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**Improving floral resources for bees and other  
flower-visiting insects:  
key ecological & human dimensions**

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Submitted for the degree of Doctor of Philosophy

Submission date: September 2020

University of Sussex

## **Declaration**

I declare that the work carried out in this thesis is entirely done by me, and that any help provided by other individuals with data collection and analysis is fully acknowledged.

I certify that this thesis has not and will not be submitted, in whole or part, to another university for the award of any other degree.

Signature:

Veronica Renée Wignall

**University of Sussex**  
**Veronica Renée Wignall, Doctor in Philosophy**

Improving floral resources for bees and other flower-visiting insects:  
key ecological and human dimensions

**Summary:**

This thesis contributes to the current field of research exploring how to improve floral resource availability for flower-visiting insects (FVI). This objective is increasingly both important and difficult, as we experience rapid global anthropogenic change and attempt to meet the food and land requirements of a growing human population sustainably. In practice enhancing floral resources is highly complex, with multiple stakeholders and interlinked ecological and human dimensions.

**Chapter Two** uses multiple complementary approaches to show that bramble, (*Rubus fruticosus* L. agg.), is a highly valuable foraging resource for bees and other FVI.

**Chapter Three** shows that nectar competition between honeybees and bumblebees varies seasonally and is stronger in summer than spring or autumn, adding to current understanding of the seasonality of resource demand and exploitative competition between bee species.

**Chapter Four** reveals patterns of competitive exclusion between pollinator groups, mediated by resource depletion by eusocial bees. The findings show a particularly strong effect of eusocial bee-mediated resource competition on solitary bee foraging behaviour and suggest a link between the strength of competition present and local floral resource availability.

**Chapter Five** discovers positive public attitudes but mixed pro-environmental behaviour relating to planting for pollinators, using questionnaires and interviews with customers in five garden centres in Sussex.

**Chapter Six** uses an online questionnaire to show that public perceptions of common wild flowering plants are influenced by conflicting factors, including aesthetic appeal, charisma and ‘weed’ status. Perceived ecological value had a small effect on liking ratings for wildflowers at an individual, but not societal, level.

## **Publications arising from this thesis**

Wignall V.R., Arscott N.A., Nudds H.E., Squire A., Green T.O. & Ratnieks F.L.W. (2020) Thug life: bramble (*Rubus fruticosus* L. agg.) is a valuable foraging resource for honeybees and diverse flower-visiting insects. *Insect Conservation and Diversity*, **13**: 543-557. **(Chapter Two)**

Wignall V.R., Campbell Harry I., Davies N.L., Kenny S.D., McMinn J.K. & Ratnieks F.L.W. (2020) Seasonal variation in exploitative competition between honeybees and bumblebees. *Oecologia*, **192**:351–361. **(Chapter Three)**

Wignall V.R., Brolly M., Uthoff C., Norton K.E., Chipperfield H.M., Balfour N.J & Ratnieks F.L.W. (2020) Exploitative competition and displacement mediated by eusocial bees: experimental evidence in a wild pollinator community. *Behavioral Ecology and Sociobiology*, **74**:152. **(Chapter Four)**

Wignall V.R., Alton K. & Ratnieks F.L.W. (2019) Garden centre customer attitudes to pollinators and pollinator-friendly planting. *PeerJ*, **7**:e7088. **(Chapter Five)**

Wignall V.R. & Ratnieks F.L.W. (*in submission*) Food for flower-visiting insects: appreciating common wild flowering plants.

Wignall V.R., Alton K. & Ratnieks F.L.W. (*in prep*) Perception roots: understanding public attitudes towards common wild flowering plants and implications for flower-visiting insects. **(Chapter Six)**

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## Chapter One: General Introduction

*“Bees are the batteries of our orchards, gardens, guard them.” ~ Carol Ann Duffy, *The Bees**

*“Long before the age of man, insects inhabited the earth” ~ Rachel Carson, *Silent Spring**

### 1.1 Floral resources for flower-visiting insects

Bees and other flower-visiting insects (FVI) require flowers as a source of nectar and pollen, which are essential for their energetic and reproductive processes. Nectar is an energy-rich food source providing carbohydrate sugars, as well as water and small quantities of minerals and amino acids (Percival 1961, Baker 1977). Pollen is an important source of protein and amino acids as well as lipids and micronutrients, required for tissue development and gamete production (Haslett 1989, Cane 2016). Different insect taxa require these resources to varying degrees. For example, the large majority of butterfly species do not consume pollen in their adult life stage, meeting their dietary needs through nectar consumption and larval-derived nutrients (Gilbert & Singer 1975). In contrast, hoverfly adults consume both nectar and pollen (Drabble & Drabble 1917), with females requiring larger pollen volumes for egg production (Haslett 1989, Rotheray & Gilbert 2011). Further differences exist between adult insects that consume only what is necessary for their individual needs (butterflies, moths, hoverflies, non-syrphid flies, solitary flower-visiting wasps and beetles) and those that are central-place foragers, which must also provision a nest to rear their larvae (bees and social flower-visiting wasps). For example, bees have relatively large requirements for nectar and pollen as the worker bee (eusocial bees) or the mated female (solitary bees) transports these back to the hive or nest in order to rear their larvae (Raw 1972, Seeley 1995, Müller et al. 2006, Cane & Tepedino 2017), as well as consuming nectar and pollen for their individual energetic and reproductive needs (Seeley 1995, Cane 2016). Intraspecific resource consumption among adult FVI relates directly to activity level, but can also vary according to sex (Boggs 1988, Haslett 1989), body size (Boggs 1988, Müller et al. 2006) and, in the case of eusocial insects, caste (Seeley 1995, Goulson 2003).

Flowers of nectar- and pollen-producing crop, wild and garden plant species are important food sources for flower-visiting insects. In turn, insects visiting flowers are

essential for healthy ecosystem function (Senapathi et al. 2015). An estimated 87.5% of flowering plant species are pollinated by insects and other animals, including crop plants (Ollerton, Winfree & Tarrant 2011). Crop pollination has important direct economic and health consequences for humans, including through food provision. While wind-pollinated plants such as wheat, rice and corn provide an important bulk of carbohydrates consumed in the human diet, animal-pollinated species provide the majority of lipids and micronutrients required for health (Eilers et al. 2011). Animal pollination, the majority of which is mediated by bees and other flower-visiting insects, also increases the yield and/or quality of 75% of crop species globally (Klein et al. 2007), with an estimated global economic value of \$235–577 billion (inflated to 2015 US\$) annually (Potts et al. 2016). In the UK, insect-pollinated crops accounted for approximately 19% of total crop value in 2007; £1057 million (Breeze et al. 2011). Insects also pollinate plants used for fuel (e.g. oil seed rape, *Brassica napus* L.), fibres, medicines and construction (IPBES 2016). However, as discussed by Senapathi et al. (2015), the economic, moral, cultural and biological reasons for conserving insect diversity extend beyond the small proportion of species that contribute to pollination (Kleijn et al. 2015), although these are often the focus of conservation efforts (Senapathi et al. 2015). For example, many FVI including cuckoo and nectar robbing bee species have little or no role in pollination, hence the use of the term ‘flower-visiting insect’, abbreviated to ‘FVI’, throughout this thesis (Senapathi et al. 2015). Insects with limited or no role in pollinating crop plants may pollinate wildflower species that provide alternative (non-crop) forage and nest sites needed to maintain crop pollinator populations (Nicholls & Altieri 2013) as well as beneficial invertebrates that reduce crop pest abundance (Krauss, Gallenberger & Steffan-Dewenter 2011, Ditner et al. 2013, Tschumi et al. 2016, Woodcock et al. 2016). Insect-pollinated non-crop flowering plants also provide food and shelter for other wildlife including invertebrates, birds, bats and rodents, supporting a complex multitude of trophic interactions. As well as the objective intrinsic value of nature (Sandler 2012), from an anthropocentric perspective these interactions are vital for biodiversity and, consequently, for human health and wellbeing (Clark et al. 2014, Sandifer, Sutton-Grier & Ward 2015).

In the UK, widespread land use and management changes since the late 19<sup>th</sup> century have reduced flower-rich habitat in favour of increased agricultural productivity (Robinson & Sutherland 2002, Ollerton et al. 2014) or land conversion to urbanised

areas with a high proportion of impervious surfaces (Swetnam 2007). This includes the loss or degradation of important habitat biotypes such as calcareous grassland, a biodiverse flower-rich habitat that supports many FVI species including several that are rare and declining (Goulson et al. 2006). This important habitat has declined significantly, with a >20% loss in the UK between 1990 and 1998 (Howard et al. 2003) and a study of habitat change in Dorset showing an 83% decline in calcareous grassland area from 1930 to 2000 (Hooftman & Bullock 2012). Widespread loss of floral resources is likely to negatively impact FVI populations. In one study, Carvell et al. (2006) found that forage plants commonly used by bumblebees had declined by 76% in Britain from 1930 to 1998. The distribution of several rare bumblebee species is now highly restricted to coastal areas and rare, fragmented biotypes without intensive agricultural management (Goulson et al. 2006, Fitzpatrick et al. 2007). Bee and flower-visiting wasp extinctions between 1851 and 1994 have been temporally linked to changes in agricultural practice that reduced wildflower availability (Ollerton et al. 2014). Predictably, areas with higher floral richness and abundance tend to have a greater species richness and abundance of flower visiting insects (*e.g.* Holzschuh et al. 2007, Goulson et al. 2006, Cole et al. 2017, Lucas et al. 2017, Baldock et al. 2019). Although only recently recognised as a major contributing factor to insect declines, with earlier research focusing on factors including specimen overcollection, urbanisation, acid rain and particularly pesticide use (Pyle, Bentzien & Opler 1981), floral resource abundance and diversity has been identified as the most important of many interacting direct factors limiting wild bee populations in at least one major review (Roulston & Goodell 2011).

Overall, lack of adequate floral resources is one of many interacting drivers thought to be contributing singly, additively or synergistically to declines in the abundance and distribution of many native insects in the UK and worldwide (Potts et al. 2010, Vanbergen et al. 2013, Goulson et al. 2015), including bumblebee (Carvell et al. 2006, Fitzpatrick et al. 2007), solitary bee (Müller et al. 2006, Scheper et al. 2014), moth (Alison et al. 2017) and butterfly species (Wallisdevries, Van Swaay & Plate 2012, Fox et al. 2015). While declines are difficult to attribute to single factors, limited or sub-optimal nutrition in adult FVI has been linked to reductions in condition (Lebeau, Wesselingh & Van Dyck 2016, Roger et al. 2017), longevity (Cahenzli & Erhardt 2012a, Lebeau, Wesselingh & Van Dyck 2016) and fecundity (Hill & Pierce 1989,

Cahenzli & Erhardt 2012b, Cane 2016). Dietary stress may also cause increased susceptibility to field-realistic levels of pesticides (Tosi et al. 2017) and to pathogens (Foley et al. 2012). Obtaining adequate nutrition may be further challenged by anthropogenic effects including climate warming, since plant-pollinator interactions are likely to be disrupted through spatial and phenological mismatches causing a reduction in floral resource availability for many FVI species (Memmott et al. 2007), and artificial light pollution which can disrupt nutrition intake by nocturnal insects such as nectar-feeding adult moths (Boyes et al. 2021).

Unsurprisingly therefore, many researchers have concluded that improving floral resource availability through habitat protection, enhancement and creation, is crucial for FVI wellbeing and the continuation of healthy populations (*e.g.* Kearns, Inouye & Waser 1998, Klein et al. 2007, Mercx et al. 2012, Scheper et al. 2014, Goulson et al. 2015, Alison et al. 2017, Carvell et al. 2017, Lucas et al. 2017, Balfour et al. 2018, Powney et al. 2019, Steele et al. 2019). This is increasingly both important and difficult, as we experience rapid global anthropogenic change and attempt to meet the food and land requirements of a growing human population sustainably. It is promising that enhancing floral richness in both urban and rural areas to benefit FVI has received increased policy interest in recent years in many parts of the world. In the UK, this is clearly stipulated in the National Pollinator Strategy for England (NPS) coordinated by the Department for Environment, Food and Rural Affairs (Defra; Defra 2014). The first of five ‘Strategy outcomes’ in the NPS Implementation Plan calls for: *“More, bigger, better, joined-up, diverse and high-quality flower-rich habitats (including nesting places and shelter) supporting our pollinators across the country”* (Defra 2018).

Progress towards this outcome is unclear. According to the State of Nature report 2019, UK government spending on biodiversity has declined consistently and by 34% since 2008/9 to £456 million of UK public sector funding in 2017/18, showing a lack of urgently needed resources for conservation including ‘more, bigger, better and more joined up’ flower-rich habitat. More positively, biodiversity spending by NGOs shows the reverse trend, increasing to reach £239 million in 2017/18 (Hayhow et al. 2019). Nevertheless, results from the National Plant Monitoring Scheme (NPMS) indicate that the abundance of indicator plant species (species selected by the NPMS as indicative of good habitat condition) in four broad habitat types surveyed by volunteers across the

UK was lower in 2019 compared to 2015, suggesting that the quality of these habitats and their value to FVI has not improved. Indicator plant abundance declined by 27% overall in arable field margins and 18% in broadleaved woodland and hedges. In bog and wet heath habitat and in lowland grassland, indicator plant abundance in 2019 was 83% and 95% of the 2015 baseline respectively (JNCC 2020). However, the total area of UK agricultural land in all higher-level or targeted agri-environment agreements increased by 20% over the same period, from 2.88 million hectares in 2015 to 3.45 million ha in 2019 (Defra 2020a). Although this figure does not reveal the area under measures specifically aiming to improve resources for pollinators, it is suggestive of an upwards trend in farmland engaged in some level of pro-biodiversity management, which can successfully improve conditions for flowering plants and FVI (Pywell et al. 2012). More specifically, since 2015 the Wild Pollinator and Farm Wildlife package within the Countryside Stewardship Scheme has supported over 13,000 ha of ‘priority field margin options’, which include cultivated flower-rich plots and field margins and sown nectar-rich seed mixes (Steele et al. 2019). Although a positive step this area is minute in the context of the UK’s total utilised agricultural area (UAA), an area made up of “all arable and horticultural crops, uncropped arable land, land used for outdoor pigs, temporary and permanent grassland and common rough grazing” which covers 17.3 million ha or 71% of the UK’s land area (Defra 2020b). It is positive that since 2013, three neonicotinoid pesticides known to be harmful to honeybees and other insects (imidacloprid, clothianidin and thiamethoxam) were severely restricted by the European Commission for use on outdoor flowering crops (Regulation (EU) No 485/2013), followed by a total moratorium in 2018 (EU Commission Implementing Regulation no. 2018/783, no. 2018/784 and no. 2018/785), which will contribute to better habitat for pollinators at risk of exposure to these substances as long as the regulations are upheld by the UK following its official departure from the EU in 2021.

Looking to the future, the Government’s 25-year Plan to Improve the Environment includes a proposed Nature Recovery Network providing 500,000 ha of wildlife habitat (HM Government 2018). Defra has supported insect conservation charity Buglife to create a map of ‘B-lines’, areas of flower-rich habitat located strategically across the UK. This project aims to restore and create 150,000 ha of wildflower habitat for FVI, in collaboration with stakeholders including farmers, local authorities and members of the public (Buglife 2020a). Meanwhile many local authorities have implemented a Local

Pollinator Strategy or Plan, signalling habitat improvements in urban as well as rural areas (Buglife 2020b), which could also contribute to greater connectivity between resources for FVI over time.

In practice, the goal of improving floral resource availability is a complex issue with clear human dimensions as well as ecological considerations. A pressing need to engender societal support for biodiversity enhancement is topical (Amel et al. 2017) and holds significant potential for positive outcomes for FVI (Hall & Martins 2020). A diverse range of stakeholders are relevant to this, including national and local government authorities, charities and non-profit organisations, land-owners, farmers, businesses and members of the public (Defra 2014), with strong partnerships recognised as being crucial in connecting conservation goals to practical outcomes (Hayhow et al. 2019).

## **1.2 Key requirements for floral resource provision**

In an optimum scenario, flower-visiting insects would be able to access sufficient, high-quality, non-toxic nectar- and pollen-rich flowers within their foraging ranges, throughout their flight period, in both urban and rural areas. Five key requirements for optimal floral resource provision for FVI are outlined in brief in this section. These are biology- and ecology- rather than management- or policy-focussed. They are adapted from the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) assessment report on pollinators, pollination and food production (IPBES 2016) and an analysis of EU Common Agricultural Policy options for improving floral resources for wild pollinators (non-managed bees and hoverflies, Cole et al. 2020). While these resources address pollinating insects, measures increasing nectar and pollen availability are highly likely also to benefit non-pollinating flower-visiting insects and less frequent pollinators.

Mass-flowering crops are discussed separately (see section 1.3) since these have mixed benefits for FVI (Westphal, Steffan-Dewenter & Tschamntke 2009) and since the planting of such crops is specifically influenced by agricultural drivers and cannot be reliably considered within conservation frameworks.



### 1.2.1 Flower-rich areas with extended flowering time

Providing non-crop flowers in the early, middle and late stages of FVI activity is necessary in order to provide species with nectar and pollen throughout their flight period, from emergence to reproduction. Resources must be available throughout the season in order to support species emerging at different times of year. For example, in a study of UK cider apple orchards Andrenid bees, the most effective pollinators, did not increase in abundance following addition of flower strips due to the lack of additional early-flowering species overlapping with the bees' flight period (Campbell et al. 2017). Early availability of flowering species is important for bumblebees (Scheper et al. 2015), when increased resource availability can enhance nest-founding, early colony growth and worker production (Westphal, Steffan-Dewenter & Tschamntke 2009). However, a study from February to November in southwest UK found that estimated daily nectar production in farmland habitat was lowest early in the year, in the period from late February to early April. The authors estimate that the sugar produced on 1 km<sup>2</sup> of farmland during March could support a maximum of 19 bumblebee queens, without considering other insects competing for available nectar. Several seasonal gaps in nectar availability were identified, including late summer months (July and particularly August; Timberlake, Vaughan & Memmott 2019).

Several researchers and experts have likewise identified a dearth of floral resources in late summer in the UK (Couvillon, Schürch & Ratnieks 2014, Balfour et al. 2018) and Europe (Cole et al. 2020), while one study also suggests that competition between eusocial bees is strongest at this time of year (Wignall et al. 2020a). Low “per-insect resource availability” in July and August, when there is a high abundance of insects compared to low availability of flowering plant species, is likely to have population-level effects: a greater-than-expected proportion of 40 aculeate wasp, bee and butterfly extinctions in the UK were late summer-flying species, a trend driven by bees (Balfour et al. 2018). There is a significant correlation between later emergence and declines in Irish and British bumblebee species (Goulson et al. 2005, Fitzpatrick et al. 2007), further suggesting that resource availability is inadequate later in the season.

Seasonal forage availability will depend on geographic location, local agricultural practice and other site-specific variables. For example, in a study in Sussex, southeast

UK, honeybee foraging distances were low in September and October in a mosaic landscape consisting of agricultural, suburban and urban land-use types, suggesting high nectar availability in this area (Couvillon, Schürch & Ratnieks 2014). This was likely to be due to the autumnal flowering of ivy, *Hedera* spp., which is abundant in the region (Garbuzov & Ratnieks 2014a). In comparison, in southwest UK, daily estimated nectar supply was low in two of four farm sites during both September and October, and low in September in three of four sites, despite the presence of flowering ivy (Timberlake, Vaughan & Memmott 2019). This may be due to methodological constraints in estimating the quantity of ivy, a vertically-climbing creeper, but reinforces the need for area-specific knowledge in enhancing season-round resource availability.

### 1.2.2 Floral abundance

It is common sense that a greater abundance of floral resources will support a larger number of FVI. Abundance of flowers had a significant positive effect on FVI abundance and species richness in a survey of all major land use types within four UK cities (Baldock et al. 2019). The abundance of preferred nectar source plant species from July to September was the key significant predictor of abundance in *Inachis io* (L.), *Pyronia tihonus* (L.), *Aglaia urticae* (L.), *Pieris brassicae* (L.), *P. rapae* (L.) and *Maniola jurtina* (L.) butterflies in uncropped arable field edges under 10 different management regimes (Feber, Smith & MacDonald 1996). In a survey of various habitats within agricultural land in southeast England, floral abundance was the main predictor of FVI abundance and species richness (Balfour et al. 2015).

Increasing floral abundance has a direct effect on FVI fitness via increased adult resource acquisition, which increases longevity and reproductive output (Haslett 1989, Cane 2016, Lebeau, Wesselingh & Van Dyck 2016). Optimal floral abundance may also have an indirect fitness effect through reducing inter- and intra-specific exploitative competition for nectar and pollen (Thomson 2016). Resource competition between adult FVI is discussed further below (1.3) and is the topic of Chapters Three and Four.

It is important to consider floral diversity as well as abundance, since providing abundant resources with restricted diversity may only benefit a limited suite of FVI species (Wood, Holland & Goulson 2017).

### 1.2.3 Floral diversity

A more diverse floral community is associated with a greater diversity of insect visitors (Potts et al. 2003, Campbell et al. 2012, Nicholls & Altieri 2013, Balfour et al. 2015). In turn, functional diversity in pollinator fauna is necessary for the persistence of plant communities (Fontaine et al. 2005). Diverse FVI assemblages are also beneficial for crop pollination (Hoehn et al. 2008, Garibaldi et al. 2013), partly due to the benefits of functional trait diversity for effective pollination (Woodcock et al. 2019). Therefore, providing a wide diversity of flowering plant species is necessary (Campbell et al. 2012, Goulson et al. 2015, Wood, Holland & Goulson 2017).

One example of the need for floral diversity is morphological variation affecting nectar accessibility to FVI, since this varies substantially between and within insect guilds. For example, larger butterflies with longer proboscides tend to visit flowers with a long corolla, while smaller, short-tongued species visit flowers with a correspondingly short corolla (Corbet 2003). Parasitoid wasps have short mouthparts and exhibit a strong preference for flowers with short corollas (Campbell et al. 2012). Many hoverfly species display a stronger preference for flowers with a short corolla (*e.g. Episyrphus balteatus* (De Geer), although some species show more general visitation to flowers with long and short corollas (*e.g. Eupeodes corollae* (Fabricius), Campbell et al. 2012). This can affect FVI populations: a widespread loss of long-corolla flowers in the UK, predominately Fabaceae, has been linked to declines in longer-tongued bumblebees that preferentially forage on these flowers (Goulson et al. 2005). Including diverse flowering species with a range of corolla lengths is therefore a crucial component of resource enhancement (Cole et al. 2020).

It is also important to optimise nutritional benefit in floral resource provision, although this is an area requiring further research (reviewed in Vaudo et al. 2015). Providing diverse flowers will meet the nutritional needs of a larger number of FVI species than habitats with low floristic diversity. Linked to this, floristic diversity must include flowering plants that support specialist FVI where these are present, such as oligolectic and monolectic solitary bees that collect pollen (and other resources such as specific

floral oils) from few or single flower species respectively (Falk & Lewington 2015), and butterfly species with specialist nectar plant preferences (Tudor et al. 2004).

#### 1.2.4 Pesticide-free flowers

The lethal and sub-lethal effect of insecticides on FVI, particularly bees, has been extensively reviewed (see Nicholls & Altieri 2013, Sánchez-Bayo & Goka 2014, Sánchez-Bayo et al. 2016). Providing both crop and non-crop flowers that are free from insecticides is an important requirement for improved floral resources for bees and other FVI (Potts et al. 2016). While this is a clear priority in agricultural contexts, pesticide use in other spaces is also a concern. For example, insecticides are commonly used in domestic gardens (Grey et al. 2006, Goddard, Dougill & Benton 2013) and have been found in concentrations high enough to harm bees in ‘bee-friendly’ ornamental plants sold to the public (Lentola et al. 2016), demonstrating a need for greater awareness of this issue in the public sphere.

#### 1.2.5 Local and landscape level resources

Adequate resource provision is needed at both local and landscape scales. Providing local resources is particularly important for less mobile species including solitary bees, the majority of which have average foraging ranges of <500 m (Zurbuchen et al. 2010a,b). At the landscape level, an adequate proportion of flower-rich habitat and connectivity between patches can mitigate negative effects of resource-scarce areas such as highly urbanised or intensively farmed agricultural land on wild insect communities (Samnegård, Persson & Smith 2011, Senapathi et al. 2017, Cole et al. 2020).

### 1.3 Mass-flowering crops

Mass-flowering crops such as field bean (*Vicia faba* L.), sunflower (*Helianthus annuus* L.) and oilseed rape (*Brassica napus* L.), provide large, dense areas of uniform flowers where and when they are in bloom. In the UK, the Utilised Agricultural Area (UAA), not including woodland, covered 17.3 million ha or 71% of land in 2020 (Defra 2020b). Of the total UAA, 2.4% was represented by oilseed crops (oilseed rape, linseed (*Linum*

*usitutum L.*) and borage (*Borago officinalis L.*)), and 1.0% by field beans. These crops provide a dense mass of flowers over a relatively short period. Other flowering crops such as potatoes (which produce pollen but not nectar), peas, legumes grown for stockfeeding and horticultural crops including orchard fruit, soft fruit, wine grapes and outdoor flowers make up a smaller area of the total UAA (DEFRA, 2020X) although within this area the provision of flowers is also likely to be high. In another example, the production of sunflowers for seeds in France covered 1.9% of the UAA (28.6 million ha or 52% of France's total land area) in 2018, or 1.0% of the total land area, while oilseed rape production covered 5.64% of the UAA, or 3.0% of the total land area (FAOSTAT 2020).

Despite their large area, mass-flowering crops have a complex role in floral resource provision for FVI in the UK and elsewhere. Crops bloom synchronously over short periods, providing a transient pulse of nectar, pollen or both for the duration or a proportion of a species' foraging period (Westphal, Steffan-Dewenter & Tscharnke 2009, Le Féon et al. 2010). For FVI emerging later than or completing their foraging prior to bloom, mass-flowering crops will evidently not provide a resource. The large-scale use of pesticides and lack of diversity that characterises monocultural cropping may also compromise any nutritional benefit provided by mass-flowering crops (Rundlöf et al. 2015), although this is unclear and often controversial (Goulson et al. 2015). Overall, several studies have concluded that although flowering crops can provide an additional food supply in agricultural landscapes, adequate availability of wild flowering plants and diverse semi-natural habitat for nesting is necessary for sustaining abundant and diverse FVI assemblages (Steffan-Dewenter et al. 2002, Le Féon et al. 2010, Holzschuh et al. 2013, Nicholls & Altieri 2013, Persson & Smith 2013, Requier et al. 2015).

#### **1.4 Per-insect resource availability: exploitative competition between flower-visiting insects**

In the UK, flower-visiting insects do not normally compete directly for nectar and pollen or other resources in interference competition. One rare example is seen in the European wool carder bee, *Anthidium manicatum* (L.). Females of this solitary bee have

an affinity to the flowering plant lamb's ear, *Stachys byzantina* K. Koch, as they line their nests with hairs collected from the downy leaves. Males aggressively defend patches of flowering lamb's ear, crushing other males or even other bees with their abdominal spines to optimise mating opportunities with females (Falk & Lewington 2015). Some hoverflies, such as the drone fly *Eristalis tenax* (L.), exhibit territorial behaviour, aggressively defending a home range that offers shelter, food, mating opportunities and other benefits (Wellington & Fitzpatrick, 1981). However, most bees and other flower visitors do not compete directly for nectar and pollen from flowers, but undergo indirect competition through resource depletion, termed resource or exploitative competition. This is the topic of Chapters Three and Four.

Pollen and nectar are produced in minute quantities by flowers (*e.g.* Fowler, Rotheray & Goulson 2016), and resources are often shared between a large range of foraging taxa (*e.g.* Wignall et al. 2020b). This results in intra- and inter-specific exploitative competition for these resources, which is likely to shape flower-visiting communities through adaptive partitioning of insect foraging behaviour. Both evolutionary adaptations and flexible shifts in foraging behaviour act to reduce foraging overlap in response to competitive resource depletion, allowing individuals to collect the resources they require. This occurs temporally (Wilms & Wiechers 1997, Walther-Hellwig et al. 2006), spatially (Walther-Hellwig et al. 2006, Lindström et al. 2016, Thomson 2016) and through morphological adaptations such as tongue length (Heinrich 1976), mouthpart morphology (Branquart & Hemptinne 2000) and body size (Torné-Noguera et al. 2016, Henry & Rodet 2018). Dietary specialisation (Raw 1974, Haslett 1989, Goulson, Lye & Darvill 2008) and differences in spatial resource use (Westphal, Steffan-Dewenter & Tscharncke 2006) can also facilitate coexistence.

Adaptive partitioning can mitigate the negative effects of exploitative competition, however, this may not be possible where floral resources are limited, or specifically, when the ratio of available floral resources to insects ("per-insect resource availability", Balfour et al. 2018) is low. In this case, dominant competitors can cause other foragers to move to alternative flowers (Thomson 2016, Wignall et al. 2020a) that may be less preferred or further away, potentially leading to fitness costs in reduced overall resource acquisition and reproductive output (Zurbuchen et al. 2010a, Hudewenz & Klein 2015, Thomson 2016). Several studies have shown that managed eusocial bees, particularly

honeybees, are competitively dominant in wild pollinator communities (reviewed in Mallinger, Gaines-Day & Gratton 2017). In contrast, certain insects may be more vulnerable to competitive resource depletion, for example species with smaller foraging ranges, notably solitary bees (*e.g.* Zurbuchen et al. 2010b, Hudewenz & Klein 2015) and specialist species (Biesmeijer et al. 2006). There are limited data for non-bee insect species (but see Lindström et al. 2016), suggesting an important knowledge gap; this is addressed in Chapter Four.

The biology of honeybees is particularly relevant when considering competitive interactions between FVI. *Apis mellifera* L. have large colonies of between 20,000 - 60,000 workers, with correspondingly large requirements for nectar and pollen: a typical honeybee colony requires 120kg nectar and 20kg pollen per year (Seeley 1995). Honeybees are floral generalists and worker bees forage over very distances; an individual forager can fly up to c. 10-12 km from the hive (Seeley 1995) while in Sussex, southeast England, worker bees covered an average radius of over 15 km<sup>2</sup> during July and August (Couvillon, Schürch & Ratnieks 2014). In addition, honeybees actively recruit nestmates to profitable patches of flowers via the waggle dance, meaning they can optimise foraging efficiency at the colony scale (Seeley 1995). As intensive, efficient and generalist resource users over large areas, there is great potential for honeybees to increase competition for floral resources where they are present. In the UK, honeybee colonies registered with BeeBase, the Animal and Plant Health Agency's (APHA) National Bee Unit website, increased from 198,711 in 2015 to 247,461 in 2017 (BeeBase data in Steele et al. 2019); however, since registration is on a voluntary basis only, this may be an underestimate. Colony numbers continue to be affected by high recent winter loss rates in England, Northern Ireland, Scotland and Wales, recorded at between 23-30% over winter 2017/2018 by surveyed beekeepers (Gray et al. 2019). Nevertheless, densities of honeybees are likely to be artificially high in many areas of the UK and elsewhere, including urban areas which have seen a growing trend for beekeeping in recent years (Alton & Ratnieks 2013, Lorenz & Stark 2015), with implications for both inter- and intraspecific floral resource competition.

Overall, it is clear that landscape management for FVI, including floral resource provision and honeybee stocking management, should consider competitive dynamics between species. This is particularly relevant in resource-poor or homogeneous

landscapes such as in built-up urban centres (Hennig & Ghazoul 2011, Geslin et al. 2013, Mattesson, Grace & Minor 2013), in rural areas under intensive agriculture (Le Féon et al. 2010) and at certain times of the year when per-insect resource availability is low (Couvillon et al. 2014, Couvillon, Schürch & Ratnieks 2014, Balfour et al. 2018).

## **1.5 Aims and objectives**

In this thesis I hope to contribute positively to the objective of improving floral resource availability for FVI through complementary ecological and social research. I address key ecological factors affecting foraging conditions for bees and other insects (Chapters Two, Three and Four), primarily through investigations of the dynamics of inter-specific floral resource competition. I then address the human dimensions of enhancing resource availability through analyses of pro-environmental attitudes among members of the public towards i) pollinators and planting for them (Chapter Five) and ii) common insect-attractive wild flowering plants (Chapter Six).



## **Chapter Two: Thug life: bramble (*Rubus fruticosus* L. agg.) is a valuable foraging resource for honeybees and diverse diurnal flower-visiting insects**

*“He told them tales of bees and flowers, the ways of trees, and the strange creatures of the Forest, about the evil things and good things, things friendly and things unfriendly, cruel things and kind things, and secrets hidden under brambles. As they listened, they began to understand the lives of the Forest, apart from themselves.”*

~ J.R.R. Tolkien, *Lord of the Rings*

*“Well I’m actually a PhD student studying the importance of bramble for pollinators and I really think you should leave it alone.”*

~ Georgia Hennessy, *The Adventures of Bramble-Lass*

### **Authors and author contribution statement**

Veronica R. Wignall, Natalie A. Arscott, Hayley E. Nudd, Annabel Squire, Thomas O. Green, Harry Dilks and Francis L.W. Ratnieks

VW and FLWR conceived the ideas; VW led the data collection, data analysis and writing of the manuscript; FLWR, NAA, HEN, AS, TOG and HD contributed to data collection

### **2.1 Abstract**

Bramble (*Rubus fruticosus* L. agg.) is a common summer-flowering plant native to the UK. Multiple complementary approaches were used to evaluate its ecological value to the honeybee (*Apis mellifera*), bumblebees (*Bombus* spp.) and other flower-visiting insects in Sussex, England. Regional surveys of insect groups at seven sites across two years showed that foraging activity on bramble was dominated by honeybees (60.2%; n = 28 surveys) and bumblebees (17.4%), compared to non-*Apis/Bombus* bees (2.8%), hoverflies (Syrphidae, 7.9%), non-syrphid Diptera (0.6%), butterflies (6.4%), wasps (0.4%) and beetles (4.4%). Foraging insect community structure was highly similar spatially but varied significantly between survey months (June and July). In detailed local surveys at one rural and one urban location, there was a diverse range of insect taxa foraging on the bramble flowers, including species of conservation concern

(*Bombus humilis*, *Coenonympha pamphilus* and *Limenitis camilla*). Pollen trapping at 12 honeybee hives in four locations showed that an average of 31% of pollen pellets collected by honeybees from late May to early August were bramble, with a peak of 66-86% per location. Bramble was present in 54 out of 60 200 x 200 m randomly selected grid squares surveyed over a large area across Sussex. Plants were recorded in multiple habitat types in both urban and rural areas. Bramble is sometimes considered an undesirable plant or a “thug” that outcompetes other wild flowers, however, these findings confirm that it is highly valuable for flower-visiting insects. We conclude that wherever conflicts of interest and management strategies allow, bramble should be maintained and promoted for wildlife and insect conservation.

## 2.2 Introduction

Bramble (*Rubus fruticosus* L. agg.; Rosaceae), also known as blackberry, is an aggregate group of over 300 closely related microspecies (Clapham, Tutin & Moore 1987, Rose 1981) that are widespread and common throughout the UK (Taylor 2005, BSBI 2019) and are native to this region and much of Europe (Royal Botanic Gardens Kew 2019). Bramble is reproductively versatile, propagating through various methods including seed dispersal, facultative apomixis and runners (Gyan & Woodell 1987a). Bramble has anti-herbivore thorns and prickles (Hanley et al. 2007), can form a dense thicket and can grow in multiple habitat types (Streeter et al. 2009). These factors contribute to its success both where native (e.g. Europe, Taylor 2005) and introduced, such as in New Zealand and Australia where naturalised bramble species are weeds of national significance subject to major control efforts (Australian Government Department of the Environment and Heritage et al. 2003).

In the UK bramble has cultural value due to the long tradition of collecting the blackberry fruits produced by the plants in early autumn (Mabey 1996). However, it is frequently considered a nuisance in both public and private land. Bramble plants are nitrophilic (Walter et al. 2016), and a recent report by the UK-based wild plant conservation charity Plantlife described the aggregate group as one of twelve plant “thugs” that thrive in nitrogen-rich road verges and outcompete other native wildflowers (Plantlife UK 2018). *Rubus fruticosus* plants are also considered problematic competitive weeds in regenerative forestry, where they can limit growth of tree saplings

(Willoughby et al. 2009). The thorny plants are often removed from nature reserves, public parks and other green spaces by local authorities (*e.g.* Phillips 2015, Bristol City Council 2019). Advice for limiting bramble growth in private gardens is also widely available from organisations such as the Royal Horticultural Society (RHS) in both printed and online publications (RHS 2019). In contrast, pro-environmental organisations such as the Royal Society for the Protection of Birds (RSPB) and Championing the Farmed Environment (CFE) encourage the creation or management of “scrub”, habitat consisting of bramble and other woody shrubs, in recognition of its value to wildlife (CFE 2019, RSPB 2019). Symptomatic perhaps of these differing attitudes, the UK government’s Department for Environment, Food and Rural Affairs (Defra) offers payment both to promote and control/clear scrub in different contexts in its Countryside Stewardship Higher Tier manual (Defra 2020c). Where scrub is encouraged, management is needed to prevent further natural succession into woodland, to promote structural and species diversity, and to prevent undesirable encroachment, for example onto species-rich grassland (Natural England 2011, CFE 2019, Defra 2020c).

