > Pav	p < 0.001			
		Gdn > Cem	p < 0.001			
		Gdn > MMS	p < 0.001			
		Gdn > NR	p < 0.001			
		Gdn > OGS	p < 0.001			
		Gdn > Par	p < 0.001			
		Gdn > Pav	p < 0.001			
		Gdn > Ver	p < 0.001			
		Par > MMS	p = 0.042			
		Ver > MMS	p = 0.005			
		Ver > Pav	p = 0.018			

Supplementary Table 5. The ten taxa with the greatest contribution to nectar sugar production in each land use are shown and all other taxa are labelled as ‘Others’. The native status is indicated by the letter ‘N’ (native) or ‘A’ (non-native alien). Some taxa were only recorded flowering in one or a few quadrats, making generalisations about their nectar sugar production in UK towns and cities unreliable from the data presented below.

Plant taxon	Native status	% of total nectar sugar	Land use
<i>Lavandula angustifolia/latifolia</i> and hybrids	A	31.3	Allotment
<i>Symphytum</i> spp.	N	9.0	Allotment
<i>Buddleja davidii</i>	A	8.4	Allotment
<i>Taraxacum</i> agg.	N	3.3	Allotment
<i>Senecio jacobaea</i>	N	2.8	Allotment
<i>Rubus fruticosus</i> agg.	N	2.3	Allotment
<i>Origanum vulgare</i>	N	1.8	Allotment
<i>Lamium album</i>	A	1.7	Allotment
<i>Rubus idaeus</i> and hybrids	N	1.6	Allotment
<i>Ribes rubrum</i>	A	1.5	Allotment
Others (244 taxa)		36.4	Allotment
<i>Trifolium pratense</i>	N	25.0	Cemetery
<i>Philadelphus</i> spp.	A	17.4	Cemetery
<i>Trifolium repens</i>	N	14.4	Cemetery
<i>Taraxacum</i> agg.	N	10.6	Cemetery
<i>Bellis perennis</i>	N	8.2	Cemetery
<i>Senecio jacobaea</i>	N	6.0	Cemetery
<i>Hypochaeris radicata</i>	N	3.0	Cemetery
<i>Prunella vulgaris</i>	N	1.9	Cemetery
<i>Anthriscus sylvestris</i>	N	1.8	Cemetery
<i>Rubus fruticosus</i> agg.	N	1.4	Cemetery
Others (98 taxa)		10.5	Cemetery
<i>Fuchsia</i> spp.	A	19.1	Garden
<i>Veronica</i> subgenus <i>Pseudoveronica</i> (<i>Hebe</i> spp.)	A	10.9	Garden
<i>Skimmia japonica</i>	A	4.1	Garden
<i>Taraxacum</i> agg.	N	3.2	Garden
<i>Lavandula angustifolia/latifolia</i> and hybrids	A	2.8	Garden
<i>Brachyglottis</i> spp.	A	2.6	Garden
<i>Berberis</i> spp.	A	2.4	Garden
<i>Ceanothus</i> spp.	A	2.4	Garden
<i>Crococsmia</i> × <i>crococsmiiflora</i>	A	2.3	Garden
<i>Ribes sanguineum</i>	A	2.2	Garden
Others (355 taxa)		48.0	Garden
<i>Berberis</i> spp.	A	64.4	Manmade surface
<i>Ceanothus</i> spp.	A	19.5	Manmade surface
<i>Taraxacum</i> agg.	N	4.3	Manmade surface
<i>Reseda lutea</i>	A	3.7	Manmade surface
<i>Senecio jacobaea</i>	N	2.2	Manmade surface
<i>Trifolium repens</i>	N	1.8	Manmade surface
<i>Symphoricarpos</i> spp.	A	1.4	Manmade surface
<i>Buddleja davidii</i>	A	1.0	Manmade surface
<i>Medicago lupulina</i>	N	0.4	Manmade surface
<i>Chamerion angustifolium</i>	N	0.3	Manmade surface
Others (27 taxa)		1.0	Manmade surface
<i>Rubus fruticosus</i> agg.	N	19.8	Nature reserve
<i>Symphytum</i> spp.	A	10.6	Nature reserve
<i>Teucrium scorodonia</i>	N	9.3	Nature reserve
<i>Impatiens glandulifera</i>	A	8.8	Nature reserve
<i>Senecio jacobaea</i>	N	7.1	Nature reserve
<i>Trifolium pratense</i>	N	6.3	Nature reserve
<i>Heracleum sphondylium</i>	N	6.1	Nature reserve
<i>Erica cinerea</i>	N	4.3	Nature reserve
<i>Taraxacum</i> agg.	N	2.8	Nature reserve
<i>Cirsium arvense</i>	N	2.7	Nature reserve
Others (95 taxa)		22.2	Nature reserve