Bramble can benefit a wide variety of wildlife. For example, small mammals, birds and invertebrates use bramble scrub for shelter and nesting (Danks 1971, Morgan 1982, Hurrell & McIntosh 1984, Flowerdew & Ellwood 2001, Bence, Stander & Griffiths 2003, Falk & Lewington 2015) or roosting (Dennis 2004), while frugivorous animals eat the blackberries when they ripen in late summer and autumn (Watts 1968, Sorensen 1981). Many phytophagous insect and mite species have been observed feeding on *R. fruticosus* plant material (Taylor 2005) with 149 herbivore invertebrate species listed in the Biological Records Centre *Database of Insects and their Food Plants* (2020).

Bramble also provides important forage for bees and other flower-visiting insects. During bloom, plants have many pink and white flowers which produce large amounts of both pollen and nectar (Gyan & Woodell 1987b, Fowler, Rotheray & Goulson 2016). A recent study found that bramble flowers have the fifth highest nectar sugar content per flower per day out of 175 species for which nectar data were available (Baude et al. 2016). The bowl-shaped flower is typical of Rosaceae, with open petals and no corolla tube (Corbet 2000), so that nectar and pollen are easily accessible to insects with either long or short tongues. Indeed, bramble flowers are visited by many insect groups

(Balfour et al. 2015, Baldock et al. 2019) including bees (Goulson et al. 2005, Falk & Lewington 2015), butterflies (Sparks & Parish 1995, Corbet 2000, Tudor et al. 2004), hoverflies (Drabble & Drabble 1927, Lucas et al. 2018a,b) and non-syrphid Diptera (Drabble & Drabble 1927). *Rubus fruticosus* has a long flowering period, which typically extends from May to September in the UK (Streeter et al. 2009, Baude et al. 2016) although flowers can be found into November (VW & FR, personal observations). Bloom typically peaks between mid-June and mid-July (Gyan & Woodell 1987a, Baude et al. 2016). Therefore, it is probable that bramble is a valuable source of both nectar and pollen for insects over much of the summer, extending into late summer months when foraging conditions are known to be challenging for honeybees and other flower-visitors due to low per-insect nectar availability (Couvillon Schürch & Ratnieks 2014, Balfour et al. 2018). However, a quantitative field study of its ecological role for pollen- and nectar-feeding insects has not previously been carried out, to our knowledge. Since many insects in the UK are undergoing widespread declines that are often linked, among other interacting factors, to the loss of flowers on a landscape scale (Carvell et al. 2006, Fox et al. 2015, Powney et al. 2019), it is important to improve our knowledge of native floral species that provide nectar and pollen for pollinating insects in order to inform conservation (Lander 2020).

The ecological value of bramble to flower-visiting insects is enhanced due to its wide geographic distribution throughout the UK in both rural and urban environments, since the different microspecies thrive in multiple habitats (Taylor 2005, BSBI 2019). In a recent study of plant-pollinator interactions in four UK cities, *R. fruticosus* was among the 20 most commonly found plants in all four, being recorded in 44 to 78% of land use types in which plant-pollinator interactions were observed (Baldock et al. 2019). In rural areas, bramble is commonly found in hedgerows, agricultural field margins and woodland edges. It can quickly establish in uncultivated fields.

In this study we combined multiple methods to provide a multi-dimensional picture of the value of *R. fruticosus* to summer-flying diurnal flower-visiting insects in our study area in Sussex, southeast UK. First, we determined the diversity and community composition of insects visiting bramble flowers by making both local, species-level surveys and regional surveys covering a wide area over Sussex in which insects were identified to group level (honeybees (*Apis mellifera* L.), bumblebees (*Bombus* spp.),

other (non-*Apis/Bombus*) bees, hoverflies, non-syrphid Diptera, butterflies and moths (Lepidoptera), beetles and wasps). Second, we assessed local *R. fruticosus* abundance within the co-flowering plant community, and its distribution and habitat type at a fine spatial scale relevant to insect foraging ranges. Third, we analysed pollen from pollen traps fitted to honeybee hives in four locations across Sussex to quantify the importance of bramble pollen for honeybees, a generalist flower visitor which has a long foraging range (Couvillon, Schürch & Ratnieks 2014) and can serve as an indicator for surveying foraging conditions for flower-visiting insects more broadly (Balfour et al. 2015).

## 2.3 Materials and Methods

Using a variety of survey techniques, we gathered field data in Sussex, southeast England, in 2018 and 2019.

### 2.3.1 Insect surveys

In each insect survey, we recorded diurnal insects foraging on bramble flowers to collect nectar and/or pollen. Data were collected from 1100 to 1600 (British Summer Time) on days that were suitable for insect activity ( $>18^{\circ}\text{C}$ , low wind, mostly sunny, no rain). We chose sites where flowering bramble was abundant. On each survey date, we recorded insects foraging on many bramble plants in bloom within the overall site area to observe sufficient insects and to prevent pseudoreplication through intensively surveying only one patch of flowers. Beetles  $<10$  mm in length were not recorded since they were difficult to identify or (smaller beetles) to see, therefore making counts inaccurate. These were mainly small pollen-feeding beetles (approx. 3 mm in length) but were not numerous. Ants were also seen but were not recorded (Baldock et al. 2015). *Bombus terrestris* (L.) and the *B. lucorum* complex comprising the cryptic species *B. lucorum* (L.), *B. magnus* Vogt and *B. cryptarum* (Fabricius) (McKendrick et al. 2017), could not be reliably separated in the field, so were grouped and recorded as *Bombus terrestris/lucorum* agg. (Fussell & Corbet 1992). It was likely that there was a difference in detectability favouring larger, slow-flying over smaller, more rapid-moving insects. However, any that were easier to detect were also quickly recorded, allowing time for smaller and/or more quick-moving insects to be tracked during their

foraging activity until they could be identified or caught. Effort was made at all times to ensure all foraging insects were recorded, pro-actively countering any potential recording bias that could otherwise have been introduced by differences in detectability.

#### *2.3.1.1 Local, detailed insect surveys (400 insects)*

Detailed surveys (approximately 400 insects per survey) were made in one urban and one rural location in and near Brighton city, southeast England, UK. The urban site was an area of disused land near the Brighton Marina on the periphery of Brighton city, next to Marine Gate flats (50°815178' N, -0°102075' W). The rural site was north of Brighton, in a meadow near Falmer village (50°870493' N, -0°084789' W), adjacent to the Sussex University campus and the South Downs. Each site was chosen due to the substantial amounts of bramble present in hedges and standalone patches. We conducted three surveys at each location between early June and late July 2018. Surveys in both locations were made over one or two days in the early, middle and late stages of the main bramble bloom period (rural: 6 June, 21 June and 5 & 6 July; urban: 13 & 15 June, 26 & 27 June and 12 & 13 July). Each rural survey was conducted approximately one week earlier than the corresponding urban survey since bramble began to flower slightly earlier at the rural site. This time difference may have introduced a small phenological bias, but since the level of bramble bloom was not noticeably different between sites in any of the three corresponding surveys any such bias was considered to be negligible.

Surveys consisted of between one and four transect walks; these were initiated between 11am-12pm and discontinued when 400 insects had been counted. Counts were made by walking slowly along the patches of bramble in a standardised route and recording all foraging insects present; transect walks were repeated from the starting point once the end of the route had been reached, ensuring at least 60-minute intervals between the start of one walk and the next. Individual foragers are unlikely to remain in one patch for more than this length of time. Therefore, if individuals revisited the patches after 60 minutes and were counted on more than one transect walk, this was considered to be an independent foraging decision, showing a genuine preference rather than an individual simply persisting in the same patch in a single visit (following Garbuzov & Ratnieks 2014b). To confirm that this gave an accurate representation of the foraging community,

we compared the proportional abundances of each insect group when all transect walks were included to when only the first walk per survey was included. These were very similar (Appendix A.1) therefore entire counts including all walks per survey are presented in the Results; summary statistics including only the first transect walk per survey are in Appendix A.1-2. Data were pooled across surveys for each site to show the overall range of insects visiting bramble flowers over the main flowering season. Surveys were conducted primarily by VW and HEN, with help from NAA, AS and TOG. All researchers were extensively trained by VW prior to the study to ensure the vast majority of common bramble-visiting insects could be identified on sight. All researchers including those newer to insect identification were encouraged to catch insects they could not ID where necessary, meaning any differences in experience were accounted for as far as possible.

Insects were identified to species where possible. Field guides for bees, hoverflies and butterflies were used to aid identification (bees: Falk & Lewington 2015, butterflies: Styles & Lewington 2001, hoverflies: Ball & Morris 2015). Any insects that could not be identified in the field were caught and identified in the laboratory using a microscope and taxonomic keys (Falk & Lewington 2015, Ball & Morris 2015). Solitary bees in the genus *Lasioglossum* were relatively common. However, it was often not possible to reliably identify foragers by eye or with a hand lens due to small size and/or microscopic distinguishing features. Therefore, we caught a representative sample (2-3 individuals) on each survey date in order to determine which species were present while minimising destructive sampling. We recorded whether honeybees were collecting pollen if this was visible in their corbiculae. This would have under-estimated the proportion of pollen foragers as some bees may have only just commenced foraging at the time of observation.

We calculated a Shannon-Wiener ( $H'$ ) diversity index for foraging FVI in the early, middle and late stages of bramble bloom at the rural and urban site using the standard equation:

$$H' = - \sum_{i=1}^R p_i \ln p_i$$

Where  $p$  ( $n/N$ ) is the proportion of the overall sample ( $N$ ) represented by genus  $i$  ( $n$ ). In both locations, genus-level foraging insect diversity was calculated separately for each survey period, including data from all transect walks. Pielou's measure of evenness ( $J$ ) was then calculated by dividing the Shannon-Wiener  $H$  index by the natural logarithm of genus richness ( $J=H'/\ln S$ ). Diversity indices were separately calculated for the first transect walk per survey (Appendix A.2).

### 2.3.1.2 Regional, group level insect surveys (100 insects)

In order to describe the community of insects visiting bramble flowers over a wider geographic area, smaller, lower-resolution surveys each of 100 insects were made by FLWR in three paired, urban and rural, sites in or near three small towns in East Sussex: Hailsham (urban: 50°86462' N, 0.25578' W, rural: 50°8672' N, 0°33744' W); Lewes (urban: 50°87243' N, 0°01754' W; rural: 50°88469 N, 0°03299 W); Uckfield (urban: 50°9691' N, 0°09899' W; rural: 50°94925' N, 0°12769' W). A further rural location was the outer border of Pevensey Levels National Nature Reserve (50°83343' N, 0°344954' W). Surveys were carried out in the same way as for the 400-insect surveys, by recording all insects observed foraging on bramble flowers along standardised walking routes, in 2018 and 2019. In each year, one survey was completed per site in June and another in July in order to cover the bloom period ( $n = 28$  surveys in total; see Appendix A.3 for survey dates).

In each survey 100 insects were recorded to the following seven groups: honeybees (*Apis mellifera* L.), bumblebees (*Bombus* spp.), other (non-*Apis/Bombus*) bees, hoverflies, non-syrphid Diptera, butterflies and moths (Lepidoptera), beetles and wasps, following Garbuzov & Ratnieks (2014a). No moths were seen in any surveys, therefore Lepidoptera are described as butterflies hereafter.

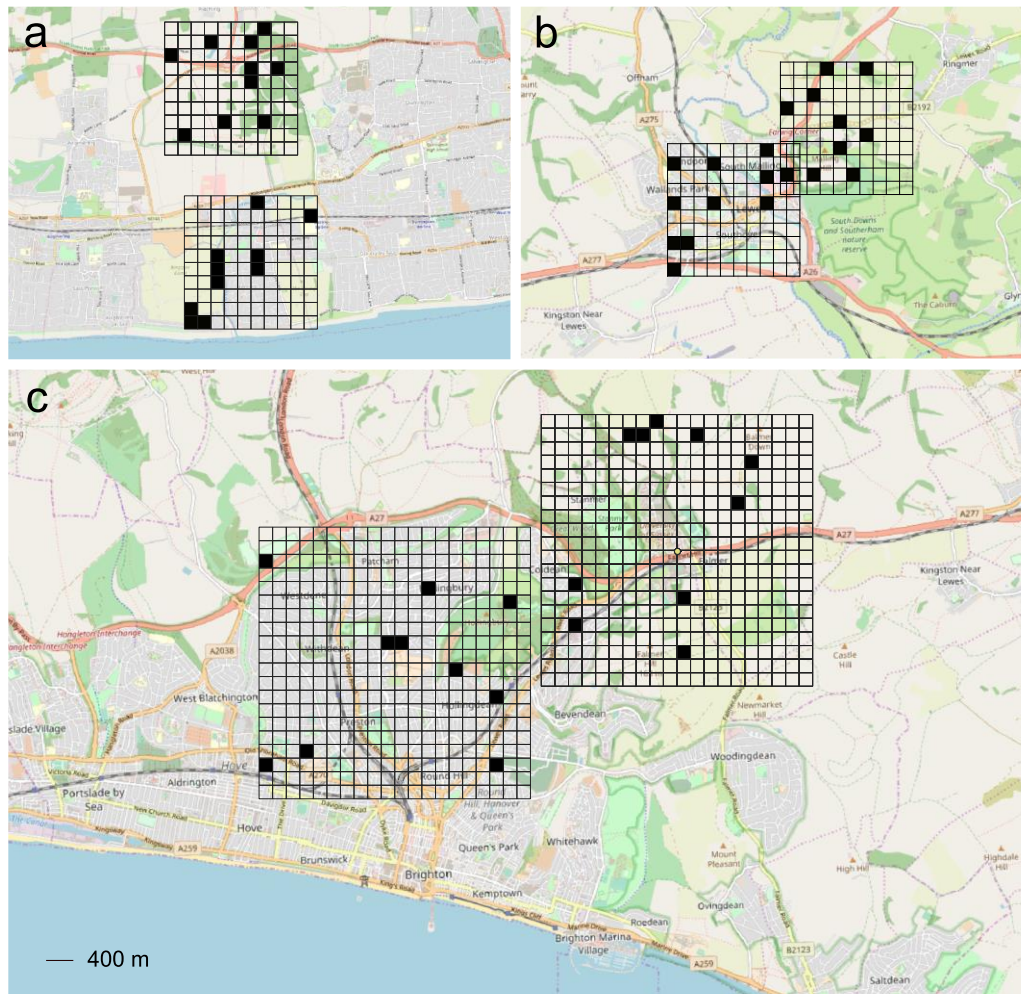
### 2.3.2 Local *R. fruticosus* abundance and habitat

We recorded the presence or absence of bramble plants on a fine spatial scale in order to determine its local availability for foraging insects, as well as the habitat types in which



it was found (following Garbuzov & Ratnieks 2014a). Surveys were made by VW and HD between July and September 2018 in ten randomly-generated 200 x 200 m squares within each of six grids in matched urban and rural locations across Sussex: Brighton, Ferring and Lewes. In the smaller towns of Ferring and Lewes, the grids were 2 x 2 km, each with 100 200 x 200 m squares (Fig. 2.1 *a, b*). In Brighton city, each 4 x 4 km area comprised 400 200 x 200 m squares (Fig. 2.1 *c*). Urban and rural grids were deliberately placed to include the largest possible proportion of the respective land use type using QGIS (version 3.0.3-Girona), although there was some unavoidable overlap between land use types within grid categories, with some peripheral urban areas in the ‘rural’ grid and vice versa (Fig. 2.1; Appendix A.4). Ten squares were randomly selected within each grid. Three squares that were dangerous to access due to roads or other hazards, or were entirely private property, were not included and new squares were randomly generated.

We accessed each 200 x 200 m square on foot and surveyed the vegetation. Presence or absence of bramble plants within each grid square was noted, along with the habitat type of the overall square and of the precise habitat in which bramble was growing, if present. Differences between observers was very unlikely due to the simple nature of this type of data collection.



**Figure 2.1.** Surveys of bramble plants in (a) Ferring, (b) Lewes and (c) Brighton areas, southeast England, UK, July to September 2018. In each location grids were placed to incorporate as much of the urban area and adjacent rural area as possible. In Ferring and Lewes, grids were 2 x 2 km each with 100 200 x 200 m squares. In Brighton, grids were 4 x 4 km each with 400 200 x 200 m squares. The 10 randomly selected squares that were surveyed for the presence or absence of bramble are in black

### 2.3.3 Local *R. fruticosus* flowering, wildflower community, and presence of raspberry *Rubus idaeus*

We recorded the (i) abundance, (ii) bloom intensity and (iii) availability of flowering bramble in a 2 km radius area surrounding our laboratory from 15 May to 30 July 2018. This was in order to determine when bramble began flowering and was at its peak, and changes in flower availability. These variables were likely to be similar over the wider study area, which extended c. 50 km east to west with similar climate and elevation

throughout the region. As well as *R. fruticosus*, we recorded other wild-growing flowering forb, shrub and tree species as an indicator of the relative importance of flowering bramble for pollinators within the local flowering plant community. All floral surveys were carried out by VW and HEN who worked together to finalise the methodology and carried out initial surveys together to ensure consistency in how the surveys were conducted.

We carried out weekly or bi-weekly 2 km fixed transect walks in northeast, northwest and southwest directions from the Laboratory of Apiculture and Social Insects (n = 26 transects in total). These included varied floral habitat types including road verge, agricultural land (fields, field margins, footpaths and bridleways) and a country park.

(i) To measure abundance, we recorded the presence of any flowering forb, shrub (including *R. fruticosus*) and tree species within 2 m (forbs and shrubs) and 5 m (trees) on either side of the transect using the DAFOR scale (1-5: 1 = Rare, 2 = Occasional, 3 = Frequent, 4 = Abundant, 5 = extremely abundant or Dominant; Kent & Coker 1992). An overall value per transect was obtained using running totals which were then converted into values on the 1-5 scale.

(ii) To record bloom intensity, we used a modified DAFOR scale to record proportional bloom as an estimated percentage of the maximum possible bloom for each species (1-5: 1 = Rare, 0-20%; 2 = Occasional, 20-40%; 3 = Frequent, 40-60%; 4 = Abundant, 60-80%; 5 = extremely abundant or Dominant, 80-100%). For species with flowering inflorescences, *e.g.* dandelion or clover species, the proportional bloom related to the density of inflorescences rather than the bloom per flowering head. An overall value per transect was obtained in the same way as before.

(iii) We then combined per-transect abundance and bloom intensity for each species, multiplying these values to give an *overall availability* score (1-25), to give a single metric representing the abundance of bloom per flowering species in the local area.

When measuring floral resource availability for pollinating insects, it is common practice to standardise floral units (flowers, capituli or umbels; Baldock et al. 2015) across species, for example by petal area (Balfour et al. 2015). Our proportional

measure of bloom intensity is not standardised across species. However, even with standardisation it is difficult to measure floral rewards accurately as nectar and pollen amounts vary greatly between and within both species and floral units due to (*e.g.*) time of day (Fowler, Rotheray & Goulson 2016). Our measure therefore gives a useful estimate of the availability of floral resources for pollinators for the purpose of this study.

During the transects we separately recorded any flowering wild *Rubus idaeus* L. (raspberry), which is similar to *R. fruticosus* but has weaker prickles and leaves that are white beneath (Streeter et al. 2009). This was in order to reduce uncertainty in our analysis of pollen pellets collected by honeybees (see Methods) since *R. idaeus* pollen is highly similar to *R. fruticosus* in both pellet colour and the microscopic features of individual grains (Sawyer 2006).

#### 2.3.4 Honeybee pollen trapping and analysis

We measured the proportion of bramble pollen collected by honeybee colonies in the study area from May to August 2018 in order to estimate the importance of *R. fruticosus* as a pollen resource for honeybees, a generalist flower visitor with a large foraging range. Using commercially available pollen traps, we collected pollen once weekly or bi-weekly from three honeybee hives in each of four locations in Sussex. Nine hives were in rural locations in East Sussex, with three at Falmer village (50°8644' N, -0°07824' W), three at Ashcombe Farm (50°87174' N, -0°03332' W) and three at Magham Down village (50°881' N, 0°285' W). Three urban hives were in Brighton city, East Sussex (50°840' N, -0°142' W). We collected pollen samples from each location on an *ad hoc* basis during May, since we expected bramble to start blooming at this time. Then, when we began to find bramble pellets in the samples, we officially began the sampling period (on 30 May). In the three rural locations we collected samples from 30 May to 3 August which covered the majority of the bramble bloom. At the urban location we collected samples from 30 May to 6 July, when sampling had to be stopped due to logistical difficulties. Hives were of different types (Commercial, Langstroth) but this was not expected to have any effect on pollen collection. Hives were in 2 or 3 hive bodies, with medium to large worker population plus queen and brood, and were

managed for swarm prevention. None was fed with supplementary sugar syrup or pollen at any stage during the pollen trapping period.

Pollen was collected once a week on days with good foraging weather, using pollen traps with a removable metal entrance grid of 5 mm diameter circular holes through which worker bees leave and enter the hive. The grid dislodges pollen pellets from the corbiculae which fall into a collecting tray beneath (Dimou, Thrasyvoulou & Tsirakoglou 2006). The grids were in place from 0900 to 1800 in three locations, or from 0800 to 2000 in one location (Magham Down village), *i.e.*, the majority of the foraging day, to account for any possible daytime variation in plants' pollen production. This small difference in sampling duration was due to researcher working hours, and was not expected to bias the results since both sampling periods include most honeybee foraging activity even in summer months. Pollen from each hive was then stored at -20°C until it was analysed.

To determine the proportion of bramble pollen in each sample we identified the pollen in a two-stage process using pellet colour and then microscopic analysis. Honeybees are flower constant (Darwin 1876) meaning that each pollen pellet is almost always from a single plant species and has a uniform colour depending on which plant species the bee was foraging (Free 1963). (Occasionally, a pollen pellet from *A. mellifera* has two colours indicating that the bee switched from one flower species to another during a foraging trip. We observed very few such pellets, <0.01% overall, and did not analyse any two-coloured pellets. Pellets consisting entirely or predominately of bramble pollen are grey which is a rare pollen colour and helped in identification. To quantify the proportion of bramble pollen in a sample we first took 2.5g from the frozen sample of pellets by shaking this into a new vial, ensuring that the 2.5g portion came from throughout the full sample and so was representative. We then sorted these pellets into colours and counted each. This was used to calculate the proportion of grey pellets. After colour sorting, VW used a compound microscope to check grey pellets in each sample for false positives (*i.e.* grey pellets that were not bramble). To determine the proportion of grey pellets that were *R. fruticosus*, we took 10 from each sorted sample and identified them at 40x magnification. Where there were <10 grey pellets in a sample, all were analysed. Pollen grains from grey pellets that were Rosaceae-type, between 25-30 µm diameter, and with a smooth non-striate, non-granular surface were

defined as *R. fruticosus* (Sawyer 2006). Following analysis of ten grey pellets, if 5 or more of these were not bramble, we tested ten more grey pellets so that the mean proportion was based on a larger sample. We then estimated the proportion of bramble in each sample, after correcting for false positives (see Appendix A.5 for details of correction procedure).

In our observations of honeybees collecting pollen from bramble flowers, pollen loads in the corbiculae were always grey. Since honeybees are flower constant (Darwin 1876; Free 1963) and we observed >240 honeybees collecting pollen from bramble flowers in this study (Table 2.1), it was assumed that there were no false negatives (*i.e.* non-grey bramble pellets) in our samples.

*Rubus idaeus* (raspberry) pollen grains are very similar to those of *R. fruticosus* (Sawyer 2006). However, in our regular transect walks during the study period (see Methods), which were representative of the countryside surrounding the hives in the three rural locations, we found flowering *R. idaeus* interspersed along one hedgerow (approx. 2 m high x 8 m long) in just two transects compared to *R. fruticosus* which was abundant in every transect ( $n = 23$  transects, see Results), suggesting that *R. idaeus* was extremely uncommon in comparison: false positives from *R. idaeus* were therefore assumed to be close to 0%.

### 2.3.5 Statistical analysis

Each low-resolution survey of 100 insects was treated as a ‘community’ for analysis, following Garbuzov & Ratnieks (2014a). We compared group-level community composition between sites using the Bray-Curtis dissimilarity index. This abundance-based index is chiefly used in ecology to compare species composition (Chao et al. 2006), and can be used to compare ecological communities at lower resolution (*e.g.* Pitman et al. 2008). Bray-Curtis indices were calculated using the function `vegdist` in the R package *vegan* (version 2.5-6, Oksanen et al. 2019). Community similarity (%) was quantified as  $(1 - \text{Bray-Curtis dissimilarity index}) \times 100$ .

For the 100 insect surveys we analysed whether any variation in bramble flower-visiting community composition, expressed by Bray-Curtis dissimilarity indices, was explained

by land use type (urban/rural) or main geographical area (Hailsham, Lewes, Uckfield) using a permutational multivariate analysis of variance (PERMANOVA, Anderson 2017), with the *adonis* function from the R package *vegan* (version 2.5-6, Oksanen et al. 2019).

Community composition at the genus level for the detailed 400 insect surveys was compared between survey periods and sites using the Bray-Curtis dissimilarity index, as sample sizes were too small for statistical comparison.

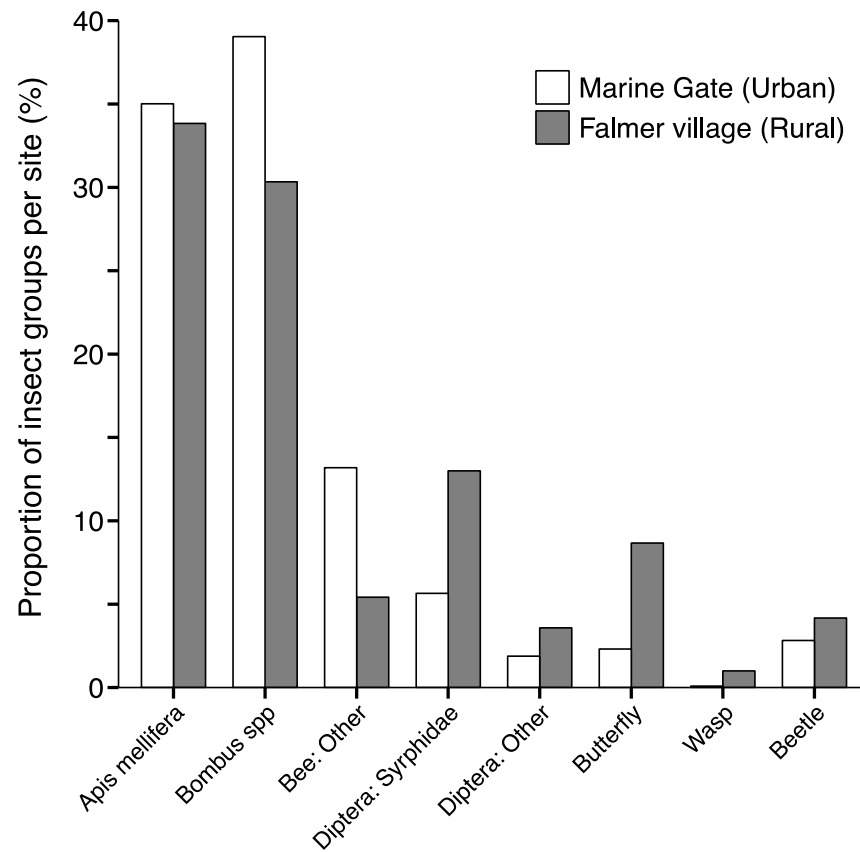
Statistical analyses were performed using RStudio version 1.1.463, R version 3.4.3 (R Core Team 2020). Values are given as mean  $\pm$  SD unless stated otherwise.

## 2.4 Results

### 2.4.1 Detailed insect surveys (400 insects)

Honeybees and bumblebees were the most abundant groups in the detailed insect surveys, each comprising 30 to 40% of the foraging insects in both urban and rural sites (urban: *Apis mellifera* 35.0%, *Bombus* spp. 39.0%,  $n = 1168$  insects; rural: *A. mellifera* 33.8%, *Bombus* spp. 30.3%,  $n = 1200$ ;  $n = 3$  surveys per site; Fig. 2.2). Less than 50% of honeybees had visible pollen in their baskets at either site (urban, 43.3%; rural, 16.5%).

Insects that were not *Apis* or *Bombus* made up a comparatively small proportion of the surveys per genus on average (urban, mean  $\pm$  SD,  $12.12 \pm 19.86$  individuals, 1.0%; rural,  $14.83 \pm 19.84$ , 1.2%; Fig. 2.3). The most species-rich genera were *Andrena*, *Bombus* and *Lasioglossum* bees. Three of the recorded species are listed as Priority Species under the UK Biodiversity Action Plan (*Bombus humilis* Illiger, *Coenonympha pamphilus* (L.) and *Limenitis camilla* (L.); UK BAP 2007). Full details of insect foraging activity in each location are in Table 2.1.



**Figure 2.2.** Foraging activity of insect groups recorded in three pooled detailed surveys at each of two sites near to Brighton, East Sussex: Marine Gate (urban, white bars, total  $n = 1168$  insects) and Falmer village (rural, grey bars, total  $n = 1200$  insects) from June to August 2018



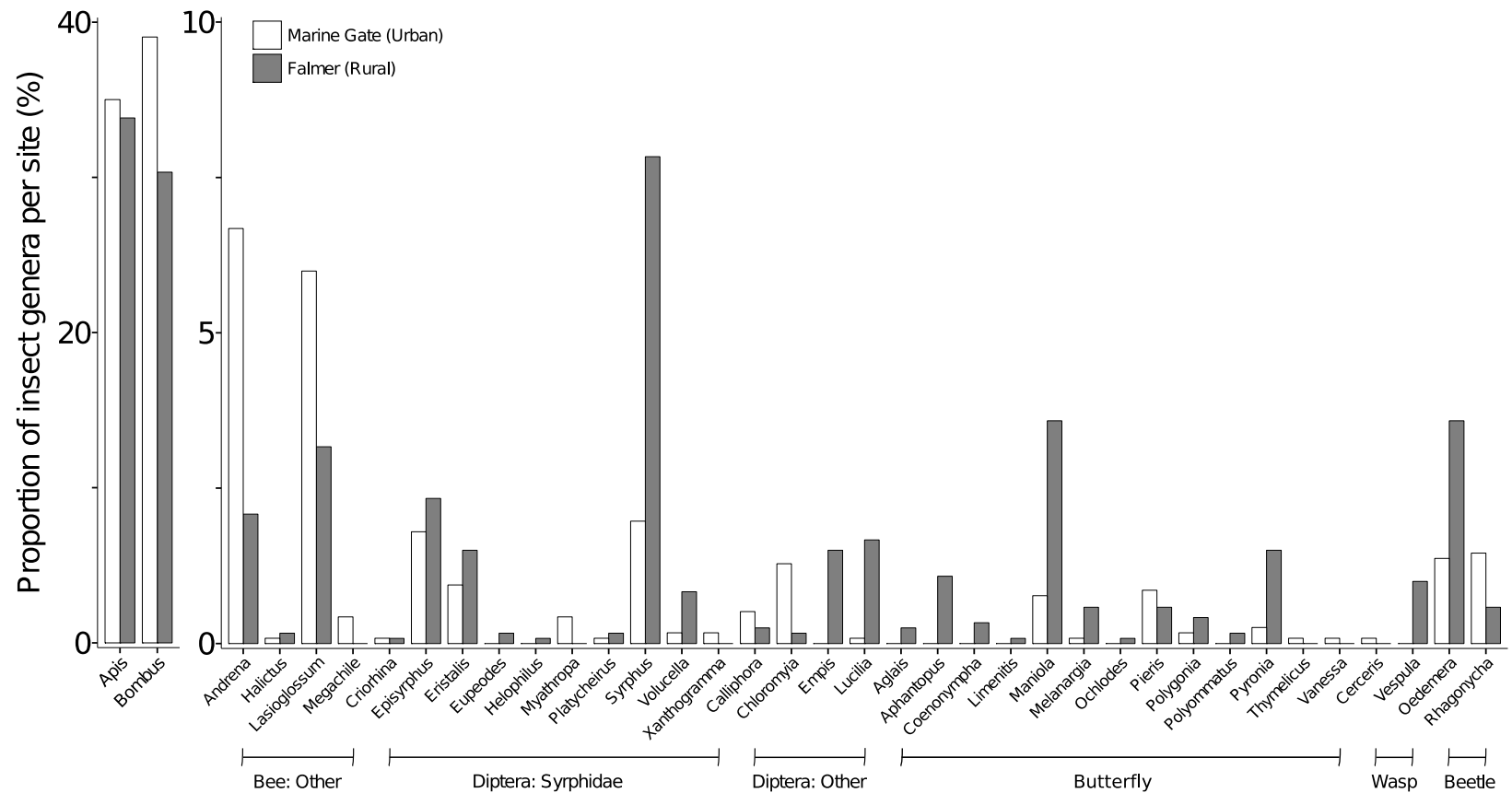
**Table 2.1.** Foraging activity of insects visiting *Rubus fruticosus* flowers in detailed insect surveys in two locations in Brighton, East Sussex, from June to July 2018. Counts are from three pooled surveys of approximately 400 insects in each location (urban: 13 & 15 June, 26 & 27 June, 12 & 13 July, n = 1168 insects in total; rural: 6 June, 21 June and 5 & 6 July, n = 1200). Bees, butterflies, beetles and wasps were identified to species. Hoverflies and non-syrphid Diptera were identified to species where possible, and to genus where this was not possible. Proportion (%) of the total number of insects per site is given for each group, and for both the overall genus and species within genus where both data are shown. Total proportion for each group may be different to the sum of proportions for each group due to rounding in the latter. Species in bold are listed as Priority Species in the UK Biodiversity Action Plan (UK BAP 2007). For *Lasioglossum* bee species, counts marked with † indicate the representative sample of bees identified using a microscope. For *Bombus* species, the number of queens recorded is shown in parentheses. For *Apis mellifera*, the number of bees collecting pollen is shown in square brackets

Group	Species	<i>Brighton urban</i>		<i>Brighton rural</i>	
		Count	Proportion (%)	Count	Proportion (%)
<i>Apis mellifera</i>	<i>Apis mellifera</i> L.	409 [177]	35	406 [67]	33.8
<i>Bombus</i> spp.	<i>Bombus</i>	456	39	364	30.3
	<i>B. hortorum</i> (L.)	1	0.1	10	0.8
	<b><i>B. humilis</i> Illiger</b>	7	0.6	0	0
	<i>B. hypnorum</i> (L.)	17 (4)	1.5	53 (2)	4.4
	<i>B. lapidarius</i> (L.)	32 (1)	2.7	34 (1)	2.8
	<i>B. pascuorum</i> (Scopoli)	113	9.7	83(1)	6.9
	<i>B. pratorum</i> (L.)	1	0.1	70	5.8
	<i>B. terrestris/lucorum</i> agg.	282 (2)	24.1	113 (6)	9.4
	<i>B. vestalis</i> (Geoffroy)	0	0	1	0.1
Other (non- <i>Apis</i> / <i>Bombus</i> ) bee		154	13.2	65	5.4

	<i>Megachile</i>	5	0.4	0	0
	<i>Megachile centuncularis</i> (L.)	3	0.3	0	0
	<i>Megachile willughbiella</i> (Kirby)	2	0.2	0	0
	<i>Andrena</i>	78	6.7	25	2.1
	<i>Andrena bicolor</i> Fabricius	1	0.1	0	0
	<i>Andrena cineraria</i> (L.)	0	0	1	0.1
	<i>Andrena dorsata</i> (Kirby)	41	3.5	18	1.5
	<i>Andrena flavipes</i> Panzer	11	0.9	0	0
	<i>Andrena fucata</i> Smith	6	0.5	0	0
	<i>Andrena haemorrhoa</i> (Fab.)	10	0.9	5	0.4
	<i>Andrena minutula</i> (Kirby)	1	0.1	0	0
	<i>Andrena scotica</i> Perkins	1	0.1	0	0
	<i>Andrena subopaca</i> Nylander	0	0	1	0.1
	<i>Andrena</i> (unknown)	7	0.6	0	0
	<i>Lasioglossum</i>	70	6.0	38	3.2
	<i>Lasioglossum calceatum</i> (Scop.)	6 †		2 †	
	<i>Lasioglossum fulvicorne</i> (Kirby)	1 †		2 †	
	<i>Lasioglossum malachurum</i> (Kirby)	0		1 †	
	<i>Lasioglossum morio</i> (Fab.)	0		1 †	
	<i>Lasioglossum pauxillum</i> (Schenck)	1 †		1 †	
	<i>Halictus tumulorum</i> (L.)	1	0.1	2	0.2
Diptera: Syrphidae		66	5.7	156	13.0
	<i>Criorhina</i>	1	0.1	1	0.1
	<i>Episyrphus balteatus</i> (De Geer)	21	1.8	28	2.3
	<i>Eristalis</i>	11	0.9	18	1.5
	<i>Eristalis horticola</i> (De G.)	1	0.1	0	0

	<i>Eristalis nemorum</i> (L.)	0	0	1	0.1
	<i>Eristalis tenax</i> (L.)	10	0.8	17	1.4
	<i>Eupeodes</i>	0	0	2	0.2
	<i>Helophilus pendulus</i> (L.)	0	0	1	0.1
	<i>Myathropa florea</i> (L.)	5	0.4	0	0
	<i>Platycheirus</i>	1	0.1	2	0.2
	<i>Syrphus</i>	23	2.0	94	7.8
	<i>Volucella</i>	2	0.2	10	0.8
	<i>Volucella bombylans</i> (L.)	2	0.2	3	0.3
	<i>Volucella pellucens</i> (L.)	0	0	6	0.5
	<i>Volucella zonaria</i> (Poda)	0	0	1	0.1
	<i>Xanthogramma pedissequum</i> (Harris)	2	0.2	0	0
Non-syrphid					
Diptera		22	1.9	43	3.6
	<i>Calliphora</i>	6	0.5	3	0.3
	<i>Chloromyia formosa</i> (Scop.)	15	1.3	2	0.2
	<i>Empis</i>	0	0	18	1.5
	<i>Lucilia sericata</i> (Meigen)	1	0.1	20	1.7
Butterfly		27	2.3	104	8.7
	<i>Aglais io</i> (L.)	0	0	3	0.3
	<i>Aphantopus hyperantus</i> (L.)	0	0	13	1.1
	<b><i>Coenonympha pamphilus</i> (L.)</b>	0	0	4	0.3
	<b><i>Limenitis camilla</i> (L.)</b>	0	0	1	0.1
	<i>Maniola jurtina</i> (L.)	9	0.8	43	3.6
	<i>Melanargia galathea</i> (L.)	1	0.1	7	0.6
	<i>Ochlodes sylvanus</i> (Esper)	0	0	1	0.1

	<i>Pieris</i>	10	0.9	7	0.6
	<i>Pieris brassicae</i> (L.)	6	0.5	3	0.3
	<i>Pieris napi</i> (L.)	0	0	3	0.3
	<i>Pieris rapae</i> (L.)	4	0.3	1	0.1
	<i>Polygonia c-album</i> (L.)	2	0.2	5	0.4
	<i>Polyommatus icarus</i> (Rottemburg)	0	0	2	0.2
	<i>Pyronia tithonus</i> (L.)	3	0.3	18	1.5
	<i>Thymelicus sylvestris</i> (Poda)	1	0.1	0	0
	<i>Vanessa atalanta</i> (L.)	1	0.1	0	0
Wasp		1	0.1	12	1.0
	<i>Cerceris rybyensis</i> (L.)	1	0.1	0	0
	<i>Vespula vulgaris</i> (L.)	0	0	12	1.0
Beetle		33	2.8	50	4.2
	<i>Oedemera nobilis</i> (Scop.)	16	1.4	43	3.6
	<i>Rhagonycha fulva</i> (Scop.)	17	1.5	7	0.6
n		1168		1200	



**Figure 2.3.** Foraging activity of insect genera recorded in three detailed surveys at each of two sites in Brighton, East Sussex: Marine Gate (urban, white bars, total  $n = 1168$  insects) and Falmer village (rural, grey bars, total  $n = 1200$  insects) from June to July 2018. *Apis* and *Bombus* are presented with a four times smaller scale (0-40%) than the non-*Apis/Bombus* genera (0-10%) for clearer visualisation of less common genera

Diversity (Shannon-Wiener  $H'$ ) and richness ( $S_{(G)}$ ) of flower-visiting genera were similar during the early and middle stages of bramble bloom, and lower during the late stage at the urban site ( $H'$ : early = 1.37, middle = 1.72, late = 1.70;  $S_{(G)}$  = 15, 17, 16) compared to the rural site ( $H'$ : 1.34, 1.95, 2.29;  $S_{(G)}$  = 13, 15, 25; Table 2.2). Fewer genera were recorded at the urban ( $S_{(G)}$  = 27) than rural site ( $S_{(G)}$  = 31) overall. These trends were similar for the first transect walks per survey period (Appendix A.2).

Community composition was similar among all six surveys at the genus level (Bray-Curtis similarity = 68.6%) and among corresponding survey periods between sites (early = 80.6%; middle = 62.8%; late = 74.5%). When data for each site were pooled over the three survey periods, giving the full range of insects foraging on bramble over its main flowering period, genus-level community composition was 79.7% similar between sites.

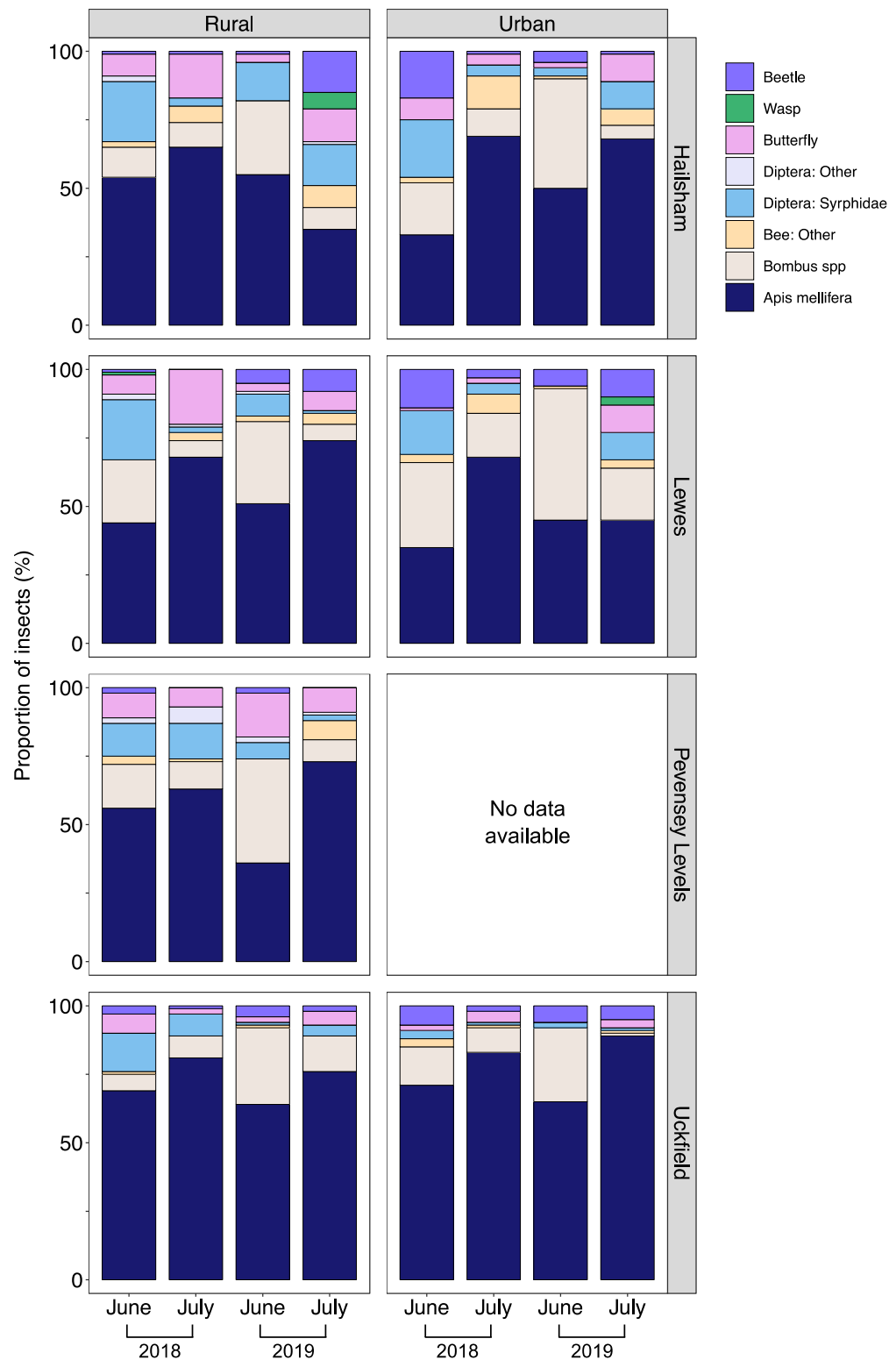
**Table 2.2.** Species richness and diversity of insects visiting *Rubus fruticosus* flowers in detailed insect surveys in two locations in Brighton, East Sussex, from June to July 2018. Data are from surveys of approximately 400 insects carried out during the early, middle and late stages of bramble bloom (urban: early = 13 & 15 June, middle = 26 & 27 June, late = 12 & 13 July,  $n$  = 1168 insects in total; rural: 6 June, 21 June and 5 & 6 July,  $n$  = 1200). Genus-level richness  $S_{(G)}$ , Shannon-Wiener diversity ( $H'$ ) and Pielou's measure of evenness ( $J$ ) are given for each survey period per location

<b>Bramble bloom stage:</b>	<b><i>Brighton urban</i></b>			<b><i>Brighton rural</i></b>		
	<b>early</b>	<b>middle</b>	<b>late</b>	<b>early</b>	<b>middle</b>	<b>late</b>
n insects	383	386	399	416	391	393
$S_{(G)}$	15	17	16	13	15	25
$H'$	1.367	1.719	1.696	1.336	1.952	2.292
$J$	0.505	0.607	0.612	0.521	0.721	0.712

#### 2.4.2 Low-resolution, group-level insect surveys (100 insects)

Honeybees were again the most abundant group, both overall and in most, 26 out of 28, of the surveys, ranging from 33 to 89% of the 100 observed insects (mean  $\pm$  SD across all sites and survey years:  $60.2 \pm 15.5$ ). Bumblebees (*Bombus* spp.) were again the second most abundant on average, ranging from 1 to 48% ( $17.4 \pm 12.1$ ). Other taxa were: hoverflies,  $7.9 \pm 6.9$  individuals per survey; butterflies,  $6.4 \pm 5.1$ ; other (non-*Apis/Bombus*) bees,  $2.8 \pm 3.0$ ; beetles,  $4.4 \pm 4.7$ , non-syrphid Diptera,  $0.6 \pm 1.3$  and wasps,  $0.4 \pm 1.25$  (Fig. 2.4).

On average, across all sites over 2018 and 2019, honeybees were proportionally 31.5% more abundant in July ( $68.4 \pm 14.2$  bees per survey,  $n = 100$  insects per survey) than June ( $52.0 \pm 12.5$ ). Bumblebees were 64% less abundant in July ( $9.1 \pm 4.5$ ) than June ( $25.6 \pm 11.8$ ; Fig. 2.4).



**Figure 2.4.** Foraging activity of insect groups (%) recorded in 28 surveys of 100 insects at seven sites in Sussex. Each stacked bar represents one survey. Surveys were made in June and July in 2018 and in 2019, in matched rural (left column) and urban (right column) sites in the overall locations, shown in vertically oriented grey bars on the



right: Hailsham, Lewes, Pevensey Levels (rural only) and Uckfield. Insect groups are shown in the legend (top right)

Group-level community composition of bramble flower-visiting insects was highly similar among all 28 surveys (Bray-Curtis similarity 72.8%). This was also similar between rural and urban surveys overall (72.3%,  $n = 16$  rural, 12 urban surveys), between sites (72.5%) and within sites (Hailsham, 70.7%; Lewes, 70.2%; Pevensey, 72.8%; Uckfield, 83.4%). Community composition, expressed by group-level Bray-Curtis dissimilarity indices, was not significantly different between land use types (urban/rural;  $F_{(1)} = 1.50$ ,  $P = 0.181$ ), between sites ( $F_{(3)} = 2.21$ ,  $P = 0.082$ ) or between years within sites ( $F_{(3)} = 0.16$ ,  $P = 1.000$ ). There was a significant difference between June and July across both years ( $F_{(1)} = 10.40$ ,  $P = 0.011$ ) and within each year (year included as an interaction term:  $F_{(1)} = 4.29$ ,  $P = 0.041$ ).

#### 2.4.3 Local *R. fruticosus* agg. abundance and habitat

Bramble plants were present in 54 of the 60 randomly selected 200 x 200 m grid squares overall across the three paired urban and rural locations in Sussex; in 80% (24/30) of urban and 100% (30/30) of rural grid squares. Plants were found in 13 main habitat types (detailed in Appendix A.4). The only surveyed habitat in which no bramble was present was in the middle of an agricultural field.

#### 2.4.4 Local *R. fruticosus* flowering, wildflower community, and presence of *R. idaeus*

Flowering bramble plants were abundant within a 2 km radius of the Laboratory of Apiculture and Social Insects throughout June and July 2018 in each of three fixed transect routes in northeast, northwest and southwest directions ( $n = 26$  transects in total). There were no flowers in mid-May ( $n = 3$  transects). We recorded the beginning of bramble bloom as 23 May 2018, when we first observed flowers on transects. On this date abundance and bloom level were low in all three transects (abundance = 1 or 2, Rare or Occasional, on the 5-point DAFOR scale; bloom intensity = 1, 0-20%, on the 5-point modified DAFOR scale; *overall availability* = 1 or 2 [maximum  $5 \times 5 = 25$ ]). The abundance of flowering plants and the level of bloom then increased to peak in mid to late June, with the highest *overall availability* of flowers recorded on 20 and 22 June on

each transect route (NE, 25/25; NW, 20/25; SW, 12/25). Flower *overall availability* decreased after this date but was still considerable on the final transects carried out in late July (Appendix A.6). Although we did not quantify floral rewards, we note that bramble pollen did not seem to be limited: large amounts were visible on the anthers of many flowers during our observations, including towards the end of the foraging day.

Relative to other forb, shrub and tree species recorded on the transects, *R. fruticosus* was one of the three species with the greatest *overall availability* of flowers from early June to early July, in 11/23 transects carried out during the bramble bloom. Bramble flower availability was highest or joint-highest of all recorded species on three NE transects and once on NW and SW routes. The most abundant other species (appearing in the top three highest *overall availability* of flowers in  $\geq 4$  transects in at least one transect route) were *Bellis perennis* L., *Cirsium arvense* (L.) Scopoli, *Epilobium angustifolium* L., *Senecio jacobaea* L., *Trifolium dubium* Sibthorp, *Trifolium repens* L. and *Vicia cracca* L. (Appendix A.7).

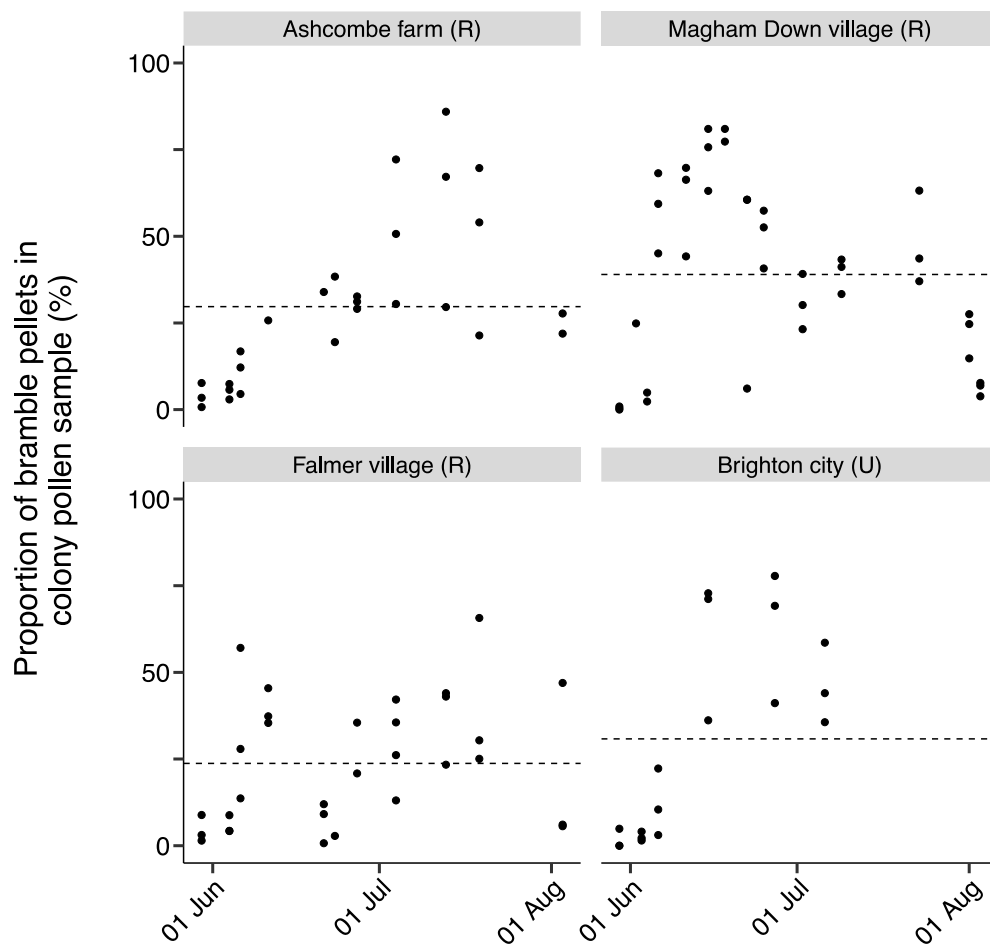
We recorded one patch, roughly 6 x 2 m, of flowering *R. idaeus* in bloom in one location on the northeast transect ( $n = 2$  transects), in a hedgerow on agricultural land, which was minimal ( $<1\%$ ) in comparison to the flowering bramble present.

#### 2.4.5 Honeybee pollen trapping

Overall, we analysed 1184 grey pollen pellets from the four locations where samples were collected in 2018 (Falmer village,  $n = 303$ ; Ashcombe Farm,  $n = 273$ ; and Magham Down village,  $n = 472$ ; Brighton city,  $n = 120$ ). *Rubus fruticosus* pollen was present in honeybee colony pellet samples in all four pollen-sampling locations from the start of the sampling period in late May (30 May) until the last sampling date for each rural location (Falmer village, Ashcombe Farm and Magham Down village, 3 August) and the urban location (Brighton city, 6 July). The proportion of bramble pellets in pollen samples fluctuated during the sampling period, with large variation between locations, and between hives in each location (Fig. 2.5).

The proportion of bramble pollen per colony per sampling date was low in each location in late May and early June then increased to a peak in mid to late June in Magham

Down village and Brighton city, and mid-July in Ashcombe farm and Falmer village (Fig. 2.5). The overall average proportion of bramble pellets over the sampling period, corrected for false positives, was 31.4% ( $n = 114$  samples), between 24% and 39% per location. The peak proportion of bramble pellets per colony sample, corrected for false positives, was  $>75\%$  in three of four locations (Table 2.3).



**Figure 2.5.** Proportion of bramble pellets in honeybee pollen samples collected in four locations in East Sussex, 2018, following correction for false positives. Each point represents pollen collected by one hive on one sampling date. Solid black lines are smoothed trend lines added using Locally Estimated Scatterplot Smoothing (LOESS). Dotted lines show the mean proportion of bramble over the sampling period in three rural (R) locations (30 May – 3 August) and one urban (U) location (30 May – 6 July)

**Table 2.3.** Proportion of bramble pellets in honeybee pollen samples in four locations in East Sussex, 2018, corrected for false positives (see Methods and Appendix A.5). Pollen was collected in three rural (R) locations (30 May – 3 August) and one urban (U) location (30 May – 6 July). The average proportion of bramble pellets in pollen samples is shown for the entire sampling period. The percent of samples in which bramble pellets comprised >50% of the pollen sample is also shown. The final two columns show the peak proportion of bramble per sampling date and per colony for each location

<b>Location (<i>Rural/Urban</i>)</b>	<b>Mean <math>\pm</math> SD proportion (%) bramble pellets over sampling period [n samples]</b>	<b>Peak proportion (%) of bramble pellets per sampling date: mean <math>\pm</math> SD, range (n hives); <i>Date</i></b>	<b>Peak proportion (%) of bramble pellets per colony; <i>Date</i></b>
Ashcombe Farm ( <i>R</i> )	29.7 $\pm$ 23.4 [27]	60.9 $\pm$ 28.7, range 85.9 – 29.6 (n = 3); 13 July	85.9; 13 July
Falmer village ( <i>R</i> )	23.7 $\pm$ 18.2 [31]	40.4 $\pm$ 22.1, range 65.7 – 25.1 (n = 3); 19 July	65.7; 19 July
Magham Down village ( <i>R</i> )	39.0 $\pm$ 25.9 [38]	79.1 $\pm$ 2.6, range 81.0 – 77.3 (n = 2); 18 June	81.0; 15 & 18 June
Brighton city ( <i>U</i> )	30.8 $\pm$ 29.1 [18]	62.7 $\pm$ 19.2, range 77.8 – 41.1 (n = 3); 27 June	77.8; 27 June

## 2.5 Discussion

Our results show that bramble flowers have an important ecological role for many species and types of flower-visiting insects, including species of conservation concern. We show that *R. fruticosus* agg. is geographically widespread and abundant in the study region, growing in many habitats in both urban and rural areas. The flowers also bloom over a long period, are highly abundant relative to co-flowering wild plant species and are a major source of pollen for a generalist flower visitor, the honeybee *Apis mellifera*, accounting for an average of 31% of pollen pellets collected from late May to early August by colonies in four locations in Sussex, UK.

Honeybees made up a large proportion of the foraging activity in our surveys (Figs. 2.2 & 2.4), which is likely to contribute to the similar community composition of foraging insects between study sites and land-use types in genus- and group-level surveys. There are many active beekeepers in Sussex and the density of managed honeybees is high in the region. Indeed, *A. mellifera* was the most abundant of the designated insect groups in 26 of the 28 surveys carried out across the Sussex region, averaging 60% of all insects overall (range 33 to 89% per survey). Together with our pollen trapping data, this indicates that bramble is an important source of forage for honey production and in maintaining managed and wild colonies. However, a wide range of other foraging insect species were recorded (Fig. 2.3), including three priority species “*identified as being the most threatened and requiring conservation action*” in the UK Biodiversity Action Plan, *Bombus humilis*, *Coenonympha pamphilus* and *Limenitis camilla* (UK BAP 2007; Table 2.1).

These findings support previous work showing the importance of *R. fruticosus* to foraging insects within the co-flowering plant community. For example, Balfour et al. (2015) found that of 38 flowering plant species surveyed on the South Downs in Sussex in July, in four habitat types (nature reserve, pasture, field margin/hedgerow and set-aside fields), bramble was ranked fifth in number of insect visitors and sixth in number of flower-visiting insects per unit petal area. In the recently established Database of Pollinator Interactions (DoPI, Balfour et al. *in prep*), which currently contains over 150,000 British plant and flower-visiting insect interactions collated from published academic literature and unpublished datasets of individuals and organisations, *R.*

*fruticosus* has the third highest number of observed flower-visitor species (210), following *Ranunculus repens* L. (260) and *Heracleum sphondylium* L. (240; data from studies using insect-flower transect data rather than observation carried out on focal species; Balfour et al. *in prep*). In agreement with the importance of bramble pollen to honeybee colonies shown in this study by pollen trapping (Fig. 2.5, Table 2.3), bramble is an important pollen source for many other insects, including bumblebees (Gyan & Woodell 1987c, Kleijn & Raemakers 2008). DNA metabarcoding of pollen loads of 11 hoverfly species in Welsh conservation grasslands also found that *R. fruticosus* was one of eight plant taxonomic groups that were the main pollen sources (Lucas et al. 2018b). Analysis of pollen loads of 47 species of solitary bee in farmland in southern England found that 4.5% by volume of the total pollen collected was from *R. fruticosus* in late June to early July, and 17.5% in late July to early August (Wood, Holland & Goulson 2017).

The relative importance of bramble as a nectar and pollen source will vary with location and over its bloom period, and will likely depend greatly on the abundance and diversity of co-flowering species. Similarly, the biodiversity of bramble-visiting insects will depend on many factors, including geographic location and the local availability of both nest sites and year-round floral resources. Nevertheless, bramble is likely often to act as a core species in insect-flower interaction networks since it offers large amounts of nectar and pollen (Gyan & Woodell 1987b, Baude et al. 2016, Fowler, Rotheray & Goulson 2016), and, as shown in this study, is locally abundant, grows in many habitat types and is highly generalist with accessible flowers that are visited by a wide range of species (Pereira Maia, Vaughan & Memmott 2019). In support of this, insect-flower interaction analyses have shown that *R. fruticosus* has high network connectivity, including in agricultural systems (Gibson et al. 2006, Power & Stout 2011) and woodland (Tiedeken & Stout 2015). Core generalist species contribute to pollination network functioning and stability and are therefore important for ecosystem resilience, as well as restoration where this is necessary (Martín González, Dalsgaard & Olesen 2010, Pereira Maia, Vaughan & Memmott 2019). They can also support populations of potential pollinators for rare plants, helping to conserve these species (Gibson et al. 2006), although successful plants such as bramble can also outcompete other wildflowers (Plantlife UK 2018), leading to conflicts of interest when considering conservation goals. It would be interesting specifically to investigate the role of *R.*

*fruticosus* in insect-flower interaction networks in varied land use types and geographic locations, to further clarify its potential ecological role as a core or even ‘keystone’ species.

Our findings show that bramble is visited by diverse insect taxa in both urban and rural locations (Figs. 2.2, 2.3 & 2.4). Bramble is common in hedgerows bordering agricultural fields, public footpaths and bridleways in rural areas (Hanley & Wilkins 2015, this study). It is also commonly found growing along transportation infrastructure including railways (Sargent 1984) and road verges, which provide a large resource for foraging insects, and can act as habitat corridors that benefit insect biodiversity and facilitate species persistence where habitats are fragmented (Dixon 2009, Hanley & Wilkins 2015). However, bramble is often removed from urban greenspace (*e.g.* Phillips 2015, Bristol City Council 2019), although it is a common feature of abandoned or derelict land and unmanaged residential gardens in urban areas (Angold et al. 2006, this study). It could be possible to further increase the tolerance of bramble in urban areas where it is not obstructive, for example in hedgerows or along fences in amenity grassland and parks, cemeteries, churchyards and other land uses that are (or could potentially be) an important foraging resource for insects within towns and cities (Baldock et al. 2019, Baldock et al. 2020). A shift in public awareness and opinion of bramble as an ecologically valuable species may be required for this to be feasible.

Our study adds to current knowledge of native floral species that provide nectar and pollen for bees and other pollinating insects in the UK, an important component in effective conservation programmes for these insects (Lander 2020). Maintaining common plants that are major forage sources for pollinators is increasingly important since many of these insects are declining in abundance in the UK (*e.g.* bumblebees: Carvell et al. 2006; butterflies: Fox et al. 2011, Fox et al. 2015; solitary bees, hoverflies: Powney et al. 2019) and globally, which is associated with several interacting drivers including loss of flowers (Carvell et al. 2006, Potts et al. 2010, Wallisdevries, Van Swaay & Plate 2012, Vanbergen et al. 2013, Goulson et al. 2015). We suggest that due to its valuable ecological role, wherever conflicts of interest and management strategies allow, bramble should be maintained and promoted as a valuable resource for flower-visiting insects and a variety of other wildlife.

### 2.5.1 Limitations and Future Research

This study aimed to provide a multi-dimensional picture of the value of *R. fruticosus* to summer-flying diurnal flower-visiting insects in our study area. While we have successfully met this aim, there are limitations of the study. For example, although we sampled foraging insects during the period of most insect activity, 11:00 – 16:00, this meant that any insects foraging before or after this sampling period will not have been recorded. We also did not sample night-flying insects, meaning that we can only comment on the value of this plant to diurnal FVI. Furthermore, the use of just three paired urban-rural sampling sites (with one additional unpaired rural site) in the group-level insect surveys means that our comparison of urban and rural habitat types is limited both descriptively and in terms of statistical power.

Future research could address these limitations through carrying out insect surveys for a larger proportion of the day, and also by sampling nocturnal visitors. Including more paired urban-rural sites across the region would allow a more detailed and reliable comparison of these land-use types. Another interesting line for future research would be to stratify the study area by habitat type and sample equally between these areas. This would allow the findings to be extrapolated more reliably to other areas in the UK, particularly those with similar climate, elevation and other biophysical attributes. To complete a thorough, high-resolution survey of the value of bramble to FVI would be difficult due to the logistics of such a study; however, a national citizen science project could be an interesting way to enable surveying on a large geographical scale at a lower resolution. Lastly, given the findings of this study and others that indirectly point to the role of bramble as a ‘keystone’ species within plant-pollinator communities (Kleijn & Raemakers 2008, Balfour et al. 2015, Wood, Holland & Goulson 2017, Lucas et al. 2018b), it would be interesting to apply an interaction network approach to analyse this empirically in a future study.



## Chapter Three: Seasonal variation in exploitative competition between honeybees and bumblebees

“What do the bees think they are doing?” ~ A.A. Milne, *The Case for the Artist* in *If I May*

### Authors and author contribution statement

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VW and FLWR conceived the ideas; VW led the data collection, data analysis and writing of the manuscript; ICH, NLD, JKM and SDK contributed to data collection

### 3.1 Abstract

Honeybees (*Apis mellifera*) and bumblebees (*Bombus* spp.) often undergo exploitative competition for shared floral resources, which can alter their foraging behaviour and flower choice, even causing competitive exclusion. This may be strongest in late summer, when foraging conditions are most challenging for bees, compared to other times of the year. However, the seasonal dynamics of competition between these major pollinator groups are not well understood. Here, we investigate whether the strength of exploitative competition for nectar between honeybees and bumblebees varies seasonally, and whether competitive pressure is greatest in late summer months. We carried out experimental bee exclusion trials from May to late September, using experimental patches of lavender, variety Grosso, in full bloom. In each trial we compared the numbers of honeybees (HB) foraging on patches from which bumblebees had been manually excluded (bumblebee excluded, BBE) versus control (CON) patches,  $HB_{(BBE-CON)}$ . This measure of exploitative competition varied significantly with season. As expected, mean  $HB_{(BBE-CON)}$  was significantly greater in late summer trials than in early summer or autumn trials. This was despite high nectar standing crop volumes in BBE patch flowers in early summer and autumn trials. Mean  $HB_{(BBE-CON)}$  was not different between early summer and autumn trials. Our results show that nectar competition between honeybees and bumblebees varies seasonally and is stronger in late summer than early summer or autumn, adding to current understanding of the seasonality of resource demand and competition between bee species. This information

may also help to inform conservation programs aiming to increase floral resources for bees by showing when these resources are most needed.

### 3.2 Introduction

Exploitative competition, in which one consumer species depletes a resource used by other species or individuals (Wootton 1994), can play an important indirect role in shaping community structure and can cause competitive exclusion (Alley 1982, Schoener 1983, Kreutzer & Lampert 1999, Balfour, Gandy & Ratnieks 2015). More generally, exploitative competition can have a wide range of effects on competing species including behavioural change in resource-use and niche partitioning (Hardin 1960, Inouye 1978, Carpenter 1979, Finke & Snyder 2008, Clink et al. 2017). The strength of competitive pressure for shared resources is expected to vary in response to per-individual resource availability, which can change seasonally in both temperate (*e.g.* Schmitt & Holbrook 1986, Balfour et al. 2018) and tropical (*e.g.* Knott 1998, Clink et al. 2017) areas. This can cause species with overlapping foraging niches to seasonally adjust their behaviour (Schmitt & Holbrook 1986), which may mitigate the effects of competition. For example, in seven co-occurring North American waterfowl species, greater competition during resource-scarce winter months caused greater specialisation in food type, habitat utilisation and foraging behaviour between species pairs compared to summer (DuBowy 1988). Conversely, seasonal periods of resource abundance can cause shifts in behavioural strategies through reduced intra- and inter-specific exploitative competition. For example, primates exhibit greater dietary selectivity when fruit availability is high in ‘mast’ years (Knott 1998, Clink et al. 2017).

Seasonal variation in exploitative competition among bee species would be expected to influence foraging behaviour, since many species are generalist nectar-feeders that can flexibly alter the flower species they visit in response to resource availability. Flower choice can be influenced directly by changes in reward quality or quantity (Heithaus 1979, Cnaani et al. 2006) or indirectly through fluctuations in competitor abundance (Heinrich 1976, Walther-Hellwig et al. 2006, Fontaine, Collin & Dajoz 2008, Balfour, Gandy & Ratnieks 2015). Several studies have shown exploitative competition between bee species (*e.g.* Heinrich 1976, Inouye 1978, Ings, Ward & Chittka 2006, Walther-Hellwig et al. 2006, Balfour, Gandy & Ratnieks 2015), but these have largely been

carried out at a particular time of year and so do not address possible seasonal variation. An April to September study of four heathland sites in southern England provided some evidence of seasonal change in the foraging-niche breadth of long-tongued bumblebees with increasing honeybee abundance, but it was not clear whether this was due to competition (Forup & Memmott 2005). Nevertheless, it is probable that the strength of exploitative competition for nectar among bee species does vary seasonally in many locations. Waggle dance decoding showed that honeybee foraging distances were greatest during July and August in Sussex, southeast England, suggesting a relative scarcity of available floral resources at this time of year compared to spring and autumn (Couvillon, Schürch & Ratnieks 2014). Since many bee and other flower-visiting insect species also demonstrate a July-August late summer peak in abundance in the UK (Falk & Lewington 2015, Balfour et al. 2018), it is likely that these factors combine to cause a predictable, seasonal, late summer increase in nectar competition.

Honeybees (*Apis mellifera* L.) and bumblebees (*Bombus* spp.) are generalist bees that overlap in floral resource use (Steffan-Dewenter & Tschardtke 2001, Forup & Memmott 2005, Thomson 2006) and are known to undergo inter-specific resource competition, which can affect foraging patterns and behaviour in both groups (*e.g.* honeybees, Balfour, Gandy & Ratnieks 2015; bumblebees, Sáez et al. 2017). *Apis-Bombus* resource competition has also been shown to cause fitness costs (reduced growth and reproduction) in bumblebees (Thomson 2004, Goulson & Sparrow 2009, Elbgami et al. 2014) though not honeybees in the existing literature (reviewed in Wojcik et al. 2018).

Both *Apis* and *Bombus* often occur in large numbers on flowers relative to other bees and insects (Garbuzov & Ratnieks 2014b) due in part to their large eusocial colonies (Seeley 1995, Goulson 2003). The absolute and relative abundance of *Apis* and *Bombus* changes over the foraging season in the UK. Bumblebees have annual colonies and are less abundant in spring/early summer and autumn when colonies are in the stages of growth and senescence respectively (Falk & Lewington 2015). In comparison, honeybees have perennial colonies and undergo much smaller seasonal fluctuations in numbers, with foragers active from March to October in our study area (Garbuzov & Ratnieks 2014a,b, Couvillon, Schürch & Ratnieks 2014) and often even earlier and later in the year. Therefore, seasonal changes in both competitor abundance and resource

availability could cause seasonal change in the strength of *Apis-Bombus* exploitative competition. However, our knowledge of this is currently limited despite the increasing (see Breeze et al. 2011) importance of these bees for pollination of crop and wildflower plant species (Corbet, Williams & Osborne 1991, Carreck & Williams 1998, Woodcock et al. 2013, Garratt et al. 2014a,b), and the potential effects of *Apis-Bombus* floral resource competition on bee fitness (growth and reproduction; Thomson 2004, Goulson & Sparrow 2009, Elbgami et al. 2014), foraging behaviour (Walther-Hellwig et al. 2006, Balfour, Gandy & Ratnieks 2015, Nielsen et al. 2017) and pollination effectiveness (Greenleaf & Kremen 2006).

Previous research in July and August has shown that bumblebees displace honeybees via exploitative competition on patches of lavender flowers (*Lavandula x intermedia* ‘Grosso’). Bumblebees outcompete honeybees in this system because they are able to visit Grosso lavender flowers at three times the rate of honeybees (Balfour, Garbuzov & Ratnieks 2013), which depletes nectar levels to a point at which honeybees cannot make an energy profit. When bumblebees were experimentally excluded honeybee numbers increased 14-fold in response to reduced resource depletion, demonstrating ecological release from competition (Balfour, Gandy & Ratnieks 2015).

In this project we aim to determine the seasonal dynamics of *Apis-Bombus* exploitative competition on lavender flowers. We extend the previous research to incorporate seasonality by carrying out foraging exclusion experiments from late May to September 2017 on patches of Grosso lavender in full bloom, thereby extending the period over which *Apis-Bombus* competition is studied. Importantly, we use a single plant variety thereby controlling the resource. We test the hypotheses that the strength of *Apis-Bombus* competition for nectar i) varies over a foraging season and ii) is greater in late summer than in early summer and autumn.