<i>Trifolium repens</i>	N	50.8	Other greenspace
<i>Taraxacum</i> agg.	N	12.4	Other greenspace
<i>Bellis perennis</i>	N	10.8	Other greenspace
<i>Hyacinthoides non-scripta/hispanica</i> and hybrids	N	3.6	Other greenspace
<i>Crataegus monogyna</i>	N	3.4	Other greenspace
<i>Rubus fruticosus</i> agg.	N	2.9	Other greenspace
<i>Centaurea nigra</i>	N	2.3	Other greenspace
<i>Prunella vulgaris</i>	N	2.0	Other greenspace
<i>Allium</i> spp.	A	1.8	Other greenspace
<i>Anthriscus sylvestris</i>	N	1.4	Other greenspace
Others (65 taxa)		8.6	Other greenspace
<i>Trifolium repens</i>	N	39.1	Park
<i>Taraxacum</i> agg.	N	34.6	Park
<i>Bellis perennis</i>	N	6.1	Park
<i>Senecio jacobaea</i>	N	3.9	Park
<i>Allium</i> spp.	A	2.6	Park
<i>Anthriscus sylvestris</i>	N	1.4	Park
<i>Euphorbia amygdaloides</i> and hybrids	N	1.4	Park
<i>Scorzoneroideis autumnalis</i>	N	1.4	Park
<i>Heracleum sphondylium</i>	N	1.2	Park
<i>Trifolium pratense</i>	N	1.2	Park
Others (71 taxa)		7.1	Park
<i>Buddleja davidii</i>	A	16.3	Pavement
<i>Valerianella</i> spp.	N	13.1	Pavement
<i>Berberis</i> spp.	A	11.8	Pavement
<i>Ceanothus</i> spp.	A	11.0	Pavement
<i>Lavandula angustifolia/latifolia</i> and hybrids	A	10.4	Pavement
<i>Calluna vulgaris</i>	N	9.5	Pavement
<i>Weigela</i> spp.	A	3.4	Pavement
<i>Euphorbia myrsinites</i>	A	3.1	Pavement
<i>Fuchsia</i> spp.	A	2.3	Pavement
<i>Trifolium repens</i>	N	2.0	Pavement
Others (79 taxa)		17.1	Pavement
<i>Trifolium repens</i>	N	37.8	Verge
<i>Taraxacum</i> agg.	N	31.7	Verge
<i>Bellis perennis</i>	N	8.4	Verge
<i>Trifolium pratense</i>	N	7.0	Verge
<i>Medicago sativa</i>	N	5.8	Verge
<i>Medicago lupulina</i>	N	1.3	Verge
<i>Scorzoneroideis autumnalis</i>	N	1.2	Verge
<i>Prunella vulgaris</i>	N	0.7	Verge
<i>Anthriscus sylvestris</i>	N	0.7	Verge
<i>Acer</i> spp.	A	0.6	Verge
Others (68 taxa)		4.9	Verge

Appendix 2: Supplementary information for Chapter 3

Supplementary Table 6. The definition of a floral unit for all plant taxa in this study.

Floral unit definition	Plant taxa
Single flower	All Acanthaceae, all Aizoaceae, <i>Alstroemeria</i> spp., all Amaranthaceae, all Amaryllidaceae, <i>Angelonia angustifolia</i> , <i>Anigozanthos</i> spp., all Apocynaceae, all Asparagaceae, all Asphodelaceae, <i>Aucuba japonica</i> , <i>Begonia</i> spp., all Berberidaceae, all Bignoniaceae, all Boraginaceae, <i>Bougainvillea</i> spp., all Brassicaceae (apart from <i>Lobularia maritima</i>), all Buxaceae, <i>Camellia japonica</i> , all Campanulaceae, <i>Canna</i> spp., all Caprifoliaceae (apart from <i>Sambucus nigra</i>), all Caryophyllaceae, all Cistaceae, all Convolvulaceae, <i>Corokia</i> × <i>virgata</i> , <i>Cotinus coggygria</i> , all Crassulaceae, all Cucurbitaceae, <i>Cyclamen</i> spp., <i>Daphne odora</i> , all Ericaceae (apart from <i>Calluna vulgaris</i>), <i>Escallonia rubra/hybrid</i> , <i>Euonymus</i> spp., all Fabaceae (apart from <i>Acacia dealbata</i> , <i>Medicago</i> spp. and <i>Trifolium</i> spp.), all Geraniaceae, <i>Grevillea rosmarinifolia</i> , all Grossulariaceae, <i>Hedera colchica/helix</i> , <i>Hemerocallis</i> spp., <i>Houttuynia cordata</i> , all Hydrangeaceae, <i>Hypericum</i> spp., <i>Ilex aquifolium</i> , <i>Impatiens</i> spp., all Iridaceae, all Lamiaceae (apart from <i>Lavandula</i> spp.), all Lardizabalaceae, <i>Laurus nobilis</i> , <i>Leptospermum scoparium</i> , all Liliaceae, <i>Limnanthes douglasii</i> , <i>Linum</i> spp., all Magnoliaceae, all Malvaceae, <i>Mercurialis perennis</i> , <i>Myrtus communis</i> , <i>Nymphaea</i> spp., all Oleaceae (apart from <i>Syringa</i> spp.), all Onagraceae, all Oxalidaceae, <i>Paeonia</i> spp., all Papaveraceae, <i>Passiflora caerulea</i> , <i>Paulownia tomentosa</i> , all Pittosporaceae, all Plumbaginaceae, all Polemoniaceae, <i>Polygala myrtifolia</i> , all Polygonaceae, all Primulaceae, all Ranunculaceae, <i>Rhodohypoxis</i> spp., all Rosaceae (apart from <i>Spiraea</i> spp.), all Rubiaceae, all Rutaceae, <i>Sagittaria sagittifolia</i> , all Sapindaceae, all Saxifragaceae, <i>Scaevola aemula</i> , all Scrophulariaceae (apart from <i>Buddleja davidii</i> and <i>Hebe</i> spp.), all Solanaceae, <i>Tropaeolum majus</i> , all Urticaceae, all Verbenaceae, <i>Viola</i> spp., all Vitaceae.
Part of panicle	<i>Spiraea</i> spp.
Secondary umbel	All Apiaceae
Single branch of capitula	<i>Solidago canadensis</i>
Single capitulum	All Asteraceae (apart from <i>Solidago canadensis</i>), all Dipsacaceae
Single catkin	<i>Salix</i> spp.
Single compound cyme	<i>Centranthus ruber</i>
Single corymb	<i>Cornus</i> spp., <i>Lobularia maritima</i> , <i>Sambucus nigra</i>
Single cyme	<i>Euphorbia</i> spp.
Single panicle	<i>Buddleja davidii</i> , <i>Syringa</i> spp.
Single raceme	<i>Acacia dealbata</i> , <i>Callistemon</i> spp., <i>Calluna vulgaris</i> , <i>Gunnera manicata</i> , <i>Hebe</i> spp., <i>Medicago</i> spp., <i>Tamarix</i> spp., <i>Trifolium</i> spp.
Single spadix	All Araceae
Single spike	<i>Lavandula</i> spp., <i>Plantago lanceolata</i>
Single thyrses	<i>Ceanothus</i> spp.

Supplementary Table 7. The 43 plant taxa which cumulatively provide 75% of the total nectar supply across all gardens. An asterisk (*) indicates a plant taxon's nectar production was estimated at the floral unit level by predictive modelling, all other taxa have empirically measured values. The native status of each taxon is indicated by the letter 'N' (native) or 'A' (non-native alien); the plant life form by the letter 'H' (herbaceous), 'T' (tree), 'S' (shrub) or 'C' (woody climber) and flower structure by the letter 'G' (generalised) or 'S' (specialised).