### **3.3 Materials and Methods**

#### **3.3.1 Study site and species**

Field work was carried out on the University of Sussex campus in southeast England (50.8671° N; 0.0879° W). We repeated 10 identical three-day exclusion trials from May

to September 2017. Data on bee foraging were collected only on days considered suitable for foraging,  $>12^{\circ}\text{C}$ , with light winds and no rain, when honeybees and bumblebees were seen to be actively foraging on the lavender plants and/or on other flowers in the study area. We ensured that both honeybees and bumblebees were active on each trial day through casual observations of flowering plants in the study vicinity (see Results section 3.4.2) and of honeybee hives in the local vicinity. There were two apiaries belonging to the Laboratory of Apiculture and Social Insects within  $<1$  km of the study site (each with between 6-10 colonies in total during the study period), plus three further apiaries within  $<2$  km, and a high density of colonies managed by beekeepers in the wider local area. Honeybees mainly forage for nectar and pollen from March to October (Couvillon, Schürch & Ratnieks 2014), and healthy colonies consist of between 20-40,000 adult bees in May-June and some 40,000 in September (Hooper 1991). Therefore, it is certain that foraging honeybees were present and abundant in the area throughout the study period.

We used the same lavender variety, *Lavandula x intermedia* ‘Grosso’ (Lamiaceae), as the previous research that demonstrated exploitative competition for nectar between *Apis* and *Bombus* in late summer (Balfour, Garbuzov & Ratnieks 2013, Balfour, Gandy & Ratnieks 2015).

A total of 700 Grosso plants in 3 L pots were obtained from Downderry Nursery, Sussex ([www.downderry-nursery.co.uk](http://www.downderry-nursery.co.uk)), the same supplier as for the previous competition studies (Balfour, Garbuzov & Ratnieks 2013, Balfour, Gandy & Ratnieks 2015). The plants had been grown in ways to cause bloom at different times. 300 plants were kept in greenhouses and polytunnels by Downderry Nursery to induce early flowering in May and June. 150 plants were grown normally, without treatment, and flowered in late July. A final batch of 250 plants were trimmed during the summer to delay bloom until September, with 150 plants used in the final two trials, 9 and 10. Some of this batch flowered in late August and 96 spare plants were used to replace plants that were near the end of their bloom in Trial 8 (21-24 August), to ensure a similar level of bloom across trials. Different growth regimes did not affect the general appearance of the plants and average nectar secretion rate was similar between batches (*Results*).

### 3.3.2 Trial design and experimental exclusions

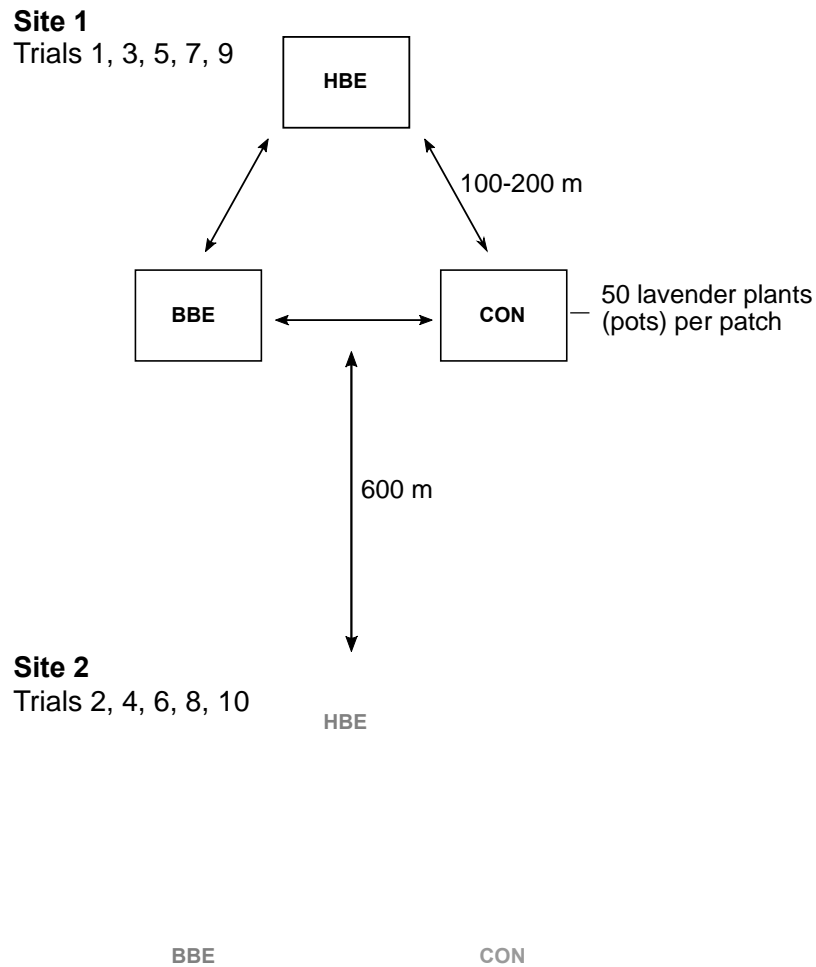
The May to September study period was categorised into three seasons, early summer (May and June), late summer (July and August), and autumn (September). July and August were combined as late summer since honeybee foraging distances are highest in the study area in these months, which indicates a dearth in overall nectar availability (Couvillon, Schürch & Ratnieks 2014). Pre-July study months were combined as early summer. Autumn was defined according to the National Met Office definition of meteorological autumn as starting on 01 September (National Met Office 2019), and also coincided with the flowering of ivy (*Hedera* spp.) in the study area from early September, following Couvillon, Schürch & Ratnieks (2014).

Each trial consisted of three exclusion days. Exact trial dates were dependent on suitable weather conditions. We aimed to carry out an even number of trials per season, but this was not possible due to poor weather conditions in early summer and the lack of lavender plants in full bloom in autumn following the final trial. We achieved three trials in early summer (1-3: 23-25 May, 31 May - 02 June and 13-15 June), five in late summer (4-8: 04-06 July, 10-13 July, 31 July - 04 August [data not collected on 02-03 August due to bad weather], 14-16 August and 21-23 August) and two in autumn (9-10: 12-14 and 19-22 September) making ten in total. We alternated trials between two sites 600 m apart on the University campus to reduce any potential local-effect bias (Fig. 3.1).

Following Balfour, Gandy & Ratnieks (2015), each three-day trial was set up using 150 plants in three patches of 50 pots, separated by 100-200 m (Fig. 3.1). Plants were selected at the start of the trial to give approximately equal total bloom per patch. Each patch was randomly assigned to a treatment: honeybees excluded (HBE), bumblebees excluded (BBE) and control (CON, no bees excluded). Following established methods (Balfour, Gandy & Ratnieks 2015), bees of the “wrong” type were excluded throughout each day using a light tap with a bamboo cane; for example, on BBE patches any bumblebees landing on the plants to forage were immediately tapped causing them to fly away. Any persistent individuals were repeatedly tapped until they left the patch. Where necessary, this required multiple individuals to monitor the patches and perform exclusions (VW, ICH, NLD, JKM and SDK). At least one individual was also present at

CON patches at all times, despite no bees being excluded, to ensure this did not introduce a difference in the patch environment for foraging insects. Researchers were all trained extensively in the experimental methodology by VW and rotated regularly between patches during each trial day, in part to relieve tedium and fatigue and also to ensure that any natural differences in researcher technique, effort or accuracy did not introduce any bias. Since many researchers were present during each trial day, including the lead author VW, a natural system of cross-monitoring between researchers was in place to ensure consistency between individuals. On all patches we excluded male wool carder bees (*Anthidium manicatum* (L.)), since these are highly territorial and aggressive towards other bee species, and the conopid fly (*Sicus ferrugineus* (L.)) which lays its eggs on foraging bumblebees (Falk & Lewington 2015), in case these insects were causing honeybees and bumblebees to avoid the lavender; both were rarely present.

We estimated the total number of flowers in each patch once during each trial by counting the number of flowering inflorescences in the patch and multiplying this by the average number of flowers calculated from 40 randomly-selected inflorescences.



**Figure 3.1.** Simplified schematic showing experimental set-up. Patches (rectangular boxes) of 50 lavender plants in pots were set up between 100-200 m apart and randomly allocated to treatment (Control, CON; Honeybees Excluded, HBE, Bumblebees Excluded, BBE) at the start of each trial. Identical three-day exclusion trials were alternated between two sites 600 m apart; see Methods section 3.3.2 for trial dates between May-September 2017

### 3.3.3 Bee count data

Data collection followed established and effective methods for counting bees visiting flowers (Garbuzov & Ratnieks 2014b, Balfour, Gandy & Ratnieks 2015). We counted bees foraging in each patch from 09:00-17:30 on each trial day. To do this we made a near instantaneous count every 30 minutes in which we scanned the patch by eye for



approximately 30 seconds and recorded any bees and other insects actively foraging at that time (Garbuzov & Ratnieks 2014b). In general, bees spend <30 minutes in a patch during a single foraging attempt. Therefore, although individuals will revisit patches, the 30-minute interval between counts means that the count data represent different visits (Garbuzov & Ratnieks 2014b). After 17:30 all patches were covered with netting to prevent insect access until targeted exclusions resumed the following morning (Balfour, Gandy & Ratnieks 2015). Counts were primarily made by VW and to a lesser extent NLD, who was trained in insect identification and the instantaneous count method by VW prior to beginning the study. A strong effort was made to reduce any natural differences in observation method between the two ‘counters’ by making simultaneous but separate counts and then checking for consistency between the recorded information. This was repeated on multiple occasions to ensure counting method and accuracy of insect identification was as consistent as possible between VW and NLD. The insects recorded on each patch were represented in large part by only a small number of species (see Results section 3.4.1 and Appendix B.2) which helped to ensure a high level of accuracy and consistency between observers.

Bumblebees, including parasitic cuckoo species (subgenus *Psithyrus*), were mostly identified according to species. *Bombus terrestris* (L.) and the *B. lucorum* complex comprising the cryptic species *B. lucorum* (L.), *B. magnus* Vogt and *B. cryptarum* (Fabricius) (McKendrick et al. 2017), could not be reliably separated in the field, so were grouped and recorded as *Bombus terrestris/lucorum* agg. (Fussell & Corbet 1992). Any non-*Apis/Bombus* bees were identified according to species where possible, or to genus. Any bees that could not be recognised by eye were caught and identified using a hand lens or microscope. The vast majority of foragers were collecting nectar only and were only ever observed carrying trace amounts of pollen, supporting previous observations in which less than 5% of the foragers on Grosso were observed with pollen in their corbiculae (Balfour, Garbuzov & Ratnieks 2013).

### 3.3.4 Nectar measurement

During each trial we measured secretion rate, standing crop and sugar concentration using microcapillary pipette tubes (Drummond Microcaps 1 µL, 64 mm, 1-000-0010-64 or 0.25 µL, 32 mm, 1-000-00025) inserted into an open flower to extract the nectar from

the base of the corolla. The length of nectar drawn up into the tube was measured using a ruler and used to calculate the per-flower volume of nectar as a proportion of the overall tube volume (Corbet 2003, Balfour, Garbuzov & Ratnieks 2013). Each microcap was used a single time only (Corbet 2003). Nectar measurements were made once per trial, between 12:00-14:00 to minimise day-to-day variation, by VW on almost every occasion. Rarely, where necessary, nectar measurements were made by NLD who was trained extensively by VW in the technique to ensure consistency between observers.

To measure the per-flower volume of nectar available to insects (standing crop) we extracted nectar from 10 flowers in each patch. Nectar sugar concentration (% Brix) was measured for each sample with sufficient volume using a hand-held refractometer (Bellingham and Stanley<sup>TM</sup>, 0-50% Brix). To measure hourly nectar secretion rate per flower we used microcaps to empty as fully as possible several flowers in the CON patch, taking care not to damage the nectaries (Corbet 2003). We marked these flowers and bagged the entire inflorescence using fine gauze bags to prevent insect access. After 60 minutes, we extracted nectar from the marked flowers individually and recorded the volume of liquid contained in the microcap.

### 3.3.5 Statistical Analysis

We analysed seasonal changes in honeybee visits to lavender flowers when bumblebees were manually excluded (BBE patch) relative to the control (CON) patch over ten trials. The following statistical analysis uses the second and third exclusion days of each trial, when bee numbers and foraging behaviour had stabilised following one full day of exclusions. This is because we observed that honeybee numbers on the BBE patch often varied considerably over the course of the first trial day, which is consistent with previous research in which honeybee numbers took approximately 1.5 days to plateau following the start of bumblebee exclusion from lavender patches (Balfour, Gandy & Ratnieks 2015). To remove this noise in the data, we removed the first trial days from analysis.

As a proxy measure of competition we calculated the absolute difference in per-day mean honeybee counts from 09:00-17:30 ( $n = 18$  counts per day) between the two patches  $((\text{mean HB}_{(\text{BBE})}) - (\text{mean HB}_{(\text{CON})}))$ , hereafter  $\text{HB}_{(\text{BBE-CON})}$ , since this metric

gives a clear indication of the increase in honeybee visits to the BBE patch compared to the control. Using daily average counts removed pseudo-replication from the raw data, and normalised the positively skewed distribution, thereby also correcting for overdispersion.  $HB_{(BBE-CON)}$  also accounts for any between-trial variation in the number of flowers.

To analyse between-season variation in  $HB_{(BBE-CON)}$  we used a linear mixed effects model (lmer, package *lme4* version 1.1-17; Bates et al. 2015) with per-day  $HB_{(BBE-CON)}$  as the response ( $n = 20$ ) and season (early summer, late summer, autumn) as a fixed effect. Trial was included in the model as a random effect since we expected between-trial variation in  $HB_{(BBE-CON)}$ , but were not directly testing differences in the response between specific trials in this model (Bolker et al. 2009). Trial day (2 or 3) and site were added as interaction terms to assess any confounding effect on  $HB_{(BBE-CON)}$  with the effect of season, but neither were significant and so were not included in the final model. Residuals were visually checked for normality and homoscedasticity, and approved. Differences between seasons were calculated using *post-hoc* pairwise comparisons across groups, using lsm (package *lsmeans*, version 2.22; Lenth 2016) within glht (package *multcomp*, version pre- 1.4-15 (Hothorn, Bretz & Westfall 2008)), with  $P$  values adjusted for multiple comparisons by the single step method.

We did not expect honeybee exclusion (HBE) to impact bumblebee visitation, given previous results (Balfour, Gandy & Ratnieks 2015), although a seasonal effect was possible and worth investigating since the previous study was conducted only in late summer (July – August). In fact, honeybee abundance on control patches was consistently low, and there was no increase in bumblebee numbers on the HBE patch relative to the control (Fig. 3.2). We confirmed this statistically through repeating the analysis as for  $HB_{(BBE-CON)}$  detailed above, using the metric  $BB_{(HBE-CON)}$  as the response variable, with season as the predictor and trial as random effect. Model fit was diagnosed in the same way. There was no difference in  $BB_{(HBE-CON)}$  between seasons ( $\chi^2_{(2)} = 2.65$ ,  $p = 0.27$ ), therefore pairwise comparisons between seasons were not assessed. We did not analyse the effects of honey- and bumblebee exclusion on other insect groups since frequencies of these were too low for statistical analysis.

Nectar standing crop volumes were compared between patch treatments in each trial using per-trial Kruskal-Wallis H tests and *post-hoc* Dunn's tests for pairwise comparisons between treatments (Ogle, Wheeler & Dinno 2018) with Bonferroni adjustment of *P* values (results in Appendix B.1). One-hour nectar secretion rates were compared between batches of lavender plants (*n* = 4 batches) and between trials (data available for eight of 10 trials), also using Kruskal-Wallis H tests for non-parametric data since data in both instances failed normality assumptions.

We determined the association between nectar standing crop volume ( $\mu\text{L}$ ) and i) daily mean honeybee count and ii) daily mean honeybee count per 1000 flowers on the BBE patch using Spearman's rank order correlation coefficient. For this we used non-pooled data from days 2 and 3 for each trial, except day 2 of Trial 1 which was removed from the analysis due to missing nectar data. In both cases daily mean honeybee count was an average of counts made between 11:00-15:00 in order to be ecologically relevant to the time at which nectar readings were taken (between 12:00-14:00).

Significance was defined at  $P < 0.05$ . All analyses were performed using RStudio version 1.1.419, R version 3.4.3 (R Core Team 2020).

### 3.4 Results

#### 3.4.1 Insect abundances on the control patch

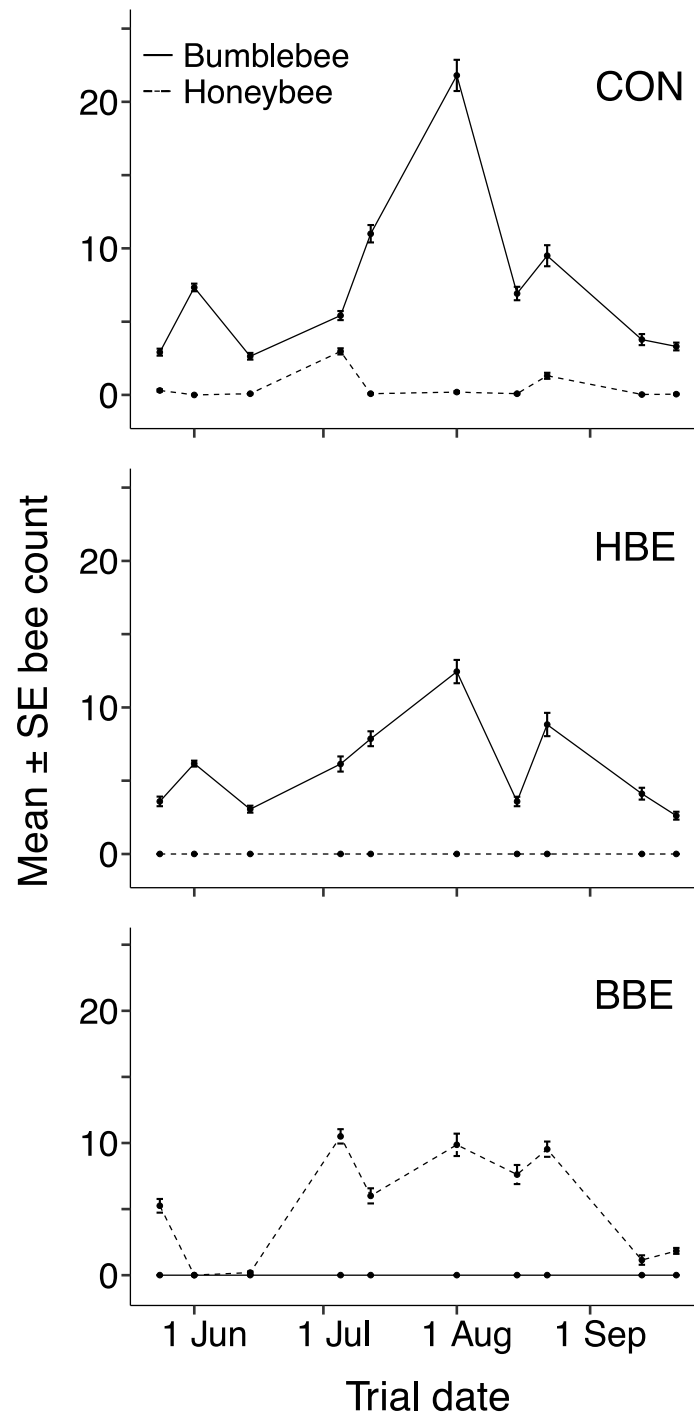
Almost all insects (96.4%, *n* = 3981 of 4128 insects in total, *n* = 30 trial days) observed foraging on the lavender control (CON) patches over the 10 trials were bumblebees (90.4%, *n* = 3733) and honeybees (6.0%, *n* = 248). Other foraging insects included butterflies and moths (1.7%, *n* = 71), hoverflies (0.7%, *n* = 27) and non-*Apis/Bombus* bees (0.6%, *n* = 24). The remaining 0.6% (*n* = 25) were classified as other insects and were mainly non-syrphid Diptera. The number of honeybees per count on the control patches was consistently low, often 0, with bumblebees approximately 15 times more numerous (overall mean  $\pm$  SD:  $0.51 \pm 1.09$  honeybees v.  $7.46 \pm 6.30$  bumblebees, *n* = 10 trials; Fig. 3.2). The abundance and species composition of bumblebee foragers on the control patch was variable over the study period, with *Bombus terrestris/lucorum* agg. And *B. pascuorum* (Scopoli) most frequent (Appendix B.2).

### 3.4.2 Honeybee response to bumblebee exclusion

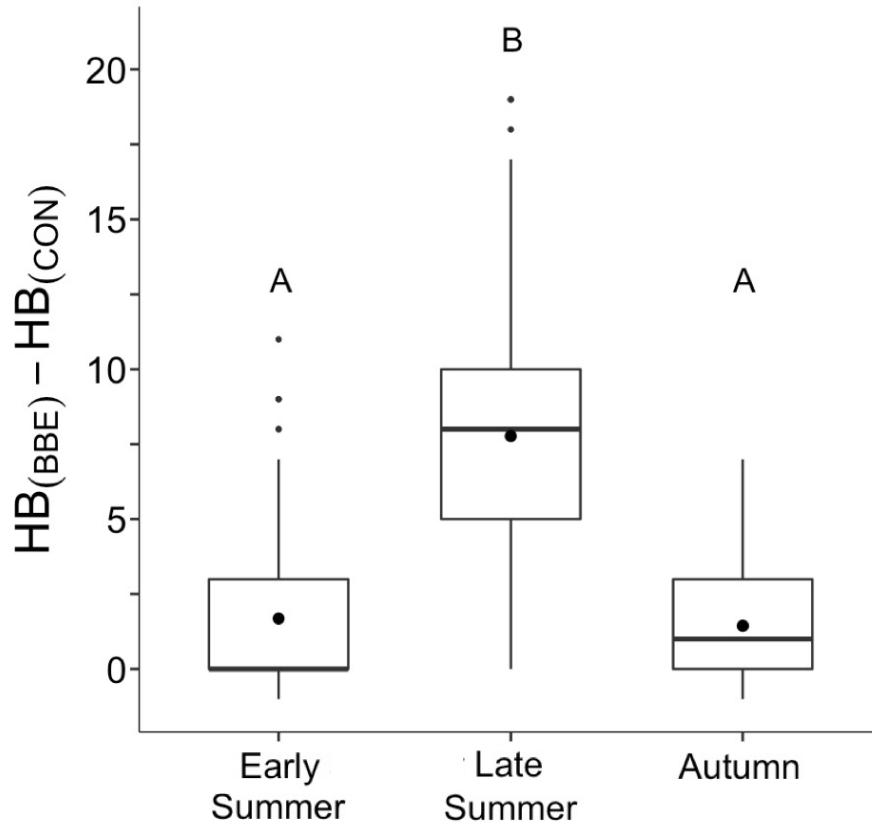
The per-trial mean number of honeybees foraging on the bumblebee excluded (BBE) patch compared to the control patch ( $HB_{(BBE-CON)}$ ) varied significantly according to season (LMER:  $\chi^2_{(2)} = 28.5$ ,  $P < 0.001$ ,  $n = 36$  counts per trial; Fig. 3.3). Importantly, the effect of bumblebee exclusion, mean  $HB_{(BBE-CON)}$ , per trial, was substantially and significantly greater in late summer trials (mean  $\pm$  SD,  $7.77 \pm 4.02$ ) than in early summer ( $1.69 \pm 2.90$ , GLHT:LSM *post-hoc*,  $t_{(7)} = 4.55$ ,  $P = 0.006$ ) or autumn trials ( $1.44 \pm 1.81$ , GLHT:LSM *post-hoc*,  $t_{(7)} = 4.13$ ,  $P = 0.010$ ). Mean  $HB_{(BBE-CON)}$  was not significantly different between early summer and autumn trials (GLHT:LSM *post-hoc*,  $t_{(7)} = 0.14$ ,  $P = 0.999$ ).

In late summer the number of honeybees visiting the BBE patch was consistently high in all five trials (mean  $\pm$  SD,  $8.7 \pm 4.27$  honeybees; Figs. 3.1 & 3.3). Mean per-trial  $HB_{(BBE-CON)}$  ranged from  $5.92 \pm 3.45$  (Trial 5) to  $9.67 \pm 5.09$  (Trial 6) in this season. In autumn, the number of honeybees visiting the BBE patch was consistently low ( $1.49 \pm 1.82$  honeybees; Figs. 3.1 & 3.3), despite many honeybees observed foraging on ivy flowers in close proximity to the study patches. Mean per-trial  $HB_{(BBE-CON)}$  was also low, from  $1.11 \pm 2.17$  (Trial 9) to  $1.78 \pm 1.31$  (Trial 10).

In early summer there was clear variation in the number of honeybees foraging on the BBE patch between trials (Figs. 3.1 & 3.3). In Trial 1, many honeybees were observed foraging on the BBE patch ( $5.25 \pm 3.11$  honeybees) compared to zero ( $0.00 \pm 0.00$ ) or few ( $0.194 \pm 0.467$ ) in Trials 2 and 3 respectively. During both Trial 2 and 3, honeybees were seen foraging on bramble flowers and other species of flowering plant in the study vicinity.



**Figure 3.2.** Numbers of honeybees (*Apis mellifera*, dashed lines) and bumblebees (*Bombus* spp., solid lines) foraging on lavender patches from which bumblebees have been excluded (BBE), honeybees have been excluded (HBE), and unmanipulated control patches (CON), across ten trials from May to September 2017. Points show the mean count per day averaged over trial days 2 and 3 ( $n = 36 = 2$  days  $\times$  18 counts per day from 09:00-17:30). Error bars show  $\pm 1$  SE



**Figure 3.3.** Seasonal change in  $HB_{(BBE)} - HB_{(CON)}$  between early summer ( $n = 3$  trials), late summer ( $n = 5$  trials) and autumn ( $n = 2$  trials) 2017.  $HB_{(BBE)} - HB_{(CON)}$  signifies the number of honeybees foraging on lavender plots from which bumblebees had been excluded (BBE) compared to unmanipulated control patches (CON;  $n = 18$  counts per day from 09:00-17:30). All data are from trial days 2 and 3. Boxplot limits are the 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers are 1.5 x the Interquartile Range, horizontal lines indicate the median, points within plots represent the mean (described as  $HB_{(BBE-CON)}$  in the text) and points outside whiskers represent outliers. Initials above plots (A, B) denote significance between per-season  $HB_{(BBE-CON)}$  means, defined at  $P < 0.05$

#### 3.4.3 Bumblebee response to honeybee exclusion

There was no increase in bumblebee numbers in response to honeybee exclusion, with similar visitation to HBE and CON patches in each trial (Fig. 3.2) and no difference in  $BB_{(HBE-CON)}$  between seasons (LMER:  $\chi^2_{(2)} = 2.65$ ,  $P = 0.27$ ). Honeybee numbers on CON patches were low throughout the study period (Fig. 3.2), and very few were ever

excluded from the HBE patches meaning that any effect on bumblebee numbers was likely to be negligible. Therefore, this result is not discussed further.

#### 3.4.4 Lavender nectar

Overall, mean hourly nectar secretion rate per flower was  $0.038 \pm 0.002 \mu\text{L}/\text{h}^{-1}$  (mean  $\pm$  SD,  $n = 154$  flowers). Mean hourly secretion rate was not different between four lavender batches grown under different regimes (Kruskal-Wallis H test:  $\chi^2_{(3)} = 6.77$ ,  $P = 0.079$ ,  $n = 4$  batches), but differed significantly between trials (Kruskal-Wallis H test:  $\chi^2_{(7)} = 25.47$ ,  $P < 0.001$ ,  $n = 8$  trials).

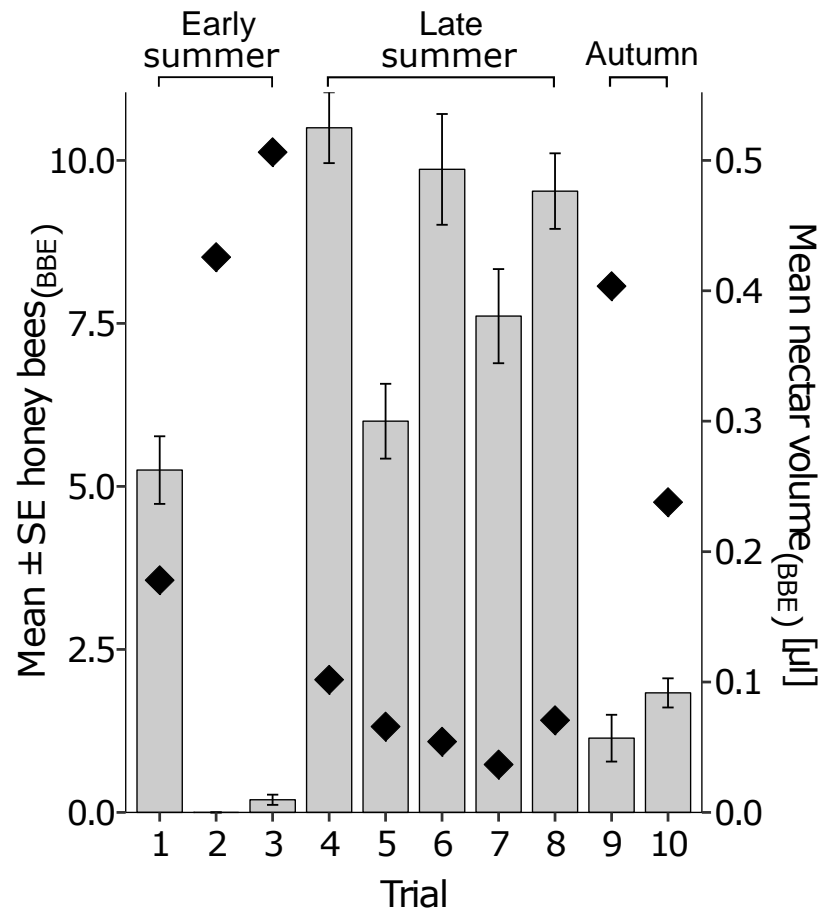
The following data refer to the per-trial average nectar standing crop volume extracted from 10 flowers per patch on days 2 and 3 of each trial ( $n = 20$  flowers per patch) except Trial 1 in which nectar was extracted only on day 2 ( $n = 10$  flowers per patch).

On the BBE patch, there was a significant negative correlation between per-day mean nectar standing crop volume ( $\mu\text{L}$ ) and i) mean honeybee count from 11:00-15:00 ( $r_s = -0.672$ ,  $P < 0.001$ ,  $n = 19$  trial days) and ii) mean honeybee count from 11:00- 15:00 per 1000 flowers ( $r_s = -0.486$ ,  $P = 0.020$ ,  $n = 19$  trial days), according to Spearman's rank order correlation tests. *I.e.*, when honeybees were visiting the flowers in large numbers, nectar standing crop volumes (both per bee per patch and per bee per 1000 flowers) were small, compared to high volumes when bees were visiting in low numbers (Fig. 3.4).

Average nectar standing crop volume was always low in the CON patch flowers (mean  $\pm$  SD over ten trials =  $0.042 \pm 0.078 \mu\text{L}$ ) and in HBE patch flowers ( $0.043 \pm 0.090 \mu\text{L}$ ). Nectar standing crop in the BBE patch ( $0.210 \pm 0.273 \mu\text{L}$ ) was higher than the control patch in every trial, which was significant in all trials apart from 1 and 4 according to per-trial Kruskal-Wallis H and *post-hoc* Dunn's tests for pairwise comparison between patch treatments (Appendix B.1). When averaged within seasons, nectar standing crop volume extracted from BBE patch flowers was 412% higher than the control patch in early summer (BBE  $0.408 \pm 0.276 \mu\text{L}$ ; CON  $0.099 \pm 0.120 \mu\text{L}$ ), 275% higher in late summer (BBE  $0.066 \pm 0.085 \mu\text{L}$ ; CON  $0.024 \pm 0.047 \mu\text{L}$ ) and 1783% higher in autumn trials (BBE  $0.321 \pm 0.361 \mu\text{L}$ ; CON  $0.018 \pm 0.019$ ).



Nectar standing crop volume in flowers in the HBE compared to CON patch was not significantly different in any trial, according to per-trial Kruskal-Wallis H and *post-hoc* Dunn's tests for pairwise comparison between patch treatments (Appendix B.1).



**Figure 3.4.** Mean number of foraging honeybees and nectar standing crop volume per flower on lavender patches from which bumblebees have been excluded (BBE) across ten trials from May to September 2017. Bars show the mean per-trial honeybee count ( $n = 18$  counts per day from 09:00-17:30), error bars show  $\pm 1$  SE. Filled diamonds indicate mean nectar standing crop volume per flower per trial ( $\mu\text{L}$ ;  $n = 10$  flowers per day). Nectar and bee count data for each trial are from days 2 and 3, except Trial 1 in which nectar was extracted only on day 2. Seasons are indicated above the bars: early summer (May – June, Trials 1-3); late summer (July – August, Trials 4-8) and autumn (September, Trials 9-10)

### 3.5 Discussion

Our results indicate, for the first time to our knowledge, that the strength of exploitative competition for nectar between two major pollinator groups can vary seasonally. As expected, *Apis-Bombus* competition on lavender Grosso flowers was greater in late summer than early summer or autumn (Fig. 3.3). On average, in late summer trials (July and August) there were 8.70 honeybees foraging on the bumblebees excluded (BBE) patch per count compared to 0.93 honeybees on the control (CON) patch, a near 10-fold increase, demonstrating ecological release from competition. In contrast, in early summer (May and June) and autumn (September) trials, honeybees were absent or very infrequent on the BBE patch, despite high levels of nectar in the flowers, suggesting the reverse, that competition for nectar was reduced in these periods. This seasonal trend was statistically significant using the metric  $HB_{(BBE-CON)}$  to compare the number of foraging honeybees on BBE vs CON patches between seasons.

Our results suggest that competition for nectar was high throughout the late summer period. Honeybees consistently visited the bumblebee excluded (BBE) patch in large numbers in each of the five July and August trials, while numbers on the control patch remained low (Fig. 3.2). Exploitative competition between coexisting species and individuals is expected to be strong when shared resources are limited, as a result of the interaction between the availability of food resources in the landscape and the abundance of competitors. Waggle dance decoding has shown that honeybees forage furthest from the nest in July and August (Couvillon, Schürch & Ratnieks 2014), and August is also the time with the largest proportion of returning foragers having empty crops (Couvillon et al. 2014). Since worker honeybees are efficient foragers that rapidly recruit nestmates to exploit the most profitable floral resources (Núñez 1982, Schmid-Hempel 1987, Requier et al. 2015), these studies imply that late summer is a period of limited overall nectar availability for bees.

Absolute nectar provision in kilograms per hectare is in fact estimated to be highest in July and August in the UK overall (Baude et al. 2016). However, this is likely to be subject to local effects. For example, late summer-flowering heather species *Erica cinerea* L. and *Calluna vulgaris* (L.) together are estimated to have contributed 16.5% of annual national nectar provision in 2007 (Baude et al. 2016), but these are virtually

absent in our study area. Additionally, non-woody flowering plants (herbs) make up the majority of insect-pollinated plant species flowering in July and August (Balfour et al. 2018). However, this floral group is known to have suffered extensive declines in the 20<sup>th</sup> century (Stroh et al. 2014) including significant decreases in the range and frequency of important summer-flowering pollinator forage plants (Carvell et al. 2006). Even if absolute nectar provision is greater later in the summer, per-insect nectar availability could still be lower in this season if there are many more nectar-feeding insects. A recent study of British phenological records showed that 62% of flower-visiting insect species (71% of aculeate wasp, 60% bee, 72% butterfly and 49% of hoverfly species) peak in abundance in July and August (Balfour et al. 2018). It is therefore possible that increased insect abundance and reduced flower availability combine to create a late summer increase in competitive pressure for pollinating insects due to lower per-insect nectar availability.

Stronger nectar competition in late summer is likely to affect competition between honey- and bumblebees since they are floral generalists that often have a high level of interspecific dietary overlap, particularly for nectar (*e.g.* Forup & Memmot 2005, Thompson 2006; but see Leonhardt & Blüthgen (2012) for differences in pollen foraging). For example, in a summer foraging ‘hotspot’ for honeybees 2-3 km from our study site, which was identified by waggle dance decoding (Couvillon, Schürch & Ratnieks 2014), honeybees and bumblebees visited similar flowers in July and August (Balfour et al. 2015). Additionally, both *Apis* and *Bombus* are eusocial and have substantial colony requirements: a typical honeybee colony requires 20kg pollen and 120kg nectar per year (Seeley 1995), while in one study *Bombus terrestris* colonies consumed on average 176g pollen and 935g sugar over a 12-week lifecycle (Rotheray, Osborne & Goulson 2017). Honeybees and 22 of 27 UK bumblebee species have a late summer peak in abundance (Falk & Lewington 2015, Balfour et al. 2018). Increased demand for limited per-insect nectar and pollen resources later in the summer is a likely explanation for our findings and previous work showing strong competition between honeybees and bumblebees at this time of the year in the UK (Goulson & Sparrow 2009, Elbgami et al. 2014, Balfour, Gandy & Ratnieks 2015) and Europe (Walther-Hellwig et al. 2006).