Plant taxon	Percentage of total nectar	Native status	Life form	Flower structure
<i>Fuchsia magellanica</i> /hybrid	23.29	A	S	S
<i>Pieris</i> spp.	6.94	A	S	S
<i>Salvia greggii</i> /microphylla	3.56	A	S	S
<i>Lonicera caprifolium</i> / <i>japonica</i> / <i>periclymenum</i>	2.79	A	C	S
<i>Erysimum linifolium</i>	2.23	A	H	S
<i>Penstemon barbatus</i>	2.03	A	H	S
<i>Crocoshmia</i> × <i>crocoshmiiflora</i>	1.83	A	H	S
<i>Philadelphus coronarius</i> /hybrid	1.79	A	S	G
<i>Tamarix</i> spp.*	1.75	A	S	G
<i>Erigeron karvinskianus</i> *	1.29	A	H	G
<i>Choisya ternata</i>	1.28	A	S	G
<i>Pyracantha</i> spp.	1.21	A	S	G
<i>Ceanothus</i> spp.	1.20	A	S	G
<i>Muscari armeniacum</i>	1.16	A	H	S
<i>Syringa vulgaris</i>	1.12	A	S	S
<i>Wisteria</i> spp.	1.12	A	C	S
<i>Skimmia japonica</i>	1.10	A	S	G
<i>Ribes sanguineum</i>	1.08	A	S	S
<i>Prunus</i> spp. (ornamental)	1.04	A	T	G
<i>Nicotiana</i> spp.	1.03	A	H	S
<i>Hedera colchica</i> / <i>helix</i>	1.02	N	C	G
<i>Dahlia</i> spp.	1.00	A	H	G
<i>Camellia japonica</i>	0.97	A	S	G
<i>Campanula portenschlagiana</i>	0.93	A	H	G
<i>Prunus laurocerasus</i>	0.90	A	S	G
<i>Campanula poscharskyana</i>	0.87	A	H	G
<i>Buddleja davidii</i>	0.85	A	S	S
<i>Erica carnea</i>	0.81	A	S	S
<i>Taraxacum</i> agg.	0.78	N	H	G
<i>Lavandula angustifolia</i>	0.77	A	S	S
<i>Bellis perennis</i>	0.76	N	H	G
<i>Weigela florida</i>	0.70	A	S	S
<i>Linaria purpurea</i>	0.69	A	H	S
<i>Cordyline australis</i> *	0.65	A	S	G
<i>Jasminum officinale</i>	0.65	A	C	S
<i>Amelanchier</i> spp.*	0.58	A	T	G
<i>Cotoneaster</i> spp. (red flowers)	0.57	A	S	G
<i>Rhododendron</i> spp. (large flower cultivar)	0.53	A	S	S
<i>Heuchera</i> spp.	0.50	A	H	G
<i>Aquilegia vulgaris</i> /hybrid	0.48	N	H	S
<i>Euonymus</i> spp.	0.46	A	S	G
<i>Sedum spectabile</i> / <i>telephium</i>	0.45	N	H	G
<i>Centaurea montana</i>	0.44	A	H	G
Other taxa (606)	24.81			

Supplementary Table 8. The 10 plant taxa with the greatest contribution to overall monthly nectar supply across the surveyed 59 gardens. An asterisk (*) indicates a plant taxon's nectar production was estimated at the floral unit level by predictive modelling, all other taxa have empirically measured values. The native status of each taxon is indicated by the letter 'N' (native) or 'A' (non-native alien).