In contrast to late summer, in early summer and autumn trials we observed that although honeybees were seen visiting flowering plant species in the close vicinity, they foraged infrequently or not at all on the BBE lavender patches despite a much greater nectar standing crop volume in the flowers, on average 6-fold greater in early summer and 5-fold greater in autumn compared to late summer (Fig. 3.4). This strongly suggests that nectar competition was reduced in these seasons, since exclusion of bumblebees caused little or no increase in honeybees: ecological release from competitive displacement was not apparent. It suggests that honeybees did not ‘need’ the lavender nectar in autumn and early summer, perhaps due to higher per-insect nectar availability in the wider local environment. This may relate partly to the seasonal bloom of certain wildflowers, which is known to have an ecologically significant impact on the amount of nectar available to bees (Seeley 1995). In autumn the apparent drop in *Apis-Bombus* competition was likely due to the blooming of ivy (*Hedera* spp.), which is abundant and a major source of pollen and nectar in autumn for many insects (Jacobs et al. 2010, Garbuzov & Ratnieks 2014a). Since ivy significantly impacts foraging behaviour when it is in flower and is likely to cause a marked increase in nectar availability (Couvillon, Schürch & Ratnieks 2014), its flowering period may also cause a seasonal reduction in inter- and intra-specific exploitative competition between insects foraging at this time of year. Similarly, in early summer trials, lower *Apis-Bombus* competition overall may have been due to a generally richer floral community in May and June than late summer months (Balfour et al. 2018).

Why did honeybees not forage on lavender flowers in early summer and autumn trials, despite the absence of the dominant competitor and resultant high nectar standing crop; what mechanism could be involved? A nectar volume of 0.019  $\mu\text{L}$  and 39% sugar concentration resulted in a substantial energetic profit for honeybees foraging on Grosso lavender, enough to cause a 14-fold increase in honeybee numbers (Balfour, Gandy & Ratnieks 2015). In this study nectar volume reached a much greater maximum per-trial average of 0.506  $\mu\text{L}$  in BBE patch flowers in early summer (concentration 41.4% sugar,  $n = 17$  flowers; Trial 3) and 0.404  $\mu\text{L}$  in autumn (concentration 32.8% sugar,  $n = 17$  flowers; Trial 9), suggesting that honeybees would certainly have been able to make a significant profit from foraging on the flowers in these seasons.

Although the high nectar standing crop in BBE-patch lavender flowers in early summer and autumn trials implies that foraging honeybees could make a profit, it is possible that lavender Grosso was nevertheless suboptimal compared to other floral resources in the environment. More abundant nectar availability in these seasons may have reduced recruitment of nestmates to the BBE patch (Seeley 1995). When colony nectar intake is high, honeybee nectar foragers adaptively raise their dance thresholds, meaning that only high-quality food sources are advertised by returning foragers (Seeley 1995). In contrast, in resource-scarce late summer months greater honeybee recruitment to the BBE flowers may be explained by a lower colony dance threshold.

Both honeybees and bumblebees are often numerically dominant foragers on a wide range of flower species (Couvillon et al. 2015, Balfour et al. 2020). This is likely often to impact the foraging behaviour of other common flower-visiting insects including non-*Apis/Bombus* bees, butterflies and hoverflies. In this study we did not analyse the effects of competitor removal on other insect groups, since these were too infrequent on the lavender flowers for the necessary statistical power. Plants with a greater number of non-*Apis/Bombus* insect foragers may be more suitable for experiments in which the exclusion method used here could begin to examine competition between honeybees, bumblebees and other insect taxa through the removal of both *Apis* and *Bombus*, as well as each group separately; this deserves further investigation.

The effect of seasonal fluctuations in exploitative competition between *Apis* and *Bombus* at a population level in areas where both are native is not clear. However, in one UK study conducted in August, workers of four bumblebee species had smaller average thorax size in sites where honeybees were present compared to where they were absent (Goulson & Sparrow 2009). It is possible that there may be negative fitness implications in times of increased competitive pressure, at least for bumblebees, although further research is needed to clarify this. Future research could also investigate whether these possible population-level effects could be compensated for by seasons in which exploitative competition is weaker.

We show here that the strength of competition for a standardised floral nectar resource between bumblebees and honeybees varies seasonally, with a late summer peak in July and August. This is similar to previous work in which waggle dance decoding showed

that honeybees forage furthest from the hive in July and August, indicating a dearth in environmental nectar availability relative to other times of the year (Couvillon, Schürch & Ratnieks 2014). Our results, therefore, also help confirm that waggle dance decoding can provide useful information about foraging conditions for honeybees. Honeybee foraging distances are thought to act as an indicator of seasonal foraging challenge for other flower-visiting insects (Couvillon, Schürch & Ratnieks 2014). We suggest that seasonal trends in competition between honeybees and bumblebees may similarly predict patterns of competitive pressure for floral resources between flower-visiting insects more broadly. While we have studied lavender as a useful phytometer with which to observe changes in *Apis-Bombus* competition, future studies should also extend this to include other locations and plant species, including native and wild-growing flowers if possible, in order to confirm our findings.

Understanding the seasonality of resource demand and competition between bee and other insect species is also important for informed conservation practice (Williams et al. 2015). Many insect species are in decline in Europe and globally (*e.g.* Potts et al. 2010, Hallmann et al. 2017, Powney et al. 2019, van Klink et al. 2020) and for flower-visitors a major driver is thought to be a widespread loss of floral resources (Goulson, Lye & Darvill 2008, Potts et al. 2010, Roulston & Goodell 2011). A need to help insect pollinators may be particularly important in July and August months, when competition for nectar seems to be increased in the UK (Couvillon, Schürch & Ratnieks 2014, Balfour et al. 2018, this study). Seasonal plant-pollinator interactions are also likely to be affected by climate change, which can be mitigated by increasing floral availability at certain times of the year (Memmott et al. 2010). Overall, there is a clear need to ensure that floral resources for bees and other insects are sustained throughout the foraging season by considering per-insect floral resource availability in local and landscape-scale resource management. A better understanding of seasonal variation in nectar competition can help in achieving this.

## Chapter Four: Exploitative competition and displacement mediated by eusocial bees: experimental evidence in a wild pollinator community

*Dedicated to Hannah Chipperfield*

### Authors and author contribution statement

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VW and FLWR conceived the ideas; VW led the data collection, data analysis and writing of the manuscript; MB, CU, KEN, HMC and NJB contributed to data collection

### 4.1 Abstract

Eusocial bees are likely to be ecologically important competitors for floral resources, although competitive effects can be difficult to quantify in wild pollinator communities. To investigate this, we excluded honeybees (HBE treatment), bumblebees (BBE), or both (HB&BBE) from wild-growing patches of bramble, *Rubus fruticosus* L. agg., flowers in two eight-day field trials at separate locations, with complementary mapping of per-site local floral resource availability. Exclusions increased per-flower volume of nectar and visitation rates of non-excluded bees, compared to control patches with no bee exclusions (CON). There was a large increase in average nectar standing crop volume both at Site 1 (+172%) and Site 2 (+137%) in HB&BBE patch flowers, and no significant change in HBE or BBE, compared to CON patches. Foraging bee responses to exclusion treatments were more pronounced at Site 2, which may be due to lower local floral resource availability, since this is likely to increase the degree of exploitative competition present. Notably, at Site 2 there was a 447% increase in larger-bodied solitary bees visiting HB&BBE patches, suggesting ecological release from competition. Hoverflies showed no response to bee removals. Numbers of other non-bee insect groups were very small and also showed no clear response to exclusions. Possible long-term implications of displacement from preferred flowers, particularly where alternative forage is reduced, are discussed. The limitations of this study, in particular the inclusion of only two sample sites in the experimental design, are also discussed.

Our results can be seen as preliminary findings regarding patterns of competitive exclusion between pollinator groups, mediated by resource depletion by eusocial bees.

## 4.2 Introduction

Flower-visiting insects gather pollen and nectar for their energetic needs and to feed their larvae. Because these resources are shared and can also be limiting, this sets the stage for exploitative competition both among individuals and species of flower-visitors. Depletion of floral resources by dominant foragers can cause others to move to alternative sources of forage, in both spatial and temporal partitioning of resources (Wilms & Wiechers 1997, Walther-Hellwig et al. 2006, Dupont et al. 2004). This can mitigate the negative effects of competition, allowing coexistence (Hardin 1960, Amarasekare 2003). However, and particularly where resources are limited, there may be fitness costs for non-dominant species following reduced overall resource acquisition and a decrease in reproductive output (Zurbuchen et al. 2010a, Hudewenz & Klein 2015, Thomson 2016).

Honeybees (*Apis mellifera* L.) and bumblebees (*Bombus* spp.) are relatively abundant in many flower-visiting insect communities (e.g. Nielsen et al. 2012, Garbuzov & Ratnieks 2014b, Balfour et al. 2015). Both have large colony requirements for nectar and pollen (Seeley 1995, Cane & Tepedino 2017, Rotheray, Osborne & Goulson 2017), which foragers extract from flowers more rapidly than many other insects, including solitary bee species (Couvillon et al. 2015). They have large foraging ranges allowing them to maximise resource use over a wide area (Seeley 1995, Walther-Hellwig & Frankl 2000), and honeybees are able to actively recruit nestmates to profitable resources via the waggle dance (Seeley 1995). Additionally, *Bombus* and particularly *Apis* are often commercially managed for pollination or (*Apis*) honey production, which can create artificially high densities particularly of honeybees. Overall, they are likely to deplete floral resources where they are present (Torné-Noguera et al. 2016), thereby exerting competitive pressure on other flower-visiting insects. This has received continuing research interest (for example, see recent reviews: Mallinger, Gaines-Day & Gratton 2017 & Wojcik et al. 2018).



Resource depletion by honey- and bumblebees can have negative effects between these groups (*e.g.* Goulson & Sparrow 2009, Thomson 2016, Sáez et al. 2017). It can also affect the many species of non-*Apis/Bombus* bees (*e.g.* Hudewenz & Klein 2015), most of which have a solitary lifecycle and are hereafter termed ‘solitary bees’ (following Baldock et al. 2015, Balfour et al. 2015). Female solitary bees build a central nest to rear their offspring, provisioning each cell with pollen and nectar. They tend to have much smaller average foraging distances than honey- and bumblebee workers (Gathmann & Tschardt 2002, Zurbuchen et al. 2010b), meaning that they may be more affected by local changes in resource availability. In one study, experimentally increasing the distance from two species of solitary bee (*Hoplitis adunca* Panzer and *Chelostoma rapunculi* Lepeletier) nests to preferred flowers increased the duration of foraging bouts for the same quantity of resources. The authors used an indirect method to show that increased foraging duration caused a decrease in reproductive output (Zurbuchen et al. 2010a). Solitary bees may therefore be particularly vulnerable to the effects of exploitative competition, particularly when resources are scarce. However, this is not well understood (see Mallinger, Gaines-Day & Gratton 2017), despite the importance of these bees for the pollination of many crop and wild plants (Williams & Kremen 2007, Garratt et al. 2014a,b, Garibaldi et al. 2014, Mallinger & Gratton 2015).

*Apis/Bombus*-mediated depletion of nectar and pollen may also affect other flower-visiting insects such as hoverflies, non-syrphid Diptera, butterflies, moths and wasps. Excepting wasps, these groups are not central-place foragers, *i.e.*, they do not have a central nest to provision. Their foraging strategies and requirements are therefore different to bees, since they do not collect resources to feed offspring, having only individual energetic needs, and can also more flexibly move away from areas where resources are depleted. As such it is possible that their foraging behaviour may be less affected by immediate local resource depletion. Previous research found that an increase in honeybee abundance caused spatial displacement of bumblebees, solitary bees and non-bee flying insects in oilseed crop fields (Lindström et al. 2016). However, there is little research investigating the effects of exploitative competition on non-bee insects.

The effects of resource competition are often studied where managed pollinators are introduced to areas where they are not native or are uncommon, thereby creating an increase in the abundance of a potential competitor (reviewed in Stout & Morales

2009). However, patterns of competition in natural flower-visiting communities can be difficult to detect (Forup & Memmott 2005, Goulson et al. 2002). Spatial and temporal niche partitioning behaviours in response to fluctuating competitive pressure facilitate coexistence among insect groups with dietary overlap, meaning that resource competition is often likely to be a key, but masked, factor in observed flower choice and foraging behaviour (Balfour, Gandy & Ratnieks 2015). Exclusion experiments in which dominant competitors are removed from flowers are a valuable way to reveal these underlying patterns of competition between insect groups (Balfour, Gandy & Ratnieks 2015). These can help to improve our understanding of the role of competition in existing pollinator communities, which can in turn help to inform conservation practice for bees and other flower visiting insects, for example by improving provision of floral resources in areas or seasons when they are most needed (Garibaldi et al. 2014, Couvillon, Schürch & Ratnieks 2014, Wignall et al. 2020a).

In this study we used established exclusion methods to investigate whether honeybees and bumblebees compete with each other and with other flower-visiting insects for a common and abundant wildflower, bramble (*Rubus fruticosus* L. agg.), which produces large quantities of nectar and pollen and is a major food source for many insects (Taylor 2005, Couvillon et al. 2015, Falk & Lewington 2015). We chose to study *R. fruticosus* as it is common throughout the UK, it has a long flowering season and its flowers are visited by a wide range of insects. Collectively, these factors mean that bramble was a useful and ecologically important species with which to investigate competition among flower visiting species, and that our findings would be of broad relevance.

We established four bee-exclusion treatments: no bees excluded (Control), honeybees excluded (HBE), bumblebees excluded (BBE) and both honey- and bumblebees excluded (HB&BBE) on patches of wild-growing *R. fruticosus* in two field trials in Sussex, southeast England. Using two study sites allowed us to make a preliminary investigation into how exclusions affected nectar availability in the bramble flowers, and flower visitation by non-excluded *Apis* or *Bombus* bees, solitary bees, hoverflies and other foraging insects. We incorporated landscape-level context by measuring local floral resource availability within a 500 m radius of each study site. The possibilities for extending this experimental design on a larger scale are explored in section 4.5.6.

### 4.3 Materials and Methods

#### 4.3.1 Study sites

Two eight-day bee-exclusion trials were carried out on the outskirts of Brighton, a city in southeast England, UK. The first trial (20.06.2019 – 02.07.2019) studied bramble growing in a semi-rural location, in a field of unimproved grassland occasionally used for sheep grazing in the South Downs, 1 km southeast of the University of Sussex campus (hereafter Site 1; 50°854374'N, -0°09413480'W). The second trial (04.07.2019 – 13.07.2019) was carried out in an area of urban greenfield with bramble growing in hedges, next to residential housing 200 m north of Brighton Marina (hereafter Site 2; 50°815178' N, -0°102075'W). In each location bramble plants were abundant and in full bloom in hedges and stand-alone patches from c. 0.5 to 4 m above ground level. Although there were no records of the number of managed or feral colonies in the study region, it was assumed that honeybee numbers would be relatively consistent between the sites since there are many active beekeepers in East Sussex and density of honeybees is high in the region (Wignall et al. 2020b). Additionally, the study sites were just over 4km apart meaning that the number of colonies between the two sites would not vary too greatly. The number of honeybees visiting control patches were similar between sites which supports this assumption (*Results*).

#### 4.3.2 Exclusions and experimental design

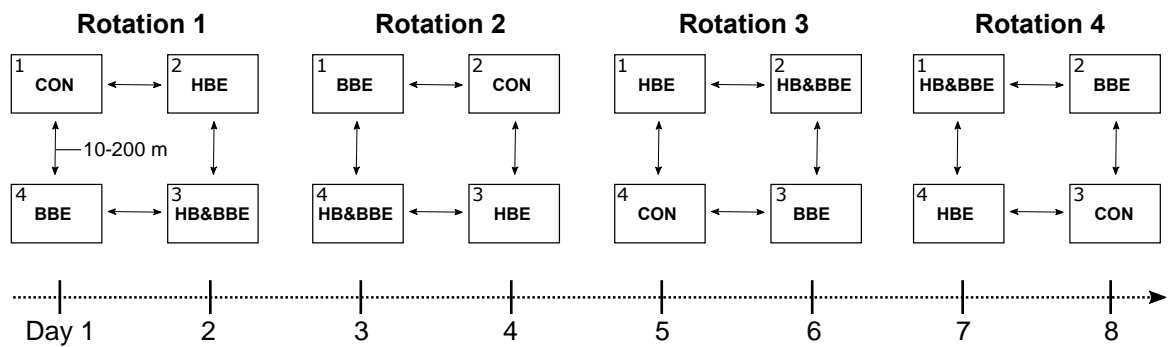
In each eight-day trial, four patches of bramble were designated and rotated through four bee-exclusion treatments: CON: control, no bees excluded; HBE: honeybees excluded; BBE: bumblebees excluded; HB&BBE: both honeybees and bumblebees excluded. This allowed us to investigate the effects of competition exerted by *Apis* and *Bombus* separately and in tandem. Using established methods, bees were continually excluded by tapping them gently with a bamboo cane. This method is very effective in reducing the excluded bee type to close to zero (Balfour, Gandy & Ratnieks 2015, Wignall et al. 2020a); in this study, numbers of excluded bee types recorded foraging on HBE, BBE and HB&BBE were between 1.4-13.1% of the total insects per treatment at Site 1 and 0.5-4.4% at Site 2 (Appendices C.1 & C.2). This required one or two researchers to monitor each patch and perform exclusions throughout the day, from

09:00 – 18:00 (VW, MB, CU, KEN, HMC and NJB). At least one individual was also present at CON patches at all times, despite no bees being excluded, to ensure consistency in the patch environment for foraging insects. Researchers were all trained extensively in the experimental methodology by VW and rotated regularly between patches during each trial day, which ensured that no bias was introduced by any natural differences in researcher technique, effort or accuracy. Since many researchers were present during each trial day, including the lead author VW, a natural system of cross-monitoring between researchers was in place which helped to ensure that research technique was consistent between observers. Due to this experimental design, in which researchers making exclusions needed to know which bees to exclude on the respective patches, it was not possible to record data blind to the patch treatment.

We chose patches of bramble in full bloom, as similar in flower density, patch size and exposure to sun and wind as possible. Each was approximately 2 x 4 m wide and was trimmed as necessary to consistent sizes and numbers of flowers. Patches were always between 10-200 m apart to ensure they were distinct. Treatments were allocated randomly to the four patches and rotated after two days of data collection, so that each patch was used for each of the four exclusion treatments, to control for any possible differences between patches, including microclimate effects or presence of bee or wasp nests in the close vicinity. Each two-day rotation was on two consecutive days so that the effect of exclusions on day 1 would directly influence day 2 (Fig. 4.1). The distance between patches meant that excluded honey- and bumblebees, which both commonly forage to distances greater than 200 m (Seeley 1995, Walther-Hellwig & Frankl 2000), would feasibly be able to move to nearby treatment patches from which they had not been removed (CON or BBE/HBE). However, the likelihood that the number of bees on other treatment patches could be inflated by excluded individuals is minimal since flowering bramble plants were abundant at both sites, with treatment patches estimated to comprise <5% of the total bramble within a 50 m radius. Bramble was also common in the wider area (Appendix C.3).

Data were collected only on days with good insect foraging conditions: >16°C, low wind, and no rain. Bees were excluded from 09:00 to 18:00, and counts of all insects foraging on the bramble flowers on each treatment patch were made every half hour from 10:00 to 17:00, the most active foraging hours (Garbuzov & Ratnieks 2014b,

Balfour, Gandy & Ratnieks 2015). This allowed treatments to be established for one hour in the morning before data collection started and continued for an hour after the counts ended in order to maintain the exclusion treatments. Counts were ended at 17:00 as by this time insect numbers generally had dropped significantly and some patches were in shade. Since the duration of time spent foraging in one patch of flowers is rarely longer than a few minutes (except for beetles which were not included in this study), 30 minutes was considered ample time to prevent counting the same insect twice. If an individual revisited the patches after 30 minutes and was counted again, this was considered to be an independent foraging decision, showing a genuine preference rather than an individual simply persisting in the same patch in a single visit (following Garbuzov & Ratnieks 2014b).



**Figure 4.1.** Experimental design per site. Four patches of bramble (boxes 1-4) between 10-200 m apart were rotated through four patch treatments: CON, control, no bees excluded; HBE, honeybees excluded; BBE, bumblebees excluded; HB&BBE, both honeybees and bumblebees excluded. Each trial consisted of 8 days in total made up of four two-day rotations

Where possible, bees, hoverflies, butterflies, moths and wasps were recorded to species on the wing as they were counted. Any that could not be were caught for closer examination in the field. Where it was not possible to identify insects in the field, specimens were taken to the lab to be identified using a microscope. For *Lasioglossum* bees, which were numerous at the second site and for the most part have microscopic identifying features, a representative sample were taken as specimens to minimise destructive sampling. We did not attempt to identify non-syrphid Diptera since these would need an expert dipterologist for accurate identification. These were not

numerous, only 0.0-2.8% of control patch insects (see Results) and were recorded in four body size categories determined by eye (very small, small, medium, large).

Any territorial hoverfly behaviour was noted, and in some instances we removed patrolling male *Eristalis tenax* L. hoverflies since these were actively preventing bees, butterflies and other insects from foraging (Wellington & Fitzpatrick 1981) and were therefore interfering with the exclusion treatments.

#### 4.3.3 Nectar standing crop volume ( $\mu\text{l}$ ) and sugar content

To quantify nectar availability to foraging insects, we measured the standing crop volume and sugar concentration of nectar in ten bramble flowers per treatment on each trial day. We extracted nectar from each flower's central nectar disc using glass microcapillary tubes (Drummond Microcap 1 $\mu\text{l}$ , 64mm, 1-000-0010-64 or 0.25 $\mu\text{l}$ , 32mm, 1-000-00025). The length of nectar drawn into the tube was measured and used to calculate the per-flower nectar volume in  $\mu\text{l}$  as a proportion of the overall volume of the tube (Corbet 2003). Nectar sugar concentration (% Brix) was measured for each sample with sufficient volume using a hand-held refractometer (Bellingham and Stanley<sup>TM</sup>, 0-50% Brix). Any samples with sugar concentration below 10% were assumed to be mostly rain or dew and discarded, and a sample taken from a new flower. Nectar measurements were made by VW between 12:00 and 14:00 each day to reduce time-dependent variation.

Per-flower nectar sugar content (mg/ml) was calculated using nectar concentration and standing crop volume. Concentration values (% Brix) were converted to sucrose content (mg) for each sample using Table 79 in the CRC handbook of chemistry and physics (1971-1972; Weast 1971). Sucrose (mg) was multiplied by standing crop volume (ml) to give the total sugar content per flower in mg/ml (Bolten et al. 1979).

Measurement of nectar concentration was subject to sampling biases. First, concentration values are bound at 50% Brix due to the 0-50% refractometer used. Actual concentration may have been higher than 50% where this was recorded, meaning that calculated averages for per-flower sugar content may be conservative. Second, concentration could not be measured for nectar samples with small volumes (Site 1:

mean standing crop volume of unmeasurable samples = 0.053  $\mu\text{l}$ ,  $n = 84$  of 320 samples; Site 2: mean = 0.059  $\mu\text{l}$ ,  $n = 186$  of 310) due to refractometer sensitivity. Nectar concentration increases at smaller droplet volumes due to a greater rate of evaporation (Corbet 2003) possibly leading to biased exclusion of samples with higher concentrations. Although any effect of this will be minimised to a degree by the very low volume of excluded samples, reported average per-flower nectar sugar content per treatment may be conservative where many samples were excluded, which disproportionately affects those with lower average standing crop volume (*Results*). Together, these factors limit the accuracy of nectar sugar content data and these should be interpreted with caution.

#### 4.3.4 Local land-use and wildflower diversity

We mapped the local habitat types and wildflower diversity within a 500 m radius of the centre of each site to add resource availability context to our study. Most solitary bees have a maximum foraging range of <500 m from their nests (Gathmann & Tscharntke 2002), while average foraging ranges tend to be far smaller than the maximum (Zurbuchen et al. 2010b). Bumblebees also often forage within 500 m of their nest, although they are capable of longer flights (Walther-Hellwig & Frankl 2000). Honeybees are able to forage much longer distances from the hive, up to c. 10-12 km, but normally forage at much lower distances (Seeley 1995, Couvillon, Schürch & Ratnieks 2014). This distance, therefore, gives a meaningful measure of the local resource availability for bees, particularly solitary bees and bumblebees.

We used QGIS 3 (version 3.0.3 Girona) to manually categorise each land-use type within the 500 m radius and to quantify the total area of each. Using this we then determined two approximate measures of the local resource availability for flower-visiting insects per site. First, the total '*flowers possible*' surface area, which included any greenspace or habitat where flowers could grow, compared to the area of impermeable surfaces and water. Within the '*flowers possible*' area we then determined the '*flowers available*' area per site, after removing arable fields, golf courses and sports pitches following site visits to verify that flowers were absent or at extremely low densities in these sub-areas. Remaining land-use types categorised as having flowers available were: (Site 1) field margins, unimproved grassland, field used as the study site

(unimproved grassland and scrub), woodland, road verges, residential gardens; (Site 2) field used as the study site (urban greenfield), woodland, nature reserve, flowery road verge, residential gardens, other urban greenspace, urban greenfield and cliff face (Appendix C.1).

Within the '*flowers available*' area, we calculated the proportion of each land-use type that could be surveyed, excluding areas such as cliff face and residential gardens that we were unable to access. We then used 200 m<sup>2</sup> belt transects to measure the presence, abundance and diversity of wildflowers in bloom within each surveyable type (see following paragraph; Balfour et al. 2015). For each site, we used the same number of transects in each type rather than stratifying by land-use area, so that linear habitats such as field margins were sampled with an equal effort since these can be important resources for pollinators (Balfour et al. 2015) despite being a smaller total area respectively. We completed eight transects per surveyable habitat type at Site 1 and four at Site 2, since the surveyable '*flowers available*' area at the first site (549,542 m<sup>2</sup>) was much greater than that of the second site (62,993 m<sup>2</sup>).

To measure species richness per habitat type, we recorded the presence of any wildflower species found within 1 m on either side of a 100 m transect. At field margins and road verges, transects were 200 m and flowers recorded within one metre on a single side, so that transects were always 200 m<sup>2</sup> in total. To quantify floral abundance (petal area) and diversity, we placed five 1 x 1 m quadrats to alternate sides of the transect at 20 m intervals (or 40 m intervals in the 200 m transects). We recorded the number of floral 'units' (flowers, capituli or umbels) of each wildflower species within the quadrat, and later standardised these using wildflower guides (Streeter 2009, Rose 1981) to give a measure of petal area for each unit, a relevant measure of floral abundance for foraging insects (Balfour et al. 2015). All surveys for each site were completed by VW and MB within one week of trial completion to ensure a relevant measure of current flower availability in the area.

#### 4.3.5 Statistical analysis

Data from each site were analysed separately to explore the effects of bee exclusion treatments on insect visitation and nectar characteristics, since the large difference in



number of insects between sites (*Results*) masked the effects of treatment when site was included as a predictor variable. Data presented and analysed include both exclusion days of each rotation to maximise statistical power, meaning reported effects will be conservative since insect response to exclusion takes approximately one day to reach its full effect (Balfour, Gandy & Ratnieks 2015), which also affects nectar volume. All statistics were calculated using RStudio version 1.2.5042, R version 3.6.3 (R Core Team 2020). Significance was taken as  $P < 0.05$ .

Insect count data included half-hourly counts between 10:00 – 17:00 on each exclusion day ( $n = 15$  counts per day per treatment, 8 days per trial). For each site the effects of exclusion treatments on counts of each insect group were analysed using zero-inflated generalised mixed effects models (GLMM) with *glmmTMB* to account for an excess of zeros in the count data (*glmmTMB* package version 0.2.3; Brooks et al. 2017). Fixed effects were treatment (CON, HBE, BBE and HB&BBE) and insect group (honeybees, bumblebees, solitary bees, hoverflies and other insects (comprising butterflies/moths, non-syrphid Diptera and wasps, grouped as ‘other insects’ due to small sample sizes, see Results)), with an interaction term between these variables. Rotation and patch were included as crossed random effects. Estimated marginal means and *post-hoc* pairwise comparisons for the effect of treatment within each insect group were calculated using *emmeans* (version 1.4.1; Lenth 2019).

At the first site, there were very low numbers of solitary bees (between 0.13 to 0.31 bees per count per treatment on average, 0 bees in 81.1% of counts; Appendix C.1), therefore this group was included as ‘solitary bees’ without subsetting for optimal model stability and reliability of results. At the second site, there were larger numbers of solitary bees (between 1.12 to 3.22 bees per count per treatment on average; Appendix C.2). Therefore, to explore whether solitary bee foraging response to bee exclusion treatment varied with body size, solitary bees were included as two separate insect groups: larger-bodied solitary bees (forewing  $>5.5$  mm (Falk & Lewington 2015); genera: *Andrena*, *Anthophora*, *Megachile*, *Osmia*) which are similar in size to honey- and bumblebees and are likely to be affected by any changes in floral reward caused by the removal of these bees (Henry & Rodet 2018), and smaller-bodied solitary bees (forewing  $\leq 5.5$  mm (Falk & Lewington 2015); genera: *Halictus*, *Hylaeus*, *Lasioglossum*) that have far smaller nectar and pollen requirements (Müller et al. 2006) and are likely

to be less affected by any changes in floral reward. Final models were compared to null models using likelihood ratio tests. Scaled residuals were plotted and visually approved for both final models using R package *DHARMa* (version 0.3.1; Hartig 2020), with further targeted goodness-of-fit tests for over- and underdispersion between the observed vs simulated residuals.

At the first site, solitary bee diversity was not compared between treatments due to very low numbers of foraging bees meaning that any differences were highly likely to be due to chance (see above and Appendix C.1). At the second site a standard measure of diversity, the Shannon-Wiener  $H'$  diversity index, was used to compare solitary bee species diversity between treatments:

$$H' = - \sum_{i=1}^R p_i \ln p_i$$

Where  $p$  ( $= n/N$ ) is the proportion of the total sample ( $N$ ) represented by species  $i$  ( $n$ ). Pielou's measure of species evenness ( $J'$ ) was also calculated for each treatment by dividing the Shannon-Wiener  $H'$  index by the natural logarithm of species richness ( $J'=H'/\ln S$ ).

For each site, One-Way Analysis of Variance (ANOVA) was used to investigate the effect of treatment on (i) nectar standing crop volume ( $\mu\text{l}$ ) and (ii) sugar content per flower ( $\text{mg/ml}$ ), with Patch and Rotation included as crossed blocking factors. Tukey's HSD *post-hoc* tests were performed for pairwise comparisons between treatments.

Wildflower diversity and species evenness was calculated for each habitat type using quadrat data and the Shannon-Wiener  $H'$  diversity index and Pielou's  $J'$  measure of evenness, as described for solitary bees. Individual transects were combined to calculate  $H'$  for each habitat type.

## 4.4 Results

### 4.4.1 Bee responses to exclusions

#### 4.4.1.1 Site 1

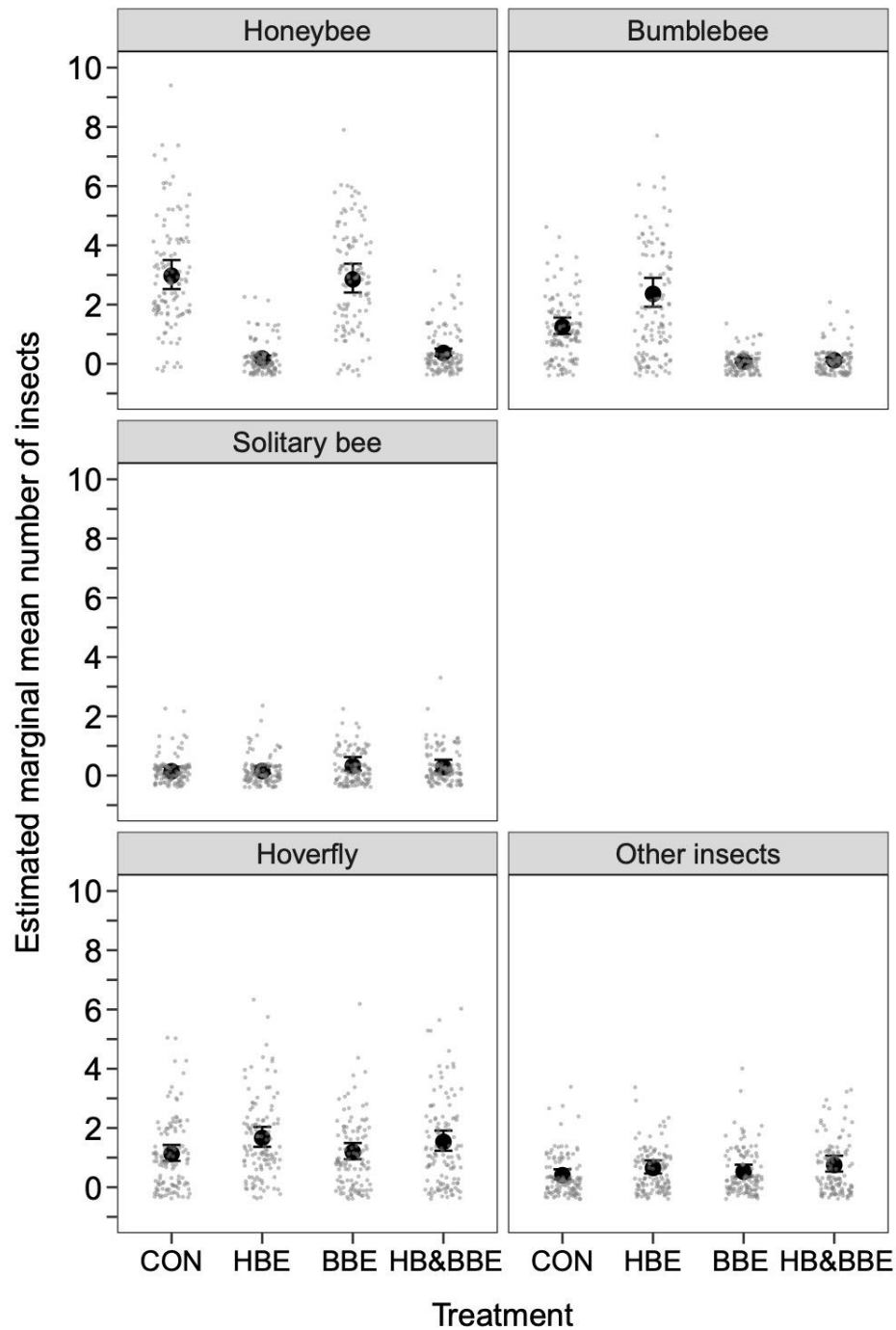
At Site 1, in the more rural location, numbers of insects observed foraging on the bramble patches were lower (total insects counted = 2070,  $n = 471$  counts) than at Site 2 ( $n = 2910$ ,  $n = 476$  counts), despite many insects seen foraging on other flower species in the area. The most numerous insects on CON patches were honeybees (52.8%) and bumblebees (20.1%; 6 species across all treatments). There were very few solitary bees (2.4%; 13 species). Among these were two cuckoo species of solitary bee, *Nomada ruficornis* L. and *Sphecodes monilicornis* Kirby, which were only 3% of recorded solitary bee individuals. Hoverflies were the most abundant non-bee insects (18.4%; 17 species). Other insects were not numerous: other non-syrphid Diptera, 2.8%; wasps, 2.1% (4 species) and Lepidoptera, 1.3% (7 species; 6 butterfly, 1 moth, *Macroglossum stellatarum* L.; Appendix C.1).

The effect of bee exclusion treatment on insect foraging response varied between insect groups, with a significant interaction between these predictor variables (treatment x insect group,  $\chi^2_{(12)} = 509.541$ ,  $P < 0.001$ ). Bumblebees were significantly affected by the exclusion of honeybees, with an 89% increase in the estimated marginal mean (EMM) count of bumblebees on HBE (EMM  $\pm$  1 SE,  $2.36 \pm 0.25$ ) vs CON ( $1.25 \pm 0.14$ ;  $P < 0.001$  in *post-hoc* pairwise comparisons between treatments). Within *Bombus* there were increases in 5/6 species (increases in *B. hypnorum*, *B. lapidarius*, *B. pascuorum*, *B. pratorum*, *B. terrestris/lucorum* agg., no increase in *B. vestalis*; between 36-583% increase in raw count data per species; raw data in Appendix C.1). Conversely, bumblebee exclusion did not affect honeybee numbers ( $P = 1.000$ ). The EMM count of honeybees on BBE treatment patches ( $2.85 \pm 0.25$ ) was 4% lower than CON ( $2.97 \pm 0.25$ ; Fig. 4.2, Table 4.1).

Solitary bees, hoverflies and other insects (comprising butterflies/moths, non-syrphid Diptera and wasps) showed no response to bee exclusion (Fig. 4.2), with all *post-hoc* pairwise comparison between treatments non-significant ( $P > 0.05$ ; Table 4.1).

**Table 4.1.** Estimated Marginal Means (EMM), standard errors and 95% confidence intervals for the effect of treatment on counts of each insect group at Site 1, estimated by a zero-inflated generalised linear mixed effects model. The results of significant *post-hoc* pairwise comparisons between treatments, calculated with Bonferroni adjustment, are shown; all other pairwise comparisons were non-significant ( $P > 0.05$ ). Raw count data for Site 1 are presented in Appendix C.1

Group	Treatment	EMM $\pm$ SE	2.5 %	97.5 %	Pairwise comparison	Post-hoc test
Honeybee	CON	2.97 $\pm$ 0.25	2.308	3.831	HBE > CON	$P < 0.001$
	HBE	0.18 $\pm$ 0.04	0.090	0.356		
	BBE	2.85 $\pm$ 0.25	2.196	3.706		
	HB&BBE	0.37 $\pm$ 0.06	0.223	0.611		
Bumblebee	CON	1.25 $\pm$ 0.14	0.889	1.761		
	HBE	2.36 $\pm$ 0.25	1.723	3.243		
	BBE	0.08 $\pm$ 0.03	0.027	0.243		
	HB&BBE	0.12 $\pm$ 0.04	0.048	0.298		
Solitary bee	CON	0.14 $\pm$ 0.05	0.045	0.442		
	HBE	0.15 $\pm$ 0.57	0.049	0.469		
	BBE	0.32 $\pm$ 0.11	0.120	0.889		
	HB&BBE	0.28 $\pm$ 0.09	0.101	0.760		
Hoverfly	CON	1.13 $\pm$ 0.14	0.781	1.623		
	HBE	1.67 $\pm$ 0.17	1.222	2.273		
	BBE	1.19 $\pm$ 0.14	0.837	1.690		
	HB&BBE	1.53 $\pm$ 0.17	1.093	2.153		
Other insects (non-syrphid Diptera, butterfly/moth, wasp)	CON	0.41 $\pm$ 0.08	0.219	0.752		
	HBE	0.65 $\pm$ 0.11	0.388	1.086		
	BBE	0.52 $\pm$ 0.10	0.293	0.931		
	HB&BBE	0.75 $\pm$ 0.13	0.437	1.287		



**Figure 4.2.** Numbers of insects foraging on patches of bramble with four bee exclusion treatments (no bees excluded (CON), honeybees excluded (HBE), bumblebees excluded (BBE) and both honey and bumblebees excluded (HB&BBE)) at Site 1. Estimated marginal means (points) with 95% confidence interval (errorbars) from a zero-inflated generalised mixed effects model are plotted in black. Grey points show the raw count data, jittered horizontally and vertically for clearer visualisation

#### 4.4.1.2 Site 2

At Site 2, in the more urban location, insect numbers were 40.6% higher overall than at Site 1 (total insects counted = 2910,  $n = 476$  counts). The most numerous insects on CON patches were honeybees (38.3%), followed by bumblebees (36.3%; 5 species across all treatments) and solitary bees (16.4%; 16 species). Within the solitary bees, larger-bodied bees made up 6.7% of the total insects on CON, and smaller-bodied 9.8%. Hoverflies were the most abundant non-bee insects (8.0%; 14 species), followed by wasps, 0.7% (2 species) and Lepidoptera (butterflies only; 4 species), 0.2%. Zero non-syrphid Diptera were counted on CON patches (Appendix C.2).

The effect of bee exclusion treatment on insect foraging response varied between insect groups, with a significant interaction between these predictor variables (treatment  $\times$  insect group,  $\chi^2_{(15)} = 578.56$ ,  $P < 0.001$ ). Honeybees and bumblebees were significantly affected by the exclusion of the ‘opposite’ bee, with a 46% increase in the estimated marginal mean (EMM) count of honeybees on BBE (EMM  $\pm 1$  SE,  $3.75 \pm 0.38$ ) vs CON ( $2.57 \pm 0.27$ ), and 47% increase in bumblebees on HBE ( $3.56 \pm 0.36$ ) vs CON ( $2.43 \pm 0.26$ ;  $P < 0.001$  in *post-hoc* pairwise comparisons; Fig. 4.3, Table 4.2).

Larger-bodied solitary bees increased significantly on each exclusion treatment (HBE, BBE and HB&BBE;  $P < 0.001$ ) relative to CON (EMM  $\pm 1$  SE,  $0.45 \pm 0.07$  bees), with the largest number of bees on HB&BBE ( $2.46 \pm 0.28$ ), an increase of 447%. Smaller-bodied solitary bees and hoverflies showed no response to bee exclusion (Fig. 4.3), with all *post-hoc* pairwise comparison between treatments non-significant ( $P > 0.05$ ; Table 4.2). At the species level, nine out of 12 larger-bodied solitary bee species were more numerous on all three exclusion treatment patches compared to CON (raw data in Appendix C.2).

The number of other insects (comprising butterflies/moths, non-syrphid Diptera and wasps) was very small on all exclusion treatments. There was a slight increase in EMM on each treatment relative to CON, with the largest on HB&BBE,  $0.35 \pm 0.07$  insects, which was significantly higher than CON ( $0.07 \pm 0.02$ ,  $P < 0.05$ ). All other *post-hoc* pairwise tests were non-significant. Hoverflies were also not numerous and numbers

were similar across treatments (between  $0.51 \pm 0.08$  (HBE) to  $0.70 \pm 0.11$  (HB&BBE);  $P > 0.05$ ; Fig. 4.3, Table 4.2).

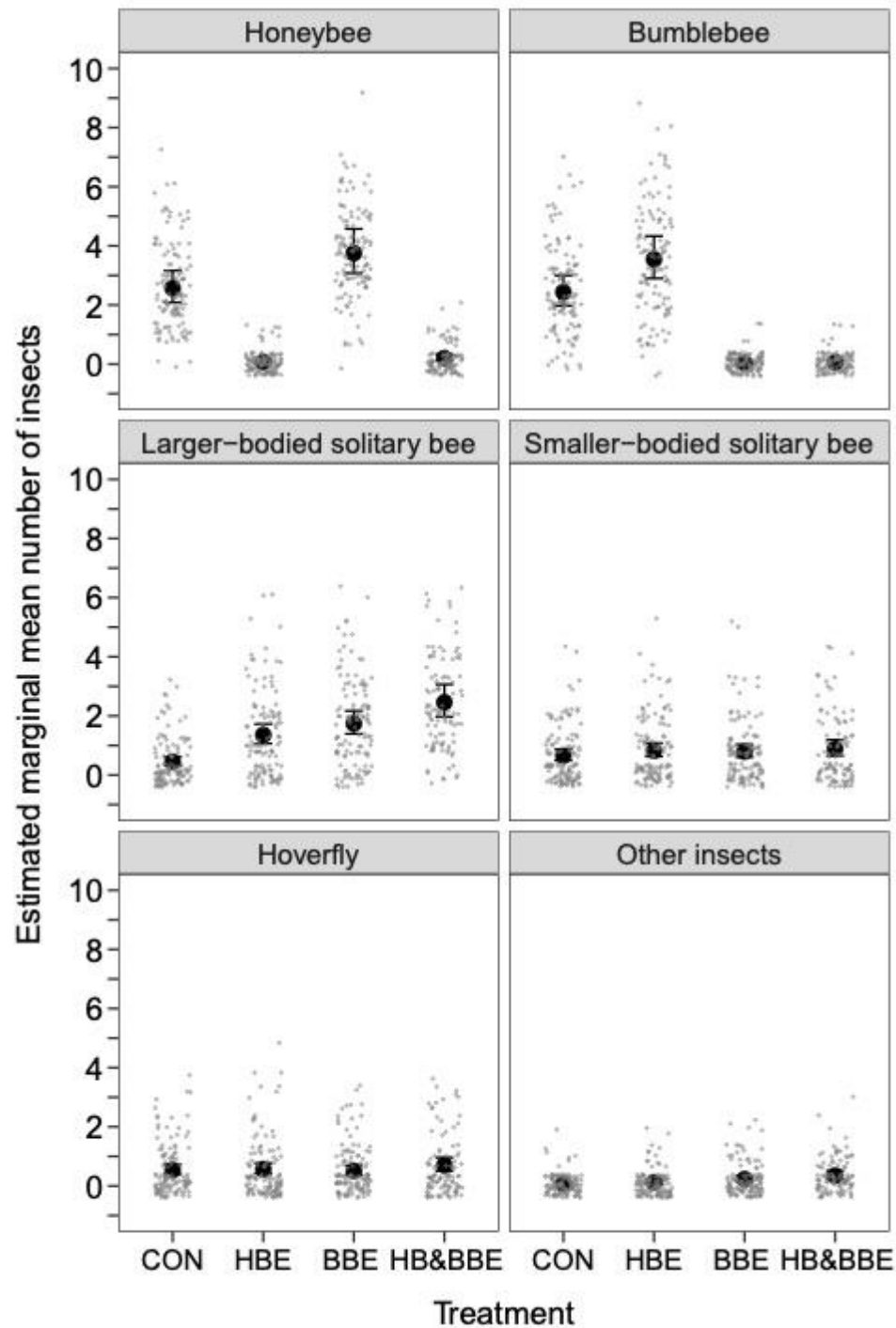
There were slight differences in solitary bee species diversity between treatments at Site 2. Shannon Wiener  $H'$  diversity index and species richness ( $S$ ) were similar on BBE ( $H' = 1.99$ ;  $S = 15$ ), HB&BBE ( $H' = 1.96$ ;  $S = 13$ ) and HBE ( $H' = 1.91$ ;  $S = 14$ ), and lowest on CON ( $H' = 1.70$ ;  $S = 10$ ). Species evenness ( $J'$ ) was similar between treatments ( $J'$ : CON, 0.74; HBE, 0.72; BBE, 0.74; HB&BBE, 0.76).

**Table 4.2.** Estimated Marginal Means (EMM), standard errors and 95% confidence intervals for the effect of treatment on counts of each insect group at Site 2, estimated by a zero-inflated generalised linear mixed effects model. The results of significant *post-hoc* pairwise comparisons between treatments, calculated with Bonferroni adjustment, are shown; all other pairwise comparisons were non-significant ( $P > 0.05$ ). Raw count data for Site 2 are presented in Appendix C.2

Group	Treatment	EMM $\pm$ 1 SE	2.5%	97.5%	Pairwise comparison	Post-hoc test
Honeybee	CON	$2.57 \pm 0.27$	1.970	3.346	BBE > CON	$P < 0.001$
	HBE	$0.07 \pm 0.03$	0.031	0.178		
	BBE	$3.75 \pm 0.38$	2.915	4.829		
	HB&BBE	$0.20 \pm 0.05$	0.110	0.378		
Bumblebee	CON	$2.43 \pm 0.26$	1.864	3.179	HBE > CON	$P < 0.001$
	HBE	$3.56 \pm 0.36$	2.745	4.577		
	BBE	$0.03 \pm 0.02$	0.009	0.117		
	HB&BBE	$0.06 \pm 0.03$	0.021	0.175		
Solitary bee: larger-bodied	CON	$0.45 \pm 0.07$	0.298	0.672	HBE > CON	$P < 0.001$
	HBE	$1.36 \pm 0.17$	0.996	1.846	BBE > CON	$P < 0.001$
	BBE	$1.74 \pm 0.20$	1.312	2.307	HB&BBE > CON	$P < 0.001$
	HB&BBE	$2.46 \pm 0.28$	1.857	3.258	HB&BBE > HBE	$P < 0.001$
Solitary bee: smaller-bodied	CON	$0.65 \pm 0.09$	0.457	0.937		
	HBE	$0.82 \pm 0.11$	0.582	1.165		
	BBE	$0.80 \pm 0.11$	0.564	1.111		
	HB&BBE	$0.88 \pm 0.14$	0.598	1.294		
Hoverfly	CON	$0.54 \pm 0.08$	0.367	0.789		
	HBE	$0.57 \pm 0.09$	0.385	0.836		
	BBE	$0.51 \pm 0.08$	0.347	0.754		
	HB&BBE	$0.70 \pm 0.11$	0.467	1.051		

Other insects	CON	$0.07 \pm 0.02$	0.026	0.164	HB&BBE > CON	$P = 0.0068$
	HBE	$0.12 \pm 0.03$	0.062	0.246		
	BBE	$0.23 \pm 0.05$	0.137	0.389		
	HB&BBE	$0.35 \pm 0.07$	0.213	0.574		





**Figure 4.3.** Numbers of insects foraging on patches of bramble with four bee exclusion treatments (no bees excluded (CON), honeybees excluded (HBE), bumblebees excluded (BBE) and both honey and bumblebees excluded (HB&BBE)) at Site 2. Estimated marginal means with 95% confidence interval from a zero-inflated generalised mixed effects model are plotted in black. Grey points show the raw count data, jittered horizontally and vertically to reduce overlap for clearer visualisation

#### 4.4.2 Nectar standing crop volume ( $\mu\text{l}$ ) and per-flower sugar content ( $\text{mg/ml}$ )

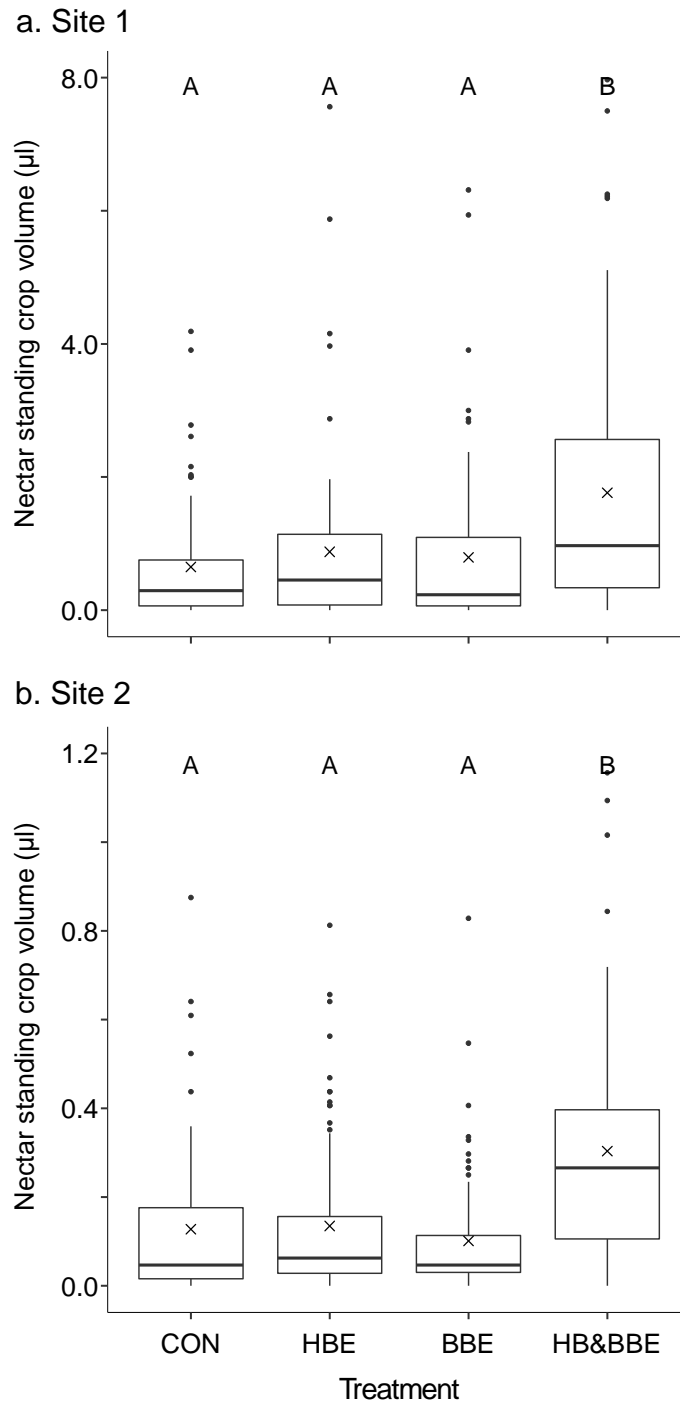
Treatment significantly affected nectar standing crop volume at Site 1 ( $F_{(3)} = 11.225$ ,  $P < 0.001$ ). Standing crop volume was significantly higher in HB&BBE patch flowers (mean  $\pm$  SD,  $1.76 \pm 1.88 \mu\text{l}$ ) compared to all other treatments (CON  $0.647 \pm 0.871 \mu\text{l}$ , +172%; HBE  $0.876 \pm 1.30 \mu\text{l}$ , +101%; BBE  $0.792 \pm 1.21 \mu\text{l}$ , +122%;  $n = 80$  flowers per treatment;  $P < 0.001$ ). Standing crop volume was not significantly different between any other treatments ( $P > 0.05$ ; Fig. 4.4 a). At Site 2, mean nectar standing crop volumes were between 80 – 87% lower in each treatment than at Site 1, although the trends were similar (Fig. 4.4). Treatment also significantly affected nectar standing crop volume at Site 2 ( $F_{(3)} = 17.679$ ,  $P < 0.001$ ). Nectar volume was significantly higher in HB&BBE patch flowers ( $0.303 \pm 0.258 \mu\text{l}$ ,  $n = 70$  flowers) compared to all other treatments (CON  $0.128 \pm 0.166 \mu\text{l}$  ( $n = 80$ ), +137%; HBE  $0.135 \pm 0.176 \mu\text{l}$  ( $n = 80$ ), +124%; BBE  $0.101 \pm 0.134 \mu\text{l}$  ( $n = 80$ ), +200%;  $P < 0.001$ ). Standing crop volume was not different between other treatments ( $P > 0.05$ ; Fig. 4.4 b). Nectar concentration was recorded as 50% (Brix) for 9 standing crop samples at Site 1 (CON 1 sample, HBE 1, BBE 3, HB&BBE 4) and 56 samples at Site 2 (CON 9, HBE 5, BBE 10, HB&BBE 32). Actual concentration may have been  $>50\%$  for these samples, meaning that calculated per-flower nectar content values may be conservative (see section 4.3.3).

Per-flower sugar content could be calculated for 73.75% of extracted nectar samples at Site 1; 84 of 320 samples had standing crop volumes that were too low (mean =  $0.053 \mu\text{l}$ ) to measure concentration (CON 22 samples, HBE 25, BBE 28, HB&BBE 8).

Nectar sugar content (calculated using available concentration data) was highest in HB&BBE patch flowers ( $0.835 \pm 0.834 \text{ mg/ml}$ ,  $n = 72$ ). This was significantly higher than CON ( $0.266 \pm 0.231 \text{ mg/ml}$ , +214%,  $n = 58$ ;  $P < 0.001$ ), BBE ( $0.371 \pm 0.469 \text{ mg/ml}$ , +125%,  $n = 52$ ;  $P < 0.001$ ) and HBE ( $0.487 \pm 0.588 \text{ mg/ml}$ , +72%,  $n = 61$ ;  $P = 0.005$ ). Sugar content per flower was not significantly different between any other treatment pairs ( $P > 0.05$ ).

At Site 2, per-flower nectar sugar content could be calculated for only 40% of samples; 186 of 310 sample volumes were too low (mean =  $0.059 \mu\text{l}$ ) to measure concentration (CON 51 samples, HBE 56, BBE 57, HB&BBE 22). Nectar sugar content (calculated

using available concentration data) was highest in HB&BBE patch flowers ( $0.240 \pm 0.164$  mg/ml,  $n = 58$ ); this was significantly higher than CON ( $0.143 \pm 0.101$  mg/ml, +68%,  $n = 29$ ;  $P = 0.009$ ) and BBE ( $0.140 \pm 0.079$  mg/ml, +71%,  $n = 23$ ;  $P = 0.013$ ), and non-significantly, 40%, higher than HBE ( $0.171 \pm 0.103$  mg/ml,  $n = 24$ ;  $P = 0.141$ ). Sugar content per flower was not significantly different between any other treatment pairs ( $P > 0.05$ ; see section 4.3.3 regarding caution in interpreting nectar sugar content data).



**Figure 4.4.** Standing crop volumes (μl) of nectar across the four bee exclusion treatments (no bees excluded (CON), honeybees excluded (HBE), bumblebees excluded (BBE) and both honey and bumblebees excluded (HB&BBE)) at Site 1 (a) and Site 2 (b). The plots show the volume of nectar collected from ten flowers per patch treatment per day over the eight-day trial (CON, HBE, BBE: n = 80 flowers in total per treatment; HB&BBE, n = 70). Horizontal lines show the median, boxplot limits are the 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers are 1.5 times the interquartile range and points outside whiskers represent outliers. Crosses within plots represent the mean nectar volume per treatment (μl). Different superscript letters above boxes (A, B) denote significant

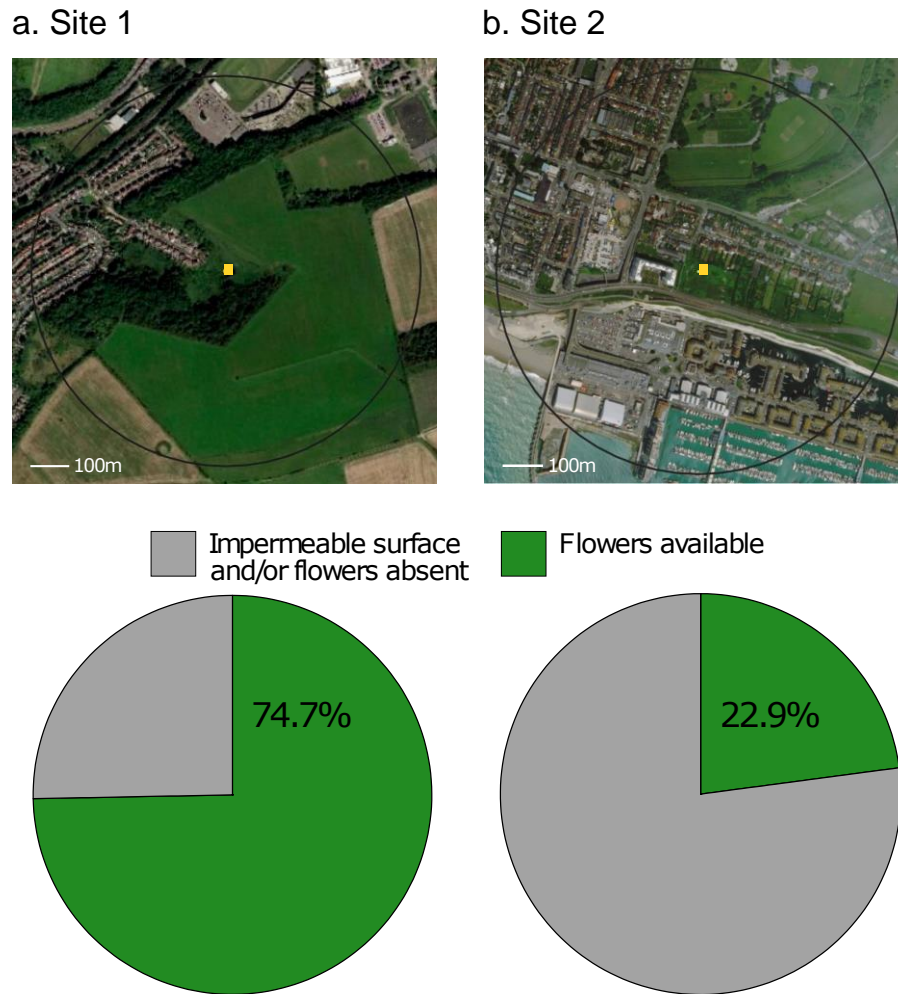
difference between treatments at  $P < 0.05$  according to ANOVA with Tukey's *post-hoc* pairwise comparisons

#### 4.4.3 Local land-use and wildflower diversity

A high proportion of the 500 m radius area (= total area 785398 m<sup>2</sup>) was successfully categorised into land-use types in each site (Site 1: 783711 m<sup>2</sup>, 99.7%; Site 2: 768107.5 m<sup>2</sup>, 97.8%). Within these areas, Site 1 had a much greater proportion of '*flowers possible*' area, comprising arable fields, broad-leaved woodland, field margins, residential gardens, sports pitches and unimproved grassland (87.2%) versus 12.8% impermeable surfaces. Site 2 had a much smaller proportion of '*flowers possible*' area, including broad-leaved woodland, cliff face, cliff top verges, field margins, golf course, nature reserve land, residential gardens, sports pitches, urban greenfield areas and other urban greenspace (38.1%) versus 61.9% impermeable surfaces or water.

The '*flowers available*' area per site, including land-use types verified to have flowers present, also comprised a much higher proportion of the overall habitat at Site 1 (74.7%; 585216/783711 m<sup>2</sup>) compared to Site 2 (22.9%; 176143.5/768107.5 m<sup>2</sup>; Fig. 4.5).

Detailed information of petal area, a measure of floral abundance, and diversity indices from transect and quadrat data for each surveyed *flowers available* habitat type is in Appendix C.3.



**Figure 4.5.** Maps showing the habitat surrounding Site 1 (a) and Site 2 (b). Black circles define the 500 m radius area surrounding the site centre, which is shown as a yellow square. White scale bars on the bottom left of maps show 100m. Corresponding pie charts show the proportion of habitat within the 500 m radius area that was found to have *flowers available* (green; Site 1 = 74.7%, Site 2 = 22.9%), compared to the proportion of area made up of impermeable surface and/or with flowers absent (grey; Site 1 = 25.3%, Site 2 = 77.1%). Maps were created using QGIS with ESRI “Satellite” base map

#### 4.5 Discussion

Our results show that visitation to wild-growing bramble flowers by honeybees and bumblebees decreases per-flower nectar volume and can reduce visits by other foragers, suggesting that *Apis* and *Bombus* displace other insects through exploitative competition. Our study is the first, to our knowledge, to demonstrate reciprocal

competition between *Apis* and *Bombus* on one flower species. Another notable finding was the strong displacement of non-*Apis/Bombus* bees (referred to here as ‘solitary bees’) in one study site, where local flower availability was somewhat limited and competition for nectar and pollen was likely to be high. The observed effects on hoverflies and other insects (butterflies, wasps and non-syrphid Diptera) were inconclusive. Although our conclusions are limited by the inclusion of only two study sites with differing characteristics (see section 4.5.6), the results can be seen as preliminary information revealing patterns of competitive exclusion between pollinator groups, mediated by resource depletion by eusocial bees.

#### 4.5.1 Reciprocal competition between *Apis* and *Bombus*

The separate removal of *Apis* or *Bombus* from bramble patches revealed reciprocal competition. Bumblebee numbers increased following honeybee removal both at Site 2 (47%) and at Site 1 (70%) compared to control patches, showing clear ecological release from competition. This was consistent for each ( $n = 5/5$ ) bumblebee species at Site 2, and all apart from *B. vestalis* Geoffroy ( $n = 5/6$ ) at Site 1. Honeybee numbers increased following bumblebee exclusion at Site 2 (45%), but did not show any release from competition at Site 1 (-4%; Figs. 4.1 & 4.2).

Honey- and bumblebees are often the most abundant foragers on *R. fruticosus* and both rapidly extract nectar from the open-structured Rosaceae-type flowers (Couvillon et al. 2015, Wignall et al. 2020b). The removal of either group should, therefore, cause an increase in nectar availability, as well as pollen. Since both honeybees (Duffield 1993, Balfour, Gandy & Ratnieks 2015) and bumblebees (Heinrich 1976) choose flowers with a higher reward, this is likely to explain the increase in the number of *Apis* and *Bombus* on patches where the ‘opposite’ bee had been removed (Figs. 4.1 & 4.2). Although we did not record an increase in per-flower nectar standing crop volume or sugar content in HBE or BBE patches compared to controls at either site, this is likely to be due to the quick depletion of any nectar by the ‘other’ (non-excluded) bee to levels similar to control patches (Fig. 4.4).

The anomalous result at Site 1, where honeybee numbers did not increase on BBE treatment patches compared to control patches, may be due to the low proportion of

bumblebees visiting the bramble flowers (20% of all insects on control patches, compared to 53% honeybees). At this site, removing bumblebees would have had only a small effect on nectar availability for honeybees, which may explain why honeybee numbers did not increase although absolute numbers remained high (Appendix C.1). In contrast, the significant increase in bumblebee numbers on HBE patches at this site showed that bumblebees were released from competitive pressure exerted by honeybees.

These patterns are in line with the ideal free distribution model, in which the number of foragers exploiting a resource is proportional to the rate of reward production in the patch, such that reward gain per forager is equal across resource patches (Fretwell & Lucas 1970).

#### 4.5.2 Solitary bees

Solitary (non-*Apis/Bombus*) bee response to *Apis* and *Bombus* exclusion varied between sites. At Site 2, a substantial and significant increase in the number of larger-bodied solitary bee visits to bramble flowers following removal of honeybees or bumblebees, and especially both, is strong evidence for ecological release from competition (Fig. 4.3). In comparison, at Site 1 there was no evidence of competition exerted by eusocial bees, with no measurable response likely due to the very low abundance of solitary bees on all treatment patches (Fig. 4.2). This between-site difference in abundance of solitary bees on bramble flowers may be due to local flower availability, which, as discussed in 4.5.4, was substantially lower at Site 2 (Fig. 4.5), although more trials would be needed to support this theory (see section 4.5.6).

At Site 2, when both honey- and bumblebees were excluded (HB&BBE), there was a very large, 447%, and significant increase in larger-bodied solitary bee visits to bramble flowers compared to control patches (Fig. 4.3). This may be partly explained by the corresponding 137% rise in nectar availability in HB&BBE patch flowers (Fig. 4.4 *b*), and 68% measured increase in per-flower sugar content (although reported sugar content data may be conservative, see sections 4.3.3 & 4.4.2). Like eusocial bees, solitary bees are sensitive to changes in nectar reward which is a key factor in flower choice and foraging patterns (Howell & Alarcón 2007, Mallinger & Prasifka 2017).



However, other factors may also have contributed, including, importantly, pollen availability since this is also a major factor driving solitary bee foraging behaviour (Tepedino & Parker 1982, Williams & Tepedino 2003) as females must provision nest cells with large quantities of pollen to rear developing larvae (Müller et al. 2006). The physical presence of honey- and bumblebees is another possible factor (Rogers et al. 2013). It would be interesting to investigate these in further studies, for example by measuring pollen availability in each treatment patch, or by decoupling bee exclusions from changes in nectar and pollen reward by experimentally adjusting these, to determine if the solitary bees respond to competitors directly or via their effect on resource amounts.

Our results also suggest that body size may affect the extent to which exploitative competition affects solitary bees, which is consistent with previous findings (Torné-Noguera et al. 2016, Henry & Rodet 2018). At Site 2, the increase in solitary bee visits to HB&BBE compared to control patches was substantial, 447%, and significant for larger-bodied solitary bees (forewing  $>5.5$  mm; genera: *Andrena*, *Anthophora*, *Megachile*, *Osmia*). In contrast, the number of smaller-bodied bees (forewing  $\leq 5.5$  mm (Falk & Lewington 2015); genera: *Hylaeus*, *Halictus*, *Lasioglossum*), was similar between treatment patches; a 35% increase on HB&BBE patches compared to control patches was not significant (Fig. 4.3, Table 4.2). Smaller bees have correspondingly smaller requirements for nectar and pollen (Müller et al. 2006) and may therefore be less affected by the depletion of these resources by honey- and bumblebees. The effect of body size may particularly relate to pollen availability, which is likely to be affected by pollen removal by honey- and bumblebees, since larger-bodied bees require large quantities to rear larvae (Müller et al. 2006). It is also possible that the very small foraging ranges of the smaller-bodied genera, particularly *Lasioglossum* species (Wright, Roberts & Collins 2015), may have prevented them from discovering the patches where bees were excluded.

Separate exclusion of honeybees or bumblebees (HBE and BBE treatments) at Site 2 also caused an increase in the number of larger-bodied solitary bee foragers (Fig. 4.3). This response was smaller than when both groups were removed (HB&BBE), which is likely to be due to the increase in *Bombus* or *Apis* visitation to HBE and BBE patches in response to the exclusion of the ‘opposite’ bee group (Fig. 4.3), which, as well as

possible un-measured factors such as pollen depletion or physical presence, depleted per-flower nectar volume to levels similar to control patches (Fig. 4.4 *b*). Nevertheless, this shows that the removal of either group singly can reduce competitive pressure to a degree that allows solitary bees to forage on flowers from which they had previously been displaced. Possible longer-term effects of competitive displacement are discussed in 4.5.5.

In contrast to Site 2, at Site 1 there were consistently very few solitary bees visiting bramble flowers in all treatment patches ( $<0.35$  per count per treatment on average, only 2.4% of all insects on control patches). This was despite substantial nectar standing crop volume and sugar content in the flowers in each patch, a 172% increase in per-flower nectar volume in HB&BBE patches compared to CON (Fig. 4.4 *a*), and observations of many solitary bees foraging on other nearby flowers. There were small increases in solitary bee visitation to exclusion treatments compared to controls but no significant differences between treatments. Overall, exploitative competition between bees for bramble flowers was much lower or non-existent in this location, which may be a result of high local flower availability (see section 4.5.4) although this inference is limited due to the two-site comparison in this study (see section 4.5.6).

#### 4.5.3 Hoverflies and other non-bee insects (butterflies, wasps and non-syrphid Diptera)

Previous research has found that experimentally-enhanced honeybee densities spatially displaced wild non-bee insects including hoverflies and non-syrphid Diptera in fields of flowering oilseed rape (Lindström et al. 2016). However, very little research has so far investigated the effect of resource depletion by *Apis* and *Bombus* on non-bee insects.

In this study, the numbers of Lepidoptera, wasps and non-syrphid Diptera at both sites were small and there was no clear response to bee exclusion. Hoverflies were more numerous, but showed a mixed response to bee removals, also with no clear effect of exclusions. It is also not clear from our data whether hoverfly flower visitation was linked to nectar reward. At Site 1, average hoverfly numbers were lowest on the two patch treatments with the lowest per-flower nectar standing crop volume and sugar content (CON and BBE). However, hoverflies were most numerous on HBE patches where per-flower nectar volume and sugar content were almost half that of HB&BBE

patches on average. At Site 2, the number of hoverflies visiting each treatment patch was highly similar between treatments, meaning that patch visitation also cannot be meaningfully linked to nectar reward.

Overall, this inconclusive result may be due to hoverflies' different life history strategy since, unlike bees, they do not rear young in a central nest. As such, they must only meet their individual energy requirements and do not have to provision a nest or feed larvae, with broader requirements including suitable oviposition sites and larval food material. This is also the case for Lepidoptera and non-syrphid Diptera. While foraging behaviour in these groups is therefore very different to bees, with requirements other than maximising efficient nectar and pollen collection, it is not clear how they are affected by immediate local resource depletion, or whether they may be more resilient to *Apis/Bombus*-mediated exploitative competition.

#### 4.5.4 Local floral resource availability

Local availability of floral resources was markedly greater at Site 1 than at Site 2 (Fig. 4.5). At Site 1, 75% of the land within 500 m was verified to have flowers growing (*'flowers available'*). Almost 60% of this was unimproved grassland immediately adjacent to the study field, which was the most flower-abundant of the surveyed habitat types at this site (Appendix C.3).

In contrast, only 23% of the land area surrounding Site 2 was found to have *flowers available*. Flower-rich habitat was patchily distributed at this location (Fig. 4.5), and 62% of the land within a 500 m radius was made up of buildings, roads, other impermeable surfaces and seawater. A further 15% was amenity grassland verified to have very few or zero flowers present. Overall, local availability of flowers for foraging insects was limited, particularly for those with small foraging ranges such as solitary bees which rarely fly further than 500 m from their nests (Gathmann & Tscharrntke 2002).

This substantial difference in surrounding land use within 500 m of the study site may explain the inconsistent solitary bee response to *Apis/Bombus* exclusion between Sites 1 (no competition evident) and 2 (evidence of strong competition), since lower flower

availability is likely to increase the strength of competition among flower-visiting insects, and vice versa. For example, a study by Thomson (2016) found that competition between bees was stronger in drought years when the availability of preferred flower species was reduced. Previous research has also suggested that exploitative competition between bees is weak when local per-insect nectar availability is high, compared to strong competition when nectar availability is low (Wignall et al. 2020a). However, further research with trials in many more sites would be needed to confirm whether the degree of exploitative competition between bees on bramble flowers can be explained by local flower availability (see Limitations and Further Research, section 4.5.6).

#### 4.5.5 Possible fitness effects of competitive displacement

We were not able to measure population-level effects of competitive exclusion from bramble flowers in this study. However, it is possible that in landscapes where floral resources are limited or bramble provides a major source of nectar and pollen, long-term displacement of bees from this abundant resource may negatively affect their reproductive output.

Competitive displacement from preferred flowers causes honeybee (Walther-Hellwig et al. 2006), bumblebee (Walther-Hellwig et al. 2006, Thomson et al. 2016) and solitary bee (Hudewenz & Klein 2015, Villanueva-Gutiérrez, Roubik & Porter-Bolland 2015) species to move to alternative sources of forage, which may be of lower quality, lower quantity, and/or further away causing longer foraging distances to find nectar and pollen. This can have a fitness cost, including reduced offspring production. For example, foraging over longer distances has been shown to reduce the number of brood cells provisioned per unit of time in two species of solitary bee (Zurbuchen et al. 2010a).