Plant taxon	Percentage of monthly nectar	Native status	Month
<i>Pieris</i> spp.	30.99	A	March
<i>Skimmia japonica</i>	10.17	A	March
<i>Muscari armeniacum</i>	9.21	A	March
<i>Camellia japonica</i>	4.97	A	March
<i>Erica carnea</i>	4.74	A	March
<i>Prunus laurocerasus</i>	4.40	A	March
<i>Prunus</i> spp. (ornamental)	4.23	A	March
<i>Salix</i> spp.	3.83	N	March
<i>Helleborus</i> × <i>hybridus</i>	3.25	A	March
<i>Bergenia cordifolia</i>	2.91	A	March
Other taxa (131)	21.29		March
<i>Pieris</i> spp.	26.07	A	April
<i>Ribes sanguineum</i>	6.99	A	April
<i>Choisya ternata</i>	5.93	A	April
<i>Syringa vulgaris</i>	5.91	A	April
<i>Wisteria</i> spp.	4.83	A	April
<i>Prunus</i> spp. (ornamental)	4.16	A	April
<i>Amelanchier</i> spp.*	4.10	A	April
<i>Taraxacum</i> agg.	3.03	N	April
<i>Camellia japonica</i>	2.92	A	April
<i>Prunus laurocerasus</i>	2.91	A	April
Other taxa (245)	33.14		April
<i>Fuchsia magellanica</i> /hybrid	11.02	A	May
<i>Philadelphus coronarius</i> /hybrid	9.82	A	May
<i>Tamarix</i> spp.*	8.89	A	May
<i>Ceanothus</i> spp.	6.65	A	May
<i>Erysimum linifolium</i>	4.48	A	May
<i>Weigela florida</i>	4.11	A	May
<i>Cotoneaster</i> spp. (red flowers)	3.21	A	May
<i>Cordyline australis</i> *	3.08	A	May
<i>Wisteria</i> spp.	2.64	A	May
<i>Choisya ternata</i>	2.59	A	May
Other taxa (302)	43.50		May
<i>Fuchsia magellanica</i> /hybrid	17.71	A	June
<i>Lonicera caprifolium</i> / <i>japonica</i> / <i>periclymenum</i>	11.08	A	June
<i>Pyracantha</i> spp.	6.06	A	June
<i>Salvia greggii</i> / <i>microphylla</i>	4.72	A	June
<i>Campanula portenschlagiana</i>	4.12	A	June
<i>Campanula poscharskyana</i>	3.93	A	June
<i>Penstemon barbatus</i>	3.55	A	June
<i>Erysimum linifolium</i>	3.23	A	June
<i>Bellis perennis</i>	2.55	N	June
<i>Erigeron karvinskianus</i> *	1.97	A	June
Other taxa (319)	41.07		June
<i>Fuchsia magellanica</i> /hybrid	32.27	A	July
<i>Salvia greggii</i> / <i>microphylla</i>	5.51	A	July
<i>Crococsmia</i> × <i>crococsmiiflora</i>	4.09	A	July
<i>Lonicera caprifolium</i> / <i>japonica</i> / <i>periclymenum</i>	3.79	A	July
<i>Penstemon barbatus</i>	3.59	A	July
<i>Lavandula angustifolia</i>	2.42	A	July
<i>Buddleja davidii</i>	2.34	A	July
<i>Nicotiana</i> spp.	2.00	A	July
<i>Linaria purpurea</i>	1.96	A	July
<i>Senecio jacobaea</i>	1.95	N	July
Other taxa (374)	40.06		July

<i>Fuchsia magellanica</i> /hybrid	42.25	A	August
<i>Crocosmia</i> × <i>crocosmiiflora</i>	9.72	A	August
<i>Salvia greggii</i> /microphylla	4.28	A	August
<i>Penstemon barbatus</i>	3.49	A	August
<i>Nicotiana</i> spp.	2.26	A	August
<i>Dahlia</i> spp.	2.22	A	August
<i>Buddleja davidii</i>	2.07	A	August
<i>Lonicera caprifolium</i> /japonica/periclymenum	1.89	A	August
<i>Lavandula angustifolia</i>	1.84	A	August
<i>Erigeron karvinskianus</i> *	1.63	A	August
Other taxa (328)	28.36		August
<i>Fuchsia magellanica</i> /hybrid	52.07	A	September
<i>Salvia greggii</i> /microphylla	5.15	A	September
<i>Sedum spectabile</i> /telephium	3.75	N	September
<i>Dahlia</i> spp.	3.53	A	September
<i>Penstemon barbatus</i>	3.03	A	September
<i>Nicotiana</i> spp.	2.46	A	September
<i>Buddleja davidii</i>	2.32	A	September
<i>Aster</i> spp.	1.94	A	September
<i>Erigeron karvinskianus</i> *	1.82	A	September
<i>Erysimum linifolium</i>	1.72	A	September
Other taxa (285)	22.21		September
<i>Fuchsia magellanica</i> /hybrid	49.00	A	October
<i>Hedera colchica</i> /helix	11.75	N	October
<i>Salvia greggii</i> /microphylla	9.91	A	October
<i>Dahlia</i> spp.	3.11	A	October
<i>Penstemon barbatus</i>	3.00	A	October
<i>Salvia</i> × <i>hybrida</i>	2.04	A	October
<i>Erigeron karvinskianus</i> *	1.70	A	October
<i>Aster</i> spp.	1.55	A	October
<i>Chrysanthemum</i> spp.*	1.44	A	October
<i>Sedum spectabile</i> /telephium	1.39	N	October
Other taxa (237)	15.12		October