Solitary bee species, many of which have undergone declines in abundance and distribution in recent decades (Falk & Lewington 2015), may be particularly vulnerable to the effects of competitive displacement as they have smaller foraging distances often of <500 m from their nests (Gathmann & Tschardt 2002, Zurbuchen et al. 2010b) compared to the larger foraging ranges of honeybees (Couvillon, Schürch & Ratnieks 2014) and many bumblebee species (Walther-Hellwig & Frankl 2000). As a result, they

have a comparatively reduced capacity to find alternative sources of forage, especially where these are limited. This is potentially concerning since solitary bees may simultaneously be particularly susceptible to the process of competitive displacement by eusocial bees, as shown in our results.

Considering these factors, it is important that in commercial management particularly of *Apis* but also *Bombus* (Steele et al. 2019), as well as in amateur beekeeping, local floral resource availability is taken into consideration not only for the health and wellbeing of managed bees but also for solitary bees, wild bumblebees and other wild FVI. For example in the UK,

#### 4.5.6 Limitations and further research

A major limitation of this study was that we completed field trials in only two locations, which was a result of time and researcher availability. This led to low statistical power since it was not possible to analyse the two trials together, due to the large masking effect of the differing numbers of insects at Site 1 and Site 2, meaning that our findings must be interpreted as preliminary. In order to more robustly analyse any effect of bee exclusions it would be necessary to carry out several trials within the same or similar locations to ensure a greater number of replicates for each treatment with a lower number of confounding variables. In this research we were interested in incorporating a measure of local floral availability to assess whether the strength of *Apis/Bombus*-mediated exploitative competition is affected by floral resource availability (and to what extent). Again, in order to assess this with a greater level of statistical robustness this would require trials in many more locations of contrasting flower availability, optimally with several replicates per location within or between study years.

In this study, it was not possible to measure floral abundance and richness in residential gardens, despite these comprising a large proportion of the *flowers available* habitat within the 500 m radius surrounding Site 1 (6.1%) and Site 2 (32.4%). In future research it would be important to incorporate this information to gain a more accurate measure of local floral resource availability, since residential gardens have been shown to host high abundance and species richness of both flowering plants and FVI (Baldock et al. 2015). This could be achieved through householder engagement to gain average

per-area measures of garden characteristics (Gaston et al. 2007, Loram et al. 2011) or through surveying front gardens in residential transects (Baldock et al. 2015). To incorporate a greater level of detail regarding nectar and pollen availability in residential gardens and other surveyed habitat types, information regarding floral abundance and richness could be combined with quantitative data detailing average reward production per flowering plant species, using secondary literature and existing datasets where necessary (*e.g.* Baude et al. 2016, Fowler Rotheray & Goulson 2016).

Further research is also needed to understand the extent of this phenomenon in flower-visiting insect communities on other wildflower and crop species, to extend the breadth of the findings and since pollinator abundance and diversity is often vital for effective pollination (Garibaldi et al. 2013). The interacting effects of landscape-scale resource availability and the abundance of managed pollinators (currently mostly honeybees) on other pollinator species deserves further attention particularly as large-scale anthropogenic changes continue to reduce net floral availability for pollinators, including agricultural intensification (Ollerton et al. 2014, Senapathi et al. 2017) and urbanisation (McKinney 2006).

Lastly, in this study we were not able to measure population-level effects of competitive displacement by *Apis* and *Bombus* on each other and other insect groups. While this would be difficult to incorporate into this small-scale study system, future research could aim to link localised manipulations of managed *Apis* and/or *Bombus* densities to foraging effort, growth and reproductive output in co-foraging species, using trap nest observations for solitary bees (Zurbuchen et al. 2010a) or pollen:nectar foraging intensity, colony weight gain, production of reproductives and male:female reproductive ratio for bumblebees (Thomson 2004, Elbgami et al. 2014).

#### 4.5.7 Conclusions

Overall, our findings preliminarily reveal multiple underlying competitive interactions within a wild pollinator community. Exploitative competition exerted by bumblebees and particularly honeybees may be widespread within and contribute to shaping wild FVI communities, with particularly strong effects where floral resources are limited, although further research is needed to explore these effects through robust statistical

analysis. Per-insect resource availability is critical for their survival and wellbeing (Balfour et al. 2018), including through buffering against other stressors such as pathogens (Brown, Loosli & Schmid-Hempel 2000, Goulson et al. 2015). Therefore, understanding patterns of competition and displacement is necessary for pollinator conservation, particularly for vulnerable or threatened species. Taking these factors into account in landscape management is important both to inform honeybee stocking densities and, importantly, to maximise provision of floral resources when and where they are most needed.

## **Chapter Five: Garden centre customer attitudes to pollinators and pollinator-friendly planting**

*“To plant a garden is to believe in tomorrow.” ~ Audrey Hepburn*

### **Authors and author contribution statement**

Veronica R. Wignall, Karin Alton & Francis L. W. Ratnieks

VW, KA and FLWR conceived the ideas; VW and KA collected the data, VW analysed the data and led the writing of the manuscript

### **5.1 Abstract**

Growing nectar- and pollen-rich flowering plant varieties in domestic gardens and other greenspace is an important pro-environmental behaviour that supports pollinating insects. Wildlife gardening is popular in the UK; however, public attitudes and behaviour relating to planting for pollinators are currently not well understood. We investigated these through questionnaires and interviews with customers in five garden centres in Sussex, southeast England, a relevant and useful consumer group representing horticulturally-engaged members of the public. Garden centre customers had strongly positive attitudes and were motivated to plant for bees and other pollinators: most (77%) grew pollinator-friendly varieties, while 64% would be more likely to buy a plant with a pollinator-friendly logo. Personal motivation to support pollinators was linked to a recent increase in personal and public awareness of their declines through (often negativistic) information from mass media sources. Practical implications of these findings in relation to the horticultural retail industry are discussed.

### **5.2 Introduction**

Growing varieties of flowering plants that support pollinating insects is one of the most effective behaviours through which the general public can directly help these insects, which are considered to be in decline in the UK and worldwide, in part due to reduced availability of nectar- and pollen-producing flowers (Carvell et al. 2006, Potts et al.



2010, Vanbergen et al. 2013, Goulson et al. 2015). Gardens and other private or community greenspace (*e.g.* allotments, cemeteries) have been shown to provide an important resource for flower-visiting insects in both rural (Bates et al. 2011, Samnegård, Persson & Smith 2011) and particularly urban environments (Ahrné, Bengtsson & Elmqvist 2009, Gunnarsson & Federsel 2014, Baldock et al. 2019). Many UK residents engage in wildlife gardening, an increasingly common pro-environmental behaviour (Gaston et al. 2007, Goddard, Dougill & Benton 2013). Furthermore, in a survey of over 500 households in Leeds, 41% of participants stated that watching or attracting wildlife was an important reason for using their garden (Goddard, Dougill & Benton 2013). However, public attitudes specifically towards flower-visiting insects and supporting these in gardens or other green space, including through planting attractive flowering plant varieties, has not been assessed to our knowledge.

One indicator that the British public are interested in bees and other pollinators is a high level of recent participation in nationwide pollinator monitoring and citizen science programmes, facilitated over the last decade through technology including widely available smartphone applications. For example, in 2018, 482,915 records of bees were submitted by 23,755 participants in the ‘Great British Bee Count’ led by environmental campaigning group Friends of the Earth (UK); 73% of these sightings were made in gardens (Friends of the Earth (UK) 2018). In 2019, a record number of transect visits (38,768) were made at a record number of sites (3,003) by volunteers monitoring butterfly numbers for the UK Butterfly Monitoring Scheme (Butterfly Conservation et al. 2019). Participation in the nationwide Hoverfly Recording Scheme increased from ~250 recorders to > 1,000 in 2017 (Hoverfly Recording Scheme 2019). Meanwhile, also in the last decade, several online resources to engage and inform the public about gardening for bees and other pollinating insects have been published by popular sources including Friends of the Earth (UK), the Wildlife Trusts and the Royal Horticultural Society. Being well-informed is a predictor of pro-environmental action (Easman, Abernethy & Godley 2018); therefore, it is possible that this recent increase in availability of online information may have also led to a corresponding growth in public interest in and motivation to plant for pollinators.

Members of the UK public commonly purchase plants from garden centres, horticultural retail outlets that sell plants and gardening material. British garden centre

customers spent £1.4 billion on garden plants in 2016 according to the Horticultural Trades Association's garden market analysis report (HTA 2017) and two thirds of adults visit a garden centre at least once a year (HTA 2018). Customers in garden centres represent a sample of the UK public that have an interest in gardening, many of whom are likely regularly to plant ornamental flowering plants to varying extents, or have the potential to do so. Therefore, this customer group is relevant and useful to understand the attitudes and behaviours of horticulturally-engaged members of the public relating to pollinators and pollinator-friendly planting. Improving our understanding of this through quantitative and qualitative investigation is an important step in improving floral resources for pollinators.

Since garden centres are a major source of ornamental flowering plants to the general public, it is also likely that increasing the availability and signposting of pollinator-friendly varieties could have a direct positive impact on resource availability for pollinators throughout the UK. However, one recent study revealed that many flowering plants on sale in garden centres were not attractive to flower-visiting insects, in some instances even when labelled as pollinator-friendly (Garbuzov, Alton & Ratnieks 2017). A second recent study identified pesticides in the nectar and pollen of a large proportion of 'bee-friendly'-labelled plants sampled in garden centres, in some cases at levels known to cause harm to bees (Lentola et al. 2017). This suggests that garden centres are not currently fulfilling a significant potential to facilitate pollinator-friendly planting. The garden retail industry is influenced by sociocultural drivers including consumer pro-environmental attitudes and behaviour (HTA 2017), therefore clarifying customer attitudes towards pollinators could have an important practical implication in respect to the garden centre industry.

This study investigates the attitudes of customers in garden centres towards pollinators and towards growing and purchasing plants that support flower-visiting insects. Our methods simultaneously assess whether there is scope for garden centres to play a more active role in facilitating pollinator-friendly planting. We collected questionnaire responses from 150 visitors to five garden centres in Sussex, southeast England. The questionnaire gathered information about (i) public attitudes to wildlife including pollinators and (ii) existing pro-environmental behaviours relating to pollinators and knowledge about pollinator-friendly plants, including awareness of plant labelling and information provided by garden centres. This was followed up with 14 in-depth

interviews with additional customers, to explore selected findings in more detail using a qualitative research approach. Possible implications of the study findings are discussed, including practical application in the garden retail industry.

### **5.3 Materials and Methods**

#### **5.3.1 Garden centres**

With permission from the managers, we gathered information from customers visiting five garden centres in Sussex, England using questionnaires and interviews. These were typical of the area, of similar sizes, and included both independent businesses ( $n = 2$ ) and branches of larger chains ( $n = 3$ ). All seemed to have a similar customer base with no notable differences in exclusivity or ‘high-end’ nature.

#### **5.3.2 Questionnaire design**

The questionnaires had three sections gathering (i) complementary information on the customer (age, sex, reason for visit etc.), (ii) attitudes to wildlife including pollinators and existing pro-environmental behaviours, and (iii) awareness of and attitude towards pollinator-friendly plants, including plant labelling and information provided by garden centres. There was space at the end for comments (Appendices D.1 & D.2).

#### **5.3.3 Garden centre visitor questionnaires and interviews**

##### ***5.3.3.1 Questionnaires***

In total, 150 questionnaires were completed, 30 per garden centre, in August and September 2018, with data gathered on one or two days mainly on weekdays (Table 5.1). VW and KA carried out the surveys with the occasional assistance of an undergraduate research assistant; each researcher was acquainted with the study aims and the need to avoid researcher and respondent bias while completing questionnaires (Saldaña 2013).

Customers were approached in the areas with plants for sale and asked if they would be happy to take part in a research study for the University of Sussex. In order not to influence the responses, researchers did not mention pollinators, wildlife, plants or anything relevant to the study, nor did they answer any questions about these topics while the participant was filling out the questionnaire. If asked any questions, we explained that we had an information sheet on the project to give them once they had completed the questionnaire (information sheet in Appendix D.3).

We found no significant difference in either the proportions of male and female customers (Chi-squared test,  $\chi^2_{(1)} = 0.106$ ,  $P = 0.745$ ) or the representation of different age groups (Fisher's exact test,  $P = 0.905$ ) between independent and chain stores, so all 150 questionnaire responses were pooled for analysis. For certain questions respondents who ticked an incorrect number of boxes were removed from the dataset, resulting in some question sample sizes of <150. Sample sizes for questionnaire responses were 150 unless noted otherwise in the text (*Results*).

#### 5.3.3.2 Interviews

After we had reviewed the questionnaire responses, we conducted 14 semi-structured interviews with separate customers (who had not previously completed the questionnaire) in October 2018 in one garden centre, to provide further insights where our findings were interesting and/or led to further questions (Goddard, Dougill & Benton 2013). We based the interviews in Wyevale garden centre, Lewes, as this is a branch of a popular large chain and was thought to have a comprehensively representative customer demographic (Table 5.1). We (VW and KA) approached customers browsing in the garden centre and asked if they would be happy to spend 10-15 minutes answering some informal questions for a research project, in exchange for free refreshments.

Interviewees were either in a pair ( $n = 11$  pairs, 22 people) or single ( $n = 3$  people). The interviewer (VW) informed the participant(s) that they would be recorded, and each was asked to read and sign an information/consent form before the interview began.

Interviews were conducted by VW. Each interview had three sections (Appendix D.4). In Section 1, the participant(s) was asked to complete one customer questionnaire. If

they were a pair, the keener gardener of the two was asked to answer the questionnaire. These 14 questionnaire responses were not included in our analysis of the 150 questionnaires completed previously. In Section 2, we asked for further details on their responses to some of the questions (Qs: 6, 8, 9, 11, 12, 13, 14, 15, 16). Section 3 asked two further questions not related to the questionnaire (Q+1: *Has your awareness of/interest in bees and other pollinators/pollinator-friendly plants changed over time? If so, could you tell me a little more about this?* and Q+2: *Where do you think you receive most information about pollinators?*).

Transcripts were manually analysed using qualitative inquiry (Saldaña 2013). Themes were drawn out using both *in vivo* and descriptive coding, to extract the most appropriate content and essence of the interviews (Saldaña 2013). After organising themes into categories and subcategories, these were cross-referenced against quantitative survey findings and integrated within these themes in the Results section.

**Table 5.1.** Details of five garden centres where questionnaires and interviews were conducted in 2018. Three were branches of a larger chain of garden centres (<sup>a</sup>) and two were independents with only a single garden centre (<sup>b</sup>). All were in Sussex. Dates of customer surveys and interviews are shown by location

Garden Centre	Surveys	Interviews
Wyevale <sup>a</sup> <i>Newhaven Road, Kingston, Lewes, BN7 3NE</i>	<i>n = 30; 5 September</i>	-
Hillier <sup>a</sup> <i>Hailsham Road, Pevensey, BN24 5BS</i>	<i>n = 30; 15 August</i>	-
Notcutts <sup>a</sup> <i>Common Ln, Ditchling, Hassocks, BN6 8TN</i>	<i>n = 30; 7 &amp; 8 August</i>	<i>n = 14; 1, 2 &amp; 5 October</i>
Stavertons Nursery <sup>b</sup> <i>Eastbourne Road, Halland, BN8 6PU</i>	<i>n = 30; 21 August</i>	-
Rushfields Plant Centre <sup>b</sup> <i>Poynings, Brighton, BN45 7AY</i>	<i>n = 30; 13 &amp; 15 September</i>	-

#### 5.3.4 Ethical approval and garden centre permissions

In each garden centre we obtained the manager's permission to survey customers on the premises. On arrival we let the staff know that we were surveying customers on that day.

All survey materials were approved by the University of Sussex Sciences & Technology Cross-Schools Research Ethics Committee (C-REC, project reference number ER/VW58/4). Interview transcriptions and corresponding signed consent forms were given unique reference codes and stored separately under password so that customers could withdraw their consent if they wished. The customer questionnaire and information sheet, and interview questions are available in the Appendices (D.2 – D.4).

### 5.3.5 Pollinator-friendly logo size on plant labels

In three garden centres, including one in the five used for questionnaires (Rushfields Plant Centre, Sussex) plus two additional (Brighton Wyevale, Sussex; Gates Garden Centre, Rutland), we surveyed the pollinator-friendly logos present in the plant and bulb stock displayed at the time, as well as seed packets on display (October 10, 2018). This was not to make a comprehensive record of the logos used but provide additional information relating to Q15 in the questionnaire *Do you think the [pollinator-friendly] labels are visible enough?* by measuring the size of a representative sample of pollinator-friendly logos found on labels and packets in the three centres as a proportion of the size of the overall label/packet. The garden centres were selected due to logistical reasons relating to researcher availability and means of transport, since the objective was to obtain a representative sample of logos on plants sold in garden centres and not to assess logo size within the centres we visited to carry out questionnaires and interviews.

We photographed any plant labels and bulb packets that included a pollinator-friendly logo with a ruler for scale. As there were very large numbers of seed packets we haphazardly selected ten packets with a pollinator-friendly logo for measurement.

We found eight different pollinator-friendly logos at the time of our surveys in the three garden centres (Fig. 5.1). The most commonly observed was the RHS (Royal

Horticultural Society) Perfect for Pollinators (Fig. 5.1 *h*). Since this logo was much more commonly seen than the others, we photographed a representative selection of plant labels that included it, including different growers and label designs ( $n = 35$ ). In order to ensure other logos were represented, we made a deliberate effort to find and photograph these. As such, the sample we collected does not reflect a proportional distribution of logo types on the plant labels displayed in the centres at the time. Sample sizes of the seven other logos found on plant labels were small (Fig. 5.1 *a-g*,  $n$ :  $a = 2$ ,  $b = 2$ ,  $c = 1$ ,  $d = 3$ ,  $e = 2$ ,  $f = 3$ ,  $g = 1$ ).

Logo area and total label size (measured as the visible part of the label, including any text that directly accompanied the label) were then measured using ImageJ (version 1.51, 2015). We also noted whether there was any mention of pollinators on the reverse side of the label.



**Figure 5.1.** Eight wildlife-friendly plant logos (*a-h*) found on plant labels in three garden centres. Photo credit: Veronica Wignall

### 5.3.6 Statistical analysis

Contingency tests were used to compare the proportions of questionnaire respondents that chose certain flowering plant features and those that were familiar with pollinator-friendly logos (male vs female; interviewees vs overall questionnaire). When all values were  $>5$ , we used Chi-squared tests, with a Yates continuity correction if any values were  $<10$  (Yates, 1934).

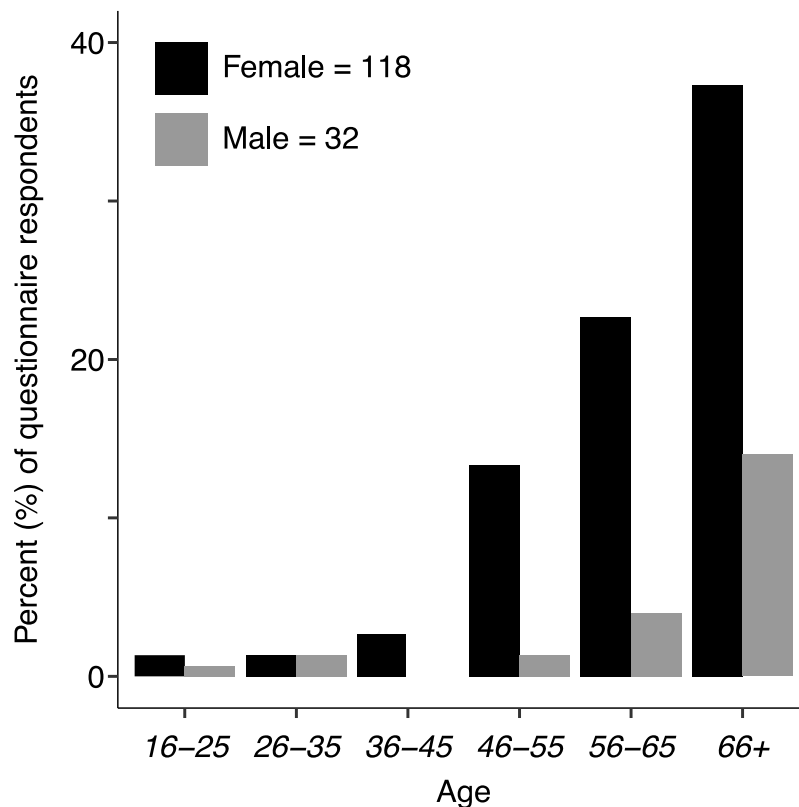
We analysed whether there was any difference in average logo size as a proportion of the total label/packet area between plants, bulbs and seeds using a Kruskal-Wallis rank sum test since data did not fit a parametric distribution.

All statistical analyses were performed using RStudio version 1.1.463 within R version 3.4.3 (R Core Team 2020).

## 5.4 Results

### 5.4.1 Questionnaire respondents' characteristics

The majority of the 150 questionnaire respondents were over the age of 55 (78%); most were female (79%; Fig. 5.2).



**Figure 5.2.** Questionnaire respondent characteristics. Age and sex distribution of garden centre customers who answered the questionnaire (n = 150)



Almost all respondents had a garden (95%). When buying plants, 68% most often looked for ornamental plants with flowers ( $n = 138$ ; 12 replies that had incorrectly ticked >1 box for this question were removed), followed by trees or shrubs (20%), vegetable/fruit plants (7%), and lastly indoor plants (5%).

In a multiple response question asking why participants were visiting the garden centre that day, the most common reason was to buy plants or seeds/bulbs (57%), followed by leisure purposes, for example browsing or visiting the cafe (52%). Others were visiting to buy other gardening items such as tools (22%) or non-gardening items (16%).

#### 5.4.2 Customer attitudes towards wildlife and pollinators (Qs 7, 8, 9, 10)

Most questionnaire respondents showed a positive interest in wildlife, with 146 (97%) answering that the decline of wildlife in Britain concerns them. Most did something in their garden or other outside space to help wildlife (97%).

In terms of pollinators specifically, almost all questionnaire respondents (97%) thought that bees and other pollinators were beneficial to their garden or other outdoor area. Most carried out several of five pollinator-friendly actions listed in the questionnaire (mean  $\pm$  SD =  $2.55 \pm 1.20$  actions, range = 0-5). The most common was to grow pollinator-friendly plants (77% of participants), followed by using limited or no pesticides (64%), providing flowers throughout the year (57%), leaving some areas unmown/unmanaged (37%) and putting up bee hotels (19%). Only four people said they did not currently help bees and other pollinators in their garden or outside area (Fig. 5.3 a).

Four interviewees mentioned that they disliked wasps. However, in general there was a positive interest in pollinators that was often particularly focused on bees and butterflies. Many interviewees even seemed to feel a psychological benefit of seeing bees and other insects in their garden or outside area, with comments including: *“I was very happy because I got a bees nest in my compost and I liked that”*, *“it can be quite therapeutic to sit and watch them [bees]”* and *“I think bees are very important, well I know bees are very important, and we like watching the bees”*. As well as this, there was a sense of a positive feeling towards environmental stewardship, with comments

such as: *“you just think if it’s keeping the natural balance of the ecosystem then it’s a good thing”*; *“I love wildlife, I love the bees, I feed the bees, and anything to help nature is better.”*

Interviewees also expressed concern for the wellbeing of pollinators, linking this to human and planetary health. One commented *“if we lose our bees, everything else follows suit, so it makes sense to wake up, and you know, start doing more to protect the environment, down from plastic to everything”*, another said *“if we run out of bees, if the bees die we die, if they don’t pollinate our flowers and our shrubs and our fruits”*, and a third remarked *“put it this way, if the bees go the humans go”*.

#### 5.4.3 Customer attitudes towards pollinator-friendly planting (Qs 6, 14)

Bee- or pollinator-friendly (53%,  $n = 145$  replies) was one of three most and equally-important features, excluding price, considered when buying flowering plants, with length of flowering (55%) and hardiness/low level of maintenance (56%). There was no significant difference among these three responses (Chi-squared test,  $\chi^2_{(2)} = 0.574$ ,  $P = 0.754$ ).

Many of the 150 questionnaire respondents said that if a plant has a ‘pollinator-friendly’ logo on the label they would be more inclined to buy that plant (64%). Almost a third of respondents answered that they would “maybe” be more inclined to buy a plant with a pollinator-friendly label (32%); only six customers (4%) answered that they would not (Fig. 5.3 b).

In the interviews, most of the participants answering the questionnaire (13/14) also stated that they would be more inclined to buy a plant that had a pollinator-friendly label. This might depend on their original purchasing motive, for example: *“I’d only buy it if it fell into my reasons for buying the plant for that space at that time of year. But if it was a choice of two that were equally..., I mean obviously you’d buy the pollinating one”*; and in another interview *“if it was between two [plants] of the same colour and one was pollinating one then I would go for the pollinator-friendly one... I might not actually but I would be tempted to”*. Several interviewees referred to a pollinator-friendly logo as an “added benefit” or “bonus” that might make them more inclined to

purchase a pollinator-friendly plant (n = 4 interviews). For example: *“We know what we like, but if it says that on there then it’s a bonus”*.

For other interview participants, the presence of a label would either assist their purchasing decision (*“if that label was on one of the...[plants] it would help me choose”*; *“if I was looking at two plants and I couldn’t make up my mind, then I would possibly go for the one that had that on [rather than] the other one didn’t”*) or provide a clear motive to buy one plant over another, for example: *“When I look through the catalogue I always look to see what all the little symbols are, and if it’s a bee-friendly one, definitely if it’s a bee-friendly one I think I can justify buying it”*.

#### 5.4.4 Perceived barriers to pollinator-friendly planting

Interviewees identified certain barriers to planting for pollinators, including allergic reaction to bee stings: *“I was stung by a bee, so I have to carry an epi-pen... we used to have the big area of wildflowers in the middle of the garden, but we don’t have that anymore”*. Concern about children being stung was also discussed: *“if you were asking us ten years ago we’d have been going ‘no I don’t want bees, I’ve got three-year olds running round the garden’... I wonder whether younger mums would be more concerned”*.

In one interview, price was mentioned as a potential barrier: *“[we would be more inclined to buy a plant with a pollinator-friendly label] as long as the cost didn’t go up because of that, because that’s what happens... I think because they’re marked as pollinator-friendly, they’d put the price up”*.

#### 5.4.5 Customer familiarity with pollinator-friendly plant logos (Q12)

Just over half the questionnaire respondents were familiar with pollinator-friendly plant logos (59%). Proportionally more female participants (F: 64%, n = 75/118) were familiar with the logos than male participants (M: 44%, n = 14/32; Chi-squared test,  $\chi^2_{(1)} = 4.094$ ,  $P = 0.043$ ).

Familiarity with pollinator-friendly plant logos among interviewees was slightly but not significantly lower than in the overall questionnaire (43%,  $n = 6/14$ ,  $v$  59%, 89/150; Chi-squared test with Yates continuity correction,  $\chi^2_{(1)} = 0.830$ ,  $P = 0.362$ ).

#### 5.4.6 Customer perception of pollinator-friendly plant logos (Qs 13, 15)

##### 5.4.6.1 Visibility

Among a subset of 89 questionnaire respondents who were familiar with the logos and were, therefore, able to comment reliably on visibility, 74% thought they were visible enough while 26% did not.

Several interviewees who were familiar with the logos commented that they were noticeable “*if you’re looking for them*” ( $n = 5$  of a total of 25 interviewees). For example: “*you have to look for them*”; in another interview “*you know if you’re looking for something you’re going to see it. If you’re not looking for it...*” and in a third “*well sometimes if you’re looking, and it’s obvious they’ve got a pollinator-friendly label, well you see it don’t you. But I don’t always look for it*”.

##### 5.4.6.2 Reliability

70% of questionnaire respondents answered Yes to Question 13: *Do you think these [pollinator-friendly] labels are reliable sources of information*, despite 28 of these customers having answered that they were not familiar with the logos. 3% did not think they are reliable sources of information, while 27% did not know.

#### 5.4.7 Pollinator-friendly logo size as a proportion of plant labels

Mean logo size overall was  $2.02 \pm 1.32\%$  of the total label or packet area (median = 1.43,  $n = 65$ ). Proportional area of the pollinator-friendly plant logo was not significantly different between plants (mean  $\pm$  SD =  $2.15 \pm 0.21\%$ ,  $n = 49$ ), seeds ( $1.73 \pm 0.26\%$ ,  $n = 10$ ) and bulbs ( $1.45 \pm 0.05$ ,  $n = 6$ ; Kruskal-Wallis rank sum test,  $H_{(2)} = 1.21$ ,  $P = 0.546$ ; Table 5.2). The smallest proportional logo type was 1.08% of the total label area (“Good for Honeybees”,  $n = 1$ , Fig. 5.1 g) and the largest logo type was

7.58% (“Bee friendly”,  $n = 1$ , Fig. 5.1 c)).

Most plant labels, seed packets and bulb packets with pollinator-friendly logos on the front did not have any information about pollinators on the reverse of the label or packet (plants: 75%; seeds: 78%; bulbs: 100% (data given for labels for which reverse information was available); Table 5.2).

**Table 5.2.** Wildlife-friendly logo sizes on plant, seed and bulb labels/packets.

Average pooled measurements of pollinator- and wildlife-friendly plant logos and the plant labels ( $n = 49$ ) and packets of seeds ( $n = 10$ ) and bulbs ( $n = 6$ ) on which they were found. Values are given as mean  $\pm$  SEM. Any mention of pollinators on the label or packet reverse is indicated for those labels/packets for which this information was available. Logo types (*a-h*) are shown in Fig. 5.1

	<i>n</i>	Logo types present	Mean logo area (mm <sup>2</sup> )	Mean total label/packet size (mm <sup>2</sup> )	Mean logo area as proportion of mean total label/packet area (%)	Mentions pollinators on label/packet reverse?
<i>Plants</i>	49	<i>a, b, c, d, e, f, g, h</i>	168.0 $\pm$ 16.9	8,495 $\pm$ 663	2.15 $\pm$ 0.21	Yes = 12/47
<i>Seeds</i>	10	<i>a</i>	216.5 $\pm$ 36.6	12,291 $\pm$ 387	1.73 $\pm$ 0.26	Yes = 2/9
<i>Bulbs</i>	6	<i>a</i>	435.2 $\pm$ 56.0	30,377 $\pm$ 4,188	1.45 $\pm$ 0.05	Yes = 0/6

#### 5.4.8 Availability of advice and information in garden centres (Q16)

Question 16 asked questionnaire respondents whether they think garden centres offer enough information about which plants are good for bees and other pollinators. The most common response was *b. No, and it would be useful to have more information* (50%), followed by *a. Yes* (35%). Just three answered *c. No, but I don't mind* (2%), and 19 answered *d. I don't know* (13%; Fig. 5.3 c).

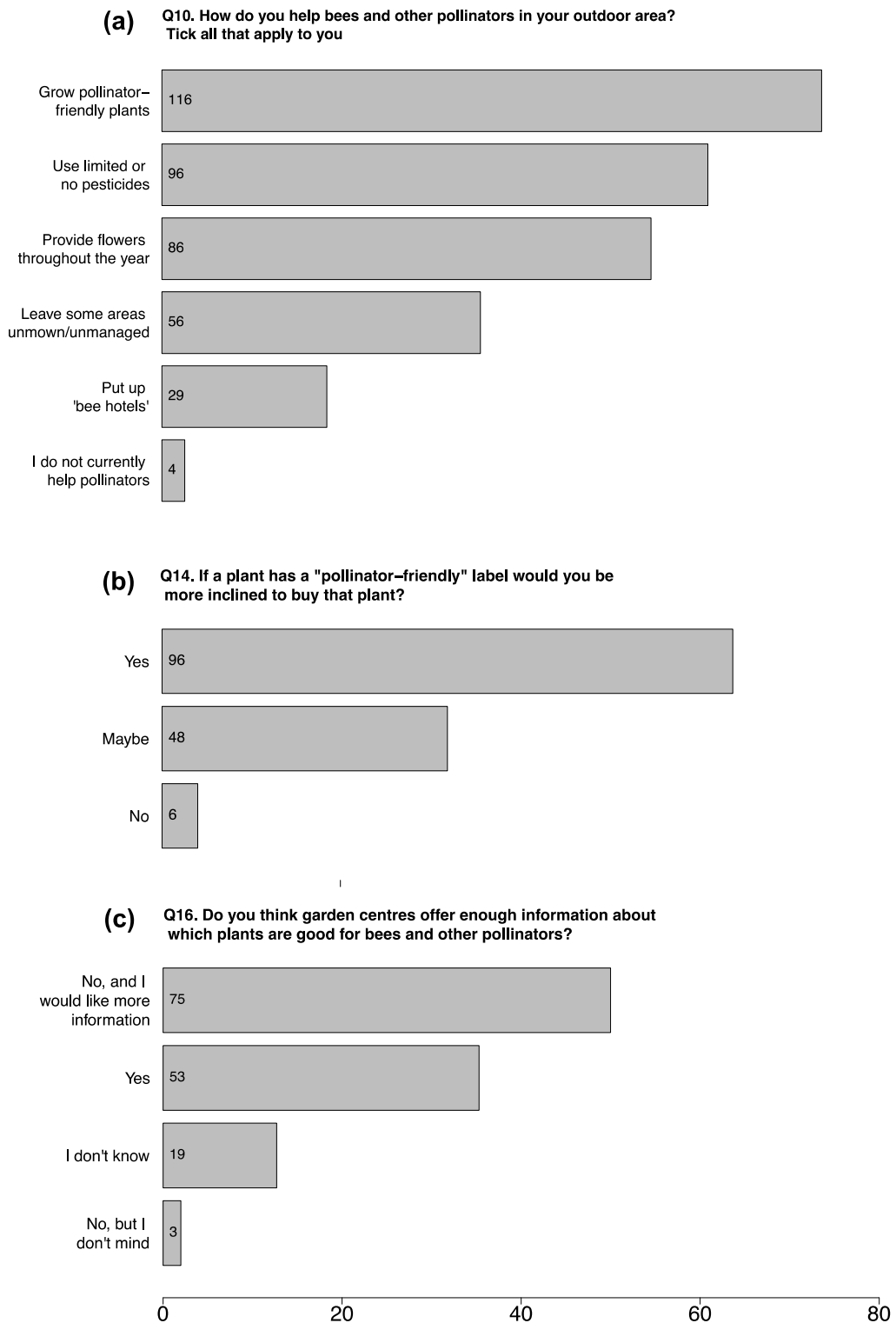
Interviewees answering the questionnaire also most commonly answered *b. No, and it would be useful to have more information* (64%, 9/14). Several commented on the

potential for garden centres to provide advice and information about pollinator-friendly plants. One interviewee commented: *“It’s probably a place where to start, the garden centres, because it’s probably where people go and buy their plants, apart from markets and things.”* For another: *“We love a garden centre don’t we, so I mean, well it’s the best place to have it really isn’t it”*, and a third noted *“it’s when you’re buying the plants that you’re thinking about pollinators, I mean not when you’re sitting in your sitting room”*.

A common theme was the lack of available information in garden centres, with several interviewees making comments similar to this example: *“I’ve never really walked round the garden centre and seen anything about it”*. Some mentioned that the information might be there if you looked for it or had a predetermined interest, for example: *“It depends whether you want to come in and you’re interested in it or not, and if you’re not, you’re just going to go round the garden centre buying the things that you want to buy”*.

Many felt that larger displays would be useful both to interest customers in pollinator-friendly plants and to provide information. One interviewee remarked *“I notice when the garden centre has a special section for bee friendly, but I can’t say I’m looking for logos”* and another that *“I think you’d have to have it with some sort of big bee display for you to actually whilst you’re chatting and looking and kids and stuff, you’d have to have a reason to look at that section”*. One interviewee noted the value of larger displays to *“make information more prominent for older eyes. Just to make people aware, just to bring the awareness, that’s the main thing.”*

Several made suggestions such as leaflets, displays, guides, posters and grouping plants in a ‘pollinator-friendly’ section to provide information and attract customer interest.



**Figure 5.3.** Garden centre customers' engagement and interest in pollinator-friendly gardening, compared to their perception of information provision by garden centres. Grey horizontal bars show the percent of questionnaire responses for each answer to three questions in (A) Question 10 "How do you help bees and other pollinators in your outdoor area? Tick all that apply to you", (B) Question 14 "If a plant has a pollinator-friendly label would you be more inclined to buy that plant" and (C) Question 16 "Do

you think garden centres offer enough information about which plants are good for bees and other pollinators”. Response details are to the left of each bar. Counts are shown within bars. Sample size was  $n = 150$  customers for each question. Question 10 was a multiple choice question.

#### 5.4.9 Current media interest in pollinators

The most common source of interviewees’ knowledge and awareness about pollinators was the media, with one or more of television, ‘the news’, newspapers and radio mentioned in 12/13 interviews in which the participant(s) were aware of pollinators. Several cited nature programmes, documentaries and/or the popular weekly BBC television program ‘*Gardener’s World*’ while other sources included gardening books, education while growing up and magazines. Social media was also acknowledged by one interviewee who received some of her knowledge from Facebook. Only two of a total of 25 interviewees said they had received any information about pollinators and/or pollinator-friendly plants in garden centres, despite many participants being regular visitors.

We asked interviewees whether they felt there had been any general change in awareness about pollinators over time. One had not been aware of pollinators prior to the interview, and in one interview neither person in the pair gave a clear response to this question. One couple did not feel their awareness of pollinators had changed. However, in 11 interviews, the participant(s) felt there had been a recent increase in the quantity and availability of information about pollinators. One said: “*Definitely, in the last four, five years, there’s been newspapers, television, documentaries about it*” while another commented “*There’s so much on the TV now, particularly on sky channels and wildlife channels. It’s everywhere*”.

Despite this, interview participants commented on a lack of reliable, comprehensive information: “*you’ve got to get your shock headlines out there to talk to people, but often there’s not enough back up information, or you’ve really got to make a concerted effort to go find out why and what and how we can do anything about it*”. Several interviewees commented on how the news media can be transient and unreliable, with comments such as: “*now the whole buzz thing has gone to plastic, and all of a sudden*



*the bee awareness has just been pushed aside a bit*"; *"Occasionally there's some news, it comes up on the news about bees and the loss of bees, but then it's all a one-day wonder"*. It was commonly noted that the public are often exposed to conflicting information through the news, including about bees and other pollinators, *"...so you think, well I don't really know what the real story is"*.

## 5.5 Discussion

Our results show that UK garden centre customers have a strongly positive attitude towards gardening for pollinators. Almost all (97%) questionnaire respondents thought that bees and other pollinators were beneficial to their garden, most (97%) reported that they already take some action to help these insects in their outside area, and many (53%) prioritised pollinator-friendly features when purchasing flowering plants. These overall conclusions were reinforced through in-depth interviews. This is the first time to our knowledge that positive attitudes towards wildlife gardening in the UK has specifically been shown to include pollinating insects; although many British households actively encourage wildlife in their garden, this often chiefly involves feeding birds (Gaston et al. 2007, Defra 2009).

Positive attitudes towards pollinators and pollinator-friendly plants is likely to influence consumer behaviour (*e.g.* Wollaeger, Getter & Behe 2015, Rihn & Khachatryan 2016). This may explain why, in our study, 96% of questionnaire respondents answered that they would ('yes' 64%; 'maybe' 32%) be more inclined to buy a plant if it had a 'pollinator-friendly' label (Fig 5.3 *b*). Insights from the interviews showed that, for some customers, knowing a plant was good for pollinators would justify their purchase or motivate them to buy a particular plant. For others, a purchasing decision would depend on initial reasons for buying a plant, but knowing one was pollinator-friendly would help them to choose between, for example, two similar varieties.

In terms of practical actions to support pollinators, 77% of questionnaire respondents stated that they currently grow pollinator-friendly plants (Fig 5.3 *a*), although it was not clear whether they had initially acquired these plants with the intention of supporting pollinators; it is possible that this was often a by-product of varieties initially planted for other reasons. However, 53% of respondents considered bee- or pollinator-friendliness

to be one of the three most important features, excluding price, when buying flowering plants. A clear incentive to help bees was also shown by a fifth of respondents who put up bee ‘hotels’. These structures aim to provide nesting habitats for solitary bees, although their efficacy is unclear (MacIvor & Packer 2015). Many people also gardened with limited or no pesticides. While this is a common pro-environmental behaviour that may reflect consumer awareness of pesticides’ negative effects on pollinating insects (Campbell, Khachatryan & Rihn 2017), participants’ motivation for this action was not investigated further in this study.

Public action to conserve pollinators is considered a necessary response to pollinator declines (Defra 2014, Cambridge Institute for Sustainability Leadership et al. 2017). Encouraging citizen action and education forms a major part of the EU Pollinators Initiative (European Commission 2018) and several national-level pollinator strategies (Defra 2014, Senapathi et al. 2017). Growing pollinator-friendly varieties of flowering plants in gardens and other private or community greenspace is one of the most effective ways in which the general public can directly help flower-visiting insects. Flower availability in both urban and countryside areas can often be reduced due to factors such as a high proportion of impervious surfaces (McKinney 2006) or intensive farming (Brassley 2000, Ollerton et al. 2014), whereas gardens can be relatively flower-rich, contain a high diversity of plant species, and even provide a resource at times of the year when native flowers are not in bloom (Smith, Warren & Thompson 2006, Stelzer et al. 2010, Baldock et al. 2015). Optimising the supply of nectar and pollen in domestic gardens and other greenspace through choosing plant varieties that attract insects (Garbuzov & Ratnieks 2014b) is therefore increasingly important in alleviating pollinator dietary stress, particularly since these areas comprise a relatively large total area in the UK (Gaston et al. 2005).

Garden centres are well-placed to facilitate this both through supplying plant varieties that will attract flower-visiting insects, and by delivering relevant advice and information to a substantial customer base. Two thirds of British adults visit a garden centre at least once a year (HTA 2018), and garden centre customers in Great Britain spent £1.4 billion on garden plants in 2016 (HTA 2017). Here, most respondents were visiting the garden centre to purchase plants, seeds or bulbs (56.7%), and when buying plants most respondents looked for ornamental plants with flowers (68.1%).

Despite this, evidence from this and previous research suggests that the potential for garden centres to facilitate pollinator-friendly planting is not being met, despite clear customer interest (Fig. 5.3). For example, it is possible for garden centres to use peer-reviewed scientific evidence to select and market varieties of flowering plants that attract pollinators (Garbuzov & Ratnieks 2014b). However, many flowering plants on sale in garden centres are in fact not attractive to flower-visiting insects, in some instances even when labelled ‘pollinator-friendly’ (Garbuzov, Alton & Ratnieks 2017).

In this study, most customers perceived garden centres’ provision of advice and information about pollinator-friendly planting to be limited (Fig. 5.3 c). The majority of questionnaire respondents thought that garden centres did not offer enough (52%) and only two interviewees had received any of their knowledge or information on this topic from garden centres compared to other sources such as television, news media and nature programmes, which were cited several times. This contrasted with a clear desire for more information, since half of all questionnaire respondents thought that it would be useful for garden centres to offer more information. Several interviewees even commented that garden centres would be the “best place” for advice about which plants are attractive to pollinators since this is most useful in context, such as when people are buying plants. Just over a third of questionnaire respondents thought there was enough information in garden centres; of these, 72% were familiar with ‘pollinator-friendly’ logos. This could indicate that a proportion of customers are generally well-informed on this issue, or alternatively that customers who answered that garden centres do offer enough information are basing this on the occurrence of pollinator-friendly logos.

Pollinator-friendly logos are one way in which garden centres advise customers about which plants are good for pollinators. These ‘eco-labels’ can be successful marketing tools. Eye-tracking technology has shown that customers who spent time looking at a pollinator-friendly label on a plant were more likely to purchase it than those who did not view the label (Khachatryan et al. 2017). In our study the majority of questionnaire respondents stated that they would be more likely to buy a plant that had a pollinator-friendly logo (64%). However, 41% were not familiar with such logos. The logos tend to be small: here, mean pollinator-friendly logo size on plant, bulb and seed labels was just 2.2% of the overall label or packet size, which may explain why many respondents were not familiar with them.

Most respondents who were familiar with pollinator-friendly logos thought that they were visible enough, possibly simply due to the fact that they had seen them. A number of interviewees commented that these logos are noticeable if you are looking for them. This is consistent with previous work investigating the potential efficacy of incentives for residential wildlife gardening, in which interviewees commented that you have to “want to know” in order to find relevant information (Goddard, Dougill & Benton 2013). Many garden centre customers, perhaps particularly younger age groups with competing time demands, are likely to have a passive approach to receiving information about which plants are attractive for pollinators, even if they have a positive attitude towards pollinator conservation. This was summarised by one interviewee: *“I think you’d have to have it with some sort of big bee display for you to actually, whilst you’re chatting and looking and kids and stuff, you’d have to have a reason to look at that section”*.

Since a lack of information has been shown to be a barrier to wildlife gardening here and in previous research (Goddard, Dougill & Benton 2013, Campbell, Khachatryan & Rihn 2017), this highlights a need for highly visible, accessible information to supplement pollinator-friendly logos on plant labels. Interviewees suggested a range of options to provide information and attract customer interest, including leaflets, displays, guides and posters. Several mentioned that grouping plants in a ‘pollinator-friendly’ section with corresponding information would be helpful. Further suggestions based on our findings could be to i) increase the size of pollinator-friendly logos to make them more visible and ii) include practical information about pollinators in combination with these logos, since only a small proportion of plant, seed and bulb labels and packets with logos had any mention of pollinators on the reverse of the packet (22.6%; Table 5.2).

Customers spend a substantial length of time in garden centres, and under 10% of the UK spend on garden plants is made online (HTA 2017). Unlike many other industries where online retail success has caused traditional stores to be non-viable, the experience of visiting a garden centre to purchase plants is clearly important to customers. This opens the possibility for garden centres to provide obvious, accurate information about pollinators that is available in context and at point-of-sale when customers are buying

flowering plants. In this study interviewees noted the usefulness of displays about other aspects of plant qualities and care. It is possible that displays about pollinator-friendly plants could be easily integrated into such pre-existing information infrastructure without significant cost, which might provide a barrier to customers should it be reflected in pollinator-friendly plant prices (Campbell, Khachatryan & Rihn 2017, this study).

We found that interviewees often spontaneously mentioned a positive emotional state associated with seeing bees and other pollinators in their gardens. Gardens and other private outside areas, including allotments, balconies and patios, can provide an important connection to nature, particularly for people living in urban environments (Dunnett & Qasim 2000, Freeman et al. 2012, Cox et al. 2017). The benefit of wildlife gardening to personal psychological wellbeing has previously been reported (Goddard, Dougill & Benton 2013), and a link between pollinators and emotional wellbeing in this study suggests that this may partly explain a personal motive for gardening for pollinators.

Interestingly, many interviewees reported a recent increase in personal and public awareness of pollinators, which was largely linked to a growth in the quantity of information published in print and broadcast media. This was often negativistic, with several participants mentioning ‘shock’ or ‘dramatic’ headlines, the need to ‘look after’ pollinators such as bees and genuine concern about their declines. This is similar to a recent survey of environmental professionals and members of the British public which found a large proportion of participants gained their information from mainstream media sources (Easman, Abernethy & Godley 2018). In this study, individuals that were more concerned about the marine environment were more likely to engage with pro-environmental actions to minimise their personal impact (Easman, Abernethy & Godley 2018). It is likely that higher awareness of and concern for pollinators would contribute to gardeners’ personal motivation to encourage pollinating insects. Concern for the status of pollinators may also have added to reported feelings of happiness associated with seeing them in their outside area, since humans disproportionately value rarity, which has been linked to increased interest in rare and threatened animal species (Angulo & Courchamp 2009).

Awareness of pollinators and factors associated with their declines can influence plant purchasing decisions based on pro-environmental attributes. In one study, consumers who were aware of neonicotinoid pesticides, which have gained widespread media attention due to their negative effects on insect pollinator health (reviewed in Van der Sluijs et al. 2013), were significantly more likely to buy plants labelled ‘neonic-free’ than those who were not aware (Rihn & Khachatryan 2016). A taste for sustainable products has been identified as a major sociocultural driver in the garden centre retail industry by the Horticultural Trade Association (HTA). For example, it is becoming important to meet a growing demand for alternatives to plastic and peat, materials considered to be environmentally unsustainable, due to increasing customer antipathy (HTA 2017). Here, several interviewees described pollinator-friendly qualities as an ‘added bonus’ to plants they might purchase primarily for other reasons. While this is a positive step, it also suggests that more could be done to harness a clear motivation of garden centre customers to support pollinators, for example by specifically advertising pollinator-friendly features to drive sales of these plants. Investigating whether featuring pollinator-friendly qualities as a primary attraction would increase sales of these plants compared to *i*) the same but un-labelled pollinator-friendly or *ii*) similar non-pollinator-friendly varieties is a logical next step, since this could show the empirical value of this type of marketing for garden centres themselves.

## 5.6 Conclusions

Growing pollinator-friendly varieties of flowering plants is one of the most effective ways in which members of the public can directly help bees and other pollinators, which are known to be in decline in the UK (*e.g.* Carvell et al. 2006) and globally (Potts et al. 2010). It is therefore important to understand public attitudes towards planting for pollinators; however, this has not been directly studied as far as we are aware. This study investigates garden centres customers’ attitudes towards pollinators and pollinator-friendly planting, since this relevant and important consumer group represents members of the UK public who are actively engaged in gardening. We show for the first time that customers have, in general, a strong current interest in and positive attitude towards pollinating insects, which translates into an impetus to plant pollinator-friendly plant varieties in private gardens or other outdoor areas. Facilitating this could have a real impact on provision of floral resources for pollinating insects, since gardens

make up a large area of the UK (Gaston et al. 2005), and are increasingly important sources of nectar and pollen for pollinators particularly in urban areas (Baldock et al. 2019).

We also suggest that our findings are relevant to the horticultural retail industry, since provision of evidence-based advice and information about pollinators and pollinator-friendly planting, as well as promotion of such plants, could potentially be increased without substantial involved costs to garden centres. We speculate that this would be likely to benefit sales due to a strong customer interest, although this deserves further study; as well as having a positive effect on the pollinators themselves.

## **Chapter Six: Perception roots: understanding public attitudes towards common wild flowering plants and implications for flower-visiting insects**

*“We're stuck in our boxes, windows open no more  
Collecting up the forget-me-nots, not recalling what they're for”  
~ Pearl Jam, *Dance of the Clairvoyants**

### **Authors and author contribution statement**

Veronica R. Wignall, Karin Alton & Francis L. W. Ratnieks

VW, KA and FLWR conceived the ideas; VW and KA designed the questionnaire, VW led the data collection, data analysis and writing of the manuscript

### **6.1 Abstract**

Common wild flowering plants can improve floral resource availability for flower-visiting insects in non-agricultural contexts. Simultaneously, allowing these plants to flourish can enhance human connection to nature, currently at a concerning level of decline in many modern, highly urbanised societies. However, while some wildflowers are widely liked, others have a low societal reputation and are commonly removed from private and public green spaces. Understanding attitudes and practice regarding common wildflowers is an important step towards creating ‘nature-friendly’ landscapes that have public support. In this study we used an online questionnaire to survey public attitudes towards common wild flowering plants using six representative species: bluebell, bramble, daffodil, dandelion, ivy and primrose. Using quantitative and qualitative data we show that perceptions of common wild flowering plants are affected by conflicting factors including aesthetic appeal, charisma and ‘weed’ status, with a small positive effect of perceived ecological function at an individual, but not societal, level. Our findings suggest that it would be worthwhile and effective to improve public perceptions of common wild flowering plants, including species considered to be a ‘weed’, through education and awareness programmes highlighting both ecological function and cultural significance.



## 6.2 Introduction

Research across traditional disciplinary boundaries has repeatedly shown that connection to the natural world can bring multiple measurable physical and mental benefits to human wellbeing (Fuller et al. 2007, Hartig et al. 2014, Sandifer, Sutton-Grier & Ward 2015, Cox et al. 2017). For example, access to greenspace provides multiple physical health benefits (Hartig et al. 2014) and can even reduce health inequalities related to socioeconomic inequality, including circulatory conditions (Mitchell & Popham 2008). Psychological benefits include reductions in stress and associated mental ill-health, and even enhanced cognitive function (Hartig et al. 2014, Sandifer, Sutton-Grier & Ward 2015). A study across three large towns in Southern England found that incidence of mild and worse depression decreased with increased neighbourhood vegetation cover and time spent in the garden (Cox et al. 2017). Experiencing biodiversity within green spaces can also have positive effects on human mental health and wellbeing, although this is complex, difficult to quantify and not consistent (Lovell et al. 2014, Marselle et al. 2019). For example, measures of psychological wellbeing in users of urban greenspace have been shown to improve with species richness of plants and birds (Fuller et al. 2007). However, an increase in perceived bird species richness was associated with more negative emotions in one study of UK citizens (Marselle et al. 2015), while in another, psychological wellbeing was positively related to perceived bird, butterfly and plant species richness in urban riparian green space, and positively associated with actual (surveyed) bird species richness, but negatively associated with actual plant species richness, with no trend observed for actual butterfly species richness (Dallimer et al. 2012). Nevertheless, a recent review found that of 24 studies investigating the association between biodiversity and mental health and wellbeing between 2001-2018, 14 reported one or more positive associations, 17 reported no significant relationship and 2 studies reported one or more negative associations (Marselle et al. 2019).

Nature, however, has been negatively affected by human activity, with large scale and accelerating global declines in biodiversity (Johnson et al. 2017) and human-driven impact on climate and ecological systems that have led to the current post-industrial period being termed the ‘Anthropocene’ (Ruddiman 2013, Waters et al. 2016). Simultaneously, human connection to nature has diminished in recent decades (Miller

2005, Soga & Gaston 2016). Underlying factors include increasing urbanisation, with 68% of the global population predicted to live in urban areas by 2050 according to the United Nations Population Division (UN 2019). Increasingly sedentary modern lifestyles and reliance on digital technology for both work and entertainment also contribute to a widespread “extinction of experience” as daily interaction with nature decreases (Miller 2005, Soga & Gaston 2016). This leads to lower affinity with nature that further reduces interaction with wildlife, causing feedback loops that lead to a low level of experience of the natural world in both children and adults. In turn this results in a concerning and ill-timed reduction in likelihood to engage in pro-environmental behaviours (Soga & Gaston 2016).

One way of ameliorating this trend is to make nature more a part of everyday life, in the spaces where we live, work, play and even commute. A cost-effective and practical means of doing this is to encourage or allow common wild plants to grow in these areas, particularly in towns, cities and along transport infrastructure, thereby increasing daily encounters with plant and associated animal life (Miller 2005, Weber, Kowarik & Säumel 2014, Soga & Gaston 2016); this is particularly relevant for individuals that do not have regular access to a private or community garden or other outdoor area (Cox et al. 2017). Such a strategy would also simultaneously benefit biodiversity and ecosystem health. For example, flowering wild plants provide nectar and pollen for flower-visiting insects (FVI), many of which also have juvenile forms that feed on vegetative parts of flowering and non-flowering species (Gilbert & Singer 1975, Rotheray & Gilbert 2011). Many FVI species are in decline worldwide (Potts et al. 2010, Vanbergen et al. 2013). In the UK, the proportions of occupied 1 km<sup>2</sup> grid squares for hoverflies and wild bees have decreased by 24% and 25% respectively between 1980 – 2012, with particularly severe declines in occupancy for non-eusocial bees (32%; Powney et al. 2019). Similarly, 37% of the UK’s 62 resident and breeding butterfly species are classified as Regionally Extinct (n = 4 species) or threatened (Critically Endangered (2), Endangered (8) or Vulnerable (9); Fox et al. 2011). Enhancing floral resources is considered to be a vital step in mitigating and reversing these declines (Carvell et al. 2006, Wallisdevries, Van Swaay & Plate 2012, Fox et al. 2015, Carvell et al. 2017). Improving conditions for insects could have cascading positive effects on biodiversity at multiple trophic levels, for example by increasing food supply for insectivorous birds (Seress et al. 2018) and bats (Bolliger et al. 2020). In urban areas, increasing vegetation cover has many positive

effects further to promoting biodiversity and human-nature connection, including local climate regulation, noise reduction and flood and pollution mitigation (Wu 2014).

Overall, encouraging common wild-growing plants could be a powerful tool in improving both public wellbeing and biodiversity in many areas. However, many spontaneously-growing flowering plants are routinely removed from residential gardens and public spaces. For example, a study of gardening behaviours in Sheffield, a large UK city, showed that mowing and weeding are performed by most householders on a regular basis, with a commonly low tolerance of weeds in domestic gardens (Loram et al. 2011). In public spaces, mowing, strimming and herbicide use by local authorities remains high in many regions, with some councils mowing verges and parks more than 10 times a year. Reflecting this, a recent study of four UK cities showed that publicly managed greenspace, including parks and road verges, made up a large proportion of land use area (27-35%), but hosted low floral abundance and particularly species richness. In parks, average floral abundance and species richness were 75% and 77% lower than in domestic gardens, respectively (Baldock et al. 2019).

Although often only simple management changes are needed to increase the abundance and species richness of wild-growing plants in areas such as domestic gardens, public parks and road verges (Noordijk et al. 2009, Garbuzov, Fensome & Ratnieks 2015, Baldock et al. 2019, Baldock 2020), managing landscapes in favour of ecological value clearly has an important human dimension. For example, reduced management in residential areas can negatively influence local people due to concerns that ‘messier’ areas can appear neglected (Nassauer 1995, Coupey et al. 2015, Nam & Dempsey 2019), which is perceived to have socio-economic consequences regarding house prices, and, linked to this, social consequences through neighbourly disapproval (Goddard, Dougill & Benton 2013). Users of urban parks may be affected both positively and negatively by changes to management that allow taller vegetation, including flowers, to grow (Garbuzov, Fensome & Ratnieks 2015). Weber, Kowarik & Säumel (2014) showed that residents in Berlin, Germany, had mixed opinions towards wild-growing roadside vegetation, with 37% of survey participants associating this with ‘disorder’ and only 15% with positive aspects of urban greening, including perceived beauty and psychological wellbeing.

Importantly, some common wild flowering plants with high ecological value have low societal appreciation, being either overlooked or disliked. In contrast, other species may be favoured. Such preferences are often independent from ecological value (Wignall & Ratnieks *in submission*), as has also been observed in invertebrates: bees and butterflies are often strongly preferred over flies and wasps despite these insects also being important pollinators (Sumner, Law & Cini 2018, Wignall, Alton & Ratnieks 2019). Possible underlying factors are complex and often context-dependent. For example, perceptions and practice (*i.e.* encouraging, tolerating or removing certain plants, or supporting such actions) may be influenced by aesthetic preferences (Clayton 2007), health reasons such as hayfever or allergy to insect stings (Wignall, Alton & Ratnieks 2019) or sociocultural norms such as neighbourhood pressure to have a tidy, ‘weed’-free lawn or garden (Blaine et al. 2012, Goddard, Dougill & Benton 2013). While ecological value may be considered positively by some members of the public, this can be a low priority, or may be overruled by or in conflict with other factors (Goddard, Dougill & Benton 2013, Sumner, Law & Cini 2018); however, this has not been investigated regarding wild flowering plants specifically. Attitudes towards wildlife and pro-nature landscapes may also be changing as more people become aware of climate and biodiversity emergencies (Wignall, Alton & Ratnieks 2019, Hall & Martins 2020; Thackeray et al. 2020), but this is not clear. Overall, understanding how people perceive common wild-flowering plant species is an important aspect of understanding current management practices as well as managing wildlife-friendly landscapes in a way that fosters public support, however, to our knowledge this has not been studied previously.

In this study we used an online questionnaire to investigate public knowledge and perceptions of common wild flowering plants, hereafter termed wildflowers, as well as possible factors influencing these. We used qualitative and quantitative data to explore the following questions: 1) Were any wildflowers more or less liked, and did any common characteristics affect this?; 2) Did perceived ecological value, specifically, influence wildflowers’ popularity or ‘weed’ status?; Did any personal attributes influence participants’ 3) liking or 4) ability to identify wildflowers? The findings relating to the six representative wildflowers chosen in this study are relevant for wildflowers more broadly and offer clues as to how to encourage popular support for wildflower-, and therefore flower-visiting insect-, friendly management in public spaces and residential areas.

## 6.3 Materials and Methods

### 6.3.1 Questionnaire design

The online questionnaire was built in Google Forms. Following a section giving information and asking for consent to participate (Appendix E.1), there were three sections which collected information about participants': (1) basic and extended attributes, including age, self-described gender, education, frequency of gardening/growing and self-reported level of interest in nature, (2) perceptions of common wildflowers and (3) knowledge of wildflowers through identification (Appendix E.2). Participants were asked to give responses that related to their attitudes and behaviours prior to the unusual state of 'lockdown' imposed by the UK Government in March 2020 in response to the coronavirus (COVID-19) pandemic.

Six representative wildflowers were chosen for the survey. These were carefully selected to include species known to be perceived both positively and negatively, so that a full range of underlying reasons and associations could be explored. Three were chosen due to their popularity in a poll by the wildflower conservation charity Plantlife in 2015: bluebell, daffodil and primrose were in the five most well-liked wildflowers for one or more of England, Northern Ireland, Scotland and Wales (Trevor Dines Plantlife UK, *personal communication*). Three further wildflowers were chosen that are known to be disliked in some contexts: bramble (Wignall et al. 2020b), dandelion (Blaine et al. 2012) and ivy (Garbuzov & Ratnieks 2014a, Wignall & Ratnieks *in submission*).

For each wildflower, photos were selected showing the plant in its flowering stage. Photos were chosen that were considered to be similarly 'photogenic' and did not give any context or extra information that may have primed associations (*e.g.* bluebells were not shown in woodland, no flower-visiting insects were present in any of the photos, no fruit was present on bramble; Fig. 6.1).

### 6.3.2 Ethical approval

All questionnaire materials were approved by the University of Sussex Sciences & Technology Cross-Schools Research Ethics Committee (C-REC, reference number ER/VW58/6). All participants were given the relevant ethical information about the survey, asked to confirm that they were over 18 years of age and to give their consent before beginning the survey. The online questionnaire and preceding information and consent form are available in Appendices E.1 & E.2.

### 6.3.3 Survey recruitment

The online survey was advertised via social media channels (Twitter, Facebook) and sent via email to the authors' personal and professional networks. This method was likely to lead to a participant bias due to a 'bubble' effect, whereby social media gathers users into cliques of like-minded individuals (Kaakinen et al. 2020), in this case, those with a pre-existing interest in plant-pollinator ecology and conservation. Therefore, we also deliberately aimed to disseminate the survey to non-specialist networks where possible. The survey was accessible from 25 May to 30 June 2020.

### 6.3.4 Processing response data

#### 6.3.4.1 Section 1: Participant characteristics

Participation in the survey was likely to be self-selecting for people with an existing interest in wildflowers or nature to a considerable extent, since these more likely to participate than those without an interest in this topic. This was likely to be further perpetuated by the recruitment process, particularly through social media channels (see section 6.3.3). Therefore, we included a question in Section 1 that asked participants to identify if they had any relevant working experience: *'Have you ever worked in a role with an environmental or horticultural focus, for example: Landscape design, garden centres, farming, greenspace management, wildlife conservation, natural sciences researcher, ecological consultancy, environmental education?'*. Any participants who answered 'Yes' (n = 819) were grouped in a 'Relevant expertise' category, which also included any remaining participants (n = 4) with education relevant to this field ('RHS qualifications', 'British Beekeeping Association exams', 'Horticultural college'; Question 10: *'What is your most recent level of education?'*). This 'Relevant expertise'

group was identified separately since respondents were likely to have a particularly strong interest in and knowledge of wild flowering plants and their ecological value.

Responses to Question 10 included '*Postgraduate University degree or equivalent*', '*Undergraduate University degree or equivalent*', '*Further Education/College*', '*School*'. Answers given in the category '*Other*' (n = 153) were manually coded into the equivalent education level category.

Responses to Question 7 ('*Do you own or have regular access to (select all that apply)*') included: '*a personal/private-owned garden*', '*allotment*', '*other personal outside space (e.g. balcony, patio)*', or '*none of the above*'. Where more than one option was selected, these were grouped into single categories that represented the level of access to an outside area ('*garden and allotment*', '*garden*', '*allotment*', '*other outside space*' and '*none of the above*'), for analysis. If '*other personal outside space (e.g. balcony, patio)*' was selected with garden and/or allotment, this was subsumed into the appropriate overarching category '*garden and allotment*', '*garden*' or '*allotment*', since this was not considered to give an additional level of engagement with an outside area above these categories.

Other attributes collected in this section were: age (18-25, 26-35, 36-45, 46-55, 56-65, 66-75, 76-85, 86+), self-described gender (*Female*, *Male*, *Prefer not to say*, *Prefer to self-describe*), where participants currently live (*City centre*, *City suburbs*, *Town centre*, *Town suburbs*, *Rural area*), how often participants partake in gardening or growing (*Daily*, *2-3 times weekly*, *Weekly*, *2-3 times monthly*, *Monthly*, *Rarely*, *Never*), and stated level of interest in nature (0-10; Appendix E.2).

#### 6.3.4.2 Section 2: Perceptions of common wildflowers

How people perceived the six flower species was assessed quantitatively and qualitatively. Respondents were asked to rate how much they liked each flowering plant using a modified Likert scale (1-5: 1, *I strongly dislike it*; 2, *I somewhat dislike it*; 3, *neutral – neither like nor dislike*; 4, *I quite like it*; 5, *I like it very much*). The proportions of each answer per wildflower were used to give a quantitative assessment of the popularity of each among the survey respondents. The ratings were also summed

per participant to give a total '*perception score*' (6-35) for statistical analysis. Respondents were also asked to select the two plants they consider to be most beneficial to wildlife including FVI, and how many (0-6) they considered to be a weed or a 'nuisance'.

Perceptions of each wildflower were assessed qualitatively by asking each respondent to give up to three words to describe the flower (following Sumner, Law & Cini 2018). For each wildflower, these data were cleaned to remove surplus blank spaces, numbers or special characters, and inconsequential words (*e.g.* 'in', 'on') using package *tm* in R (version 0.7-7; Feinerer & Hornik 2019) and further corrected manually to remove plurals (*e.g.* woodland, woodlands) and for spelling mistakes. Where short phrases were given it was ensured as far as possible that these were not separated into single words (*e.g.* 'bee friendly', 'blackberry pie', 'wild flower'). Species names, prominent colours (*e.g.* for bluebell: blue and purple) and the word 'flower(s)' and 'wildflower(s)' were also removed. Word clouds were made using the package *wordcloud* in R (version 2.6; Fellows 2018) to visually represent the frequencies of the 100 most common word responses. Then, for each wildflower, all words and short phrases that were given by 10 or more participants were manually coded into 'perception root' categories so that key factors influencing perceptions could be identified. The 20 most common words given for each wildflower with their associated perception root categories were extracted as a per-species 'profile' (modified from Sumner, Law & Cini 2018).

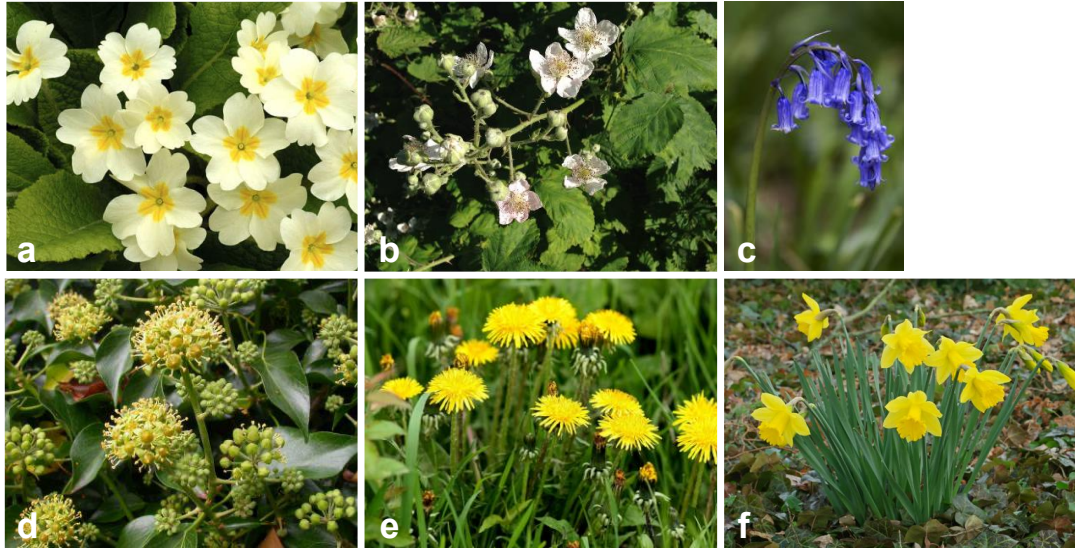
Participants were then asked to select two of the six wildflowers they thought to be '*most beneficial to wildlife*', and to select any (or none) of the six wildflowers they thought to be '*a weed or a nuisance*'.

#### 6.3.4.3 Section 3: Wildflower identification

Questions 26-31 asked participants to name the six representative wildflowers. Shortenings such as 'daffs' were accepted as correct. Commonly used colloquial names (*e.g.* 'johnquil' for daffodil) were accepted. Latin names were accepted, but if solely the Genus was given where there was possible ambiguity ("*Rubus*" and "*Primula*") this was marked as incorrect. Answers were marked as incorrect if more than one species was



named as this was ambiguous. The total number of correct answers (0-6), or ‘*knowledge score*’, was calculated for each participant.



**Figure 6.1.** Photos used in the online questionnaire for each wildflower species: *a.* primrose, *Primula vulgaris* Huds.; *b.* bramble, *Rubus fruticosus* L. agg.; *c.* bluebell, *Hyacinthoides non-scripta* (L.); *d.* ivy, *Hedera* spp.; *e.* dandelion, *Taraxacum officinale* agg. and *f.* daffodil *Narcissus pseudonarcissus* L.. Photos sourced from Wikimedia Commons

#### 6.3.5 Statistical analysis

Many of the participant attributes were associated and were tested for independence using contingency Chi-square tests, with Kendall’s tau-b to calculate the strength of association between two ordinal variables, Freeman’s *theta* for one nominal and one ordinal variable and Cramer’s V for two nominal variables.

Following graphical exploration to identify variables of interest, we used regression models to explore which participant attributes affected i) wildflower liking rating and ii) ability to identify wildflowers (*knowledge score*). There were strong associations between growing or gardening frequency and access to outside space ( $\chi^2_{(4)} = 227.81$ ,  $P < 0.001$ ; Freeman’s *theta* = 0.421; Freeman 1976) and growing or gardening frequency and stated level of interest in nature ( $Z = 15.67$ ,  $P < 0.001$ , Kendall’s tau-b = 0.317;

Brown & Benedetti 1977), therefore these variables were included separately in statistical models to avoid multicollinearity. Before selecting final models, multicollinearity between model variables was further tested using the function *vif* in the R package *car* (version 3.0-10; Fox & Weisberg 2019). Best-fitting models were selected using Aikake-Information Criteria (Bolker et al. 2020) and comparison to a null model using likelihood ratio tests.

Only five participants were age 86+, therefore to improve model stability these were merged with the age group 75-85 for analysis. Similarly, stated level of interest in nature was given as '1' out of ten by just one participant and '3' by three participants. Therefore, for model stability these were merged with '4', since this level represents a similarly low level of interest in nature.

Participants' liking rating for the six wildflowers was analysed using a proportional odds logistic regression model, with rating on the Likert-type scale (1-5) as the ordered factor response variable. Predictor variables for the best-fitting model were wildflower species and participant age and stated level of interest in nature. The proportional odds assumption was tested using visual representation of surrogate response variables, and confirmed.

Participants' ability to identify the six wildflowers was analysed using a Poisson regression model, with respondents' number of correct answers or *knowledge score* (0-6) as the response variable and a Poisson family link for count data. Predictor variables for the best-fitting model were age and level of interest in nature. An interaction term between these variables was not significant ( $P = 1.000$ ) and therefore was not included in the final model. Residuals were plotted and visually approved using R package *DHARMa* (version 0.3.1; Hartig 2020), with targeted goodness-of-fit tests for over- and underdispersion between the observed vs simulated residuals. Follow-up pairwise comparisons between model estimated marginal means within groups were calculated using *emmeans* (in package *emmeans*, version 1.4.1; Lenth 2019) with  $P$  values adjusted for multiple comparisons by the Bonferonni method.

For each wildflower species we tested whether considering a plant to be beneficial to wildlife affected its i) liking rating and ii) perception as a 'weed'. First, we tested

whether the flower's liking rating (1-5) varied among participants who had selected that wildflower as one of the two plants they considered '*most beneficial to wildlife*' and those that had not, using Mann-Whitney-Wilcoxon tests between these groups (de Winter & Dodou 2010). Effect sizes ( $r$ ) were calculated using the formula  $r = Z/\sqrt{N}$  (obs) and interpreted using the standard boundaries: small = 0.1 - < 0.3, medium = 0.3 - < 0.5, large  $\geq 0.5$  (Mangiafico 2020). Second, we analysed whether the proportion of participants that selected each wildflower as a weed was equal among participants that thought of that flower as beneficial to wildlife and those that did not, using a test of equal proportions.

To explore whether stated level of interest in nature was linked to perception of wildflowers as 'weeds', we used Kruskal-Wallis tests for differences in the mean ranks number of wildflowers selected as a weed/nuisance, with nature interest (4-10) as the grouping factor and *post-hoc* Dunn's tests for pairwise comparisons between groups. This was repeated with access to outside space as the grouping factor (garden, allotment, garden and allotment, patio or other non-garden outside area, none).

Significance was defined at  $P < 0.05$ . All analyses were performed using RStudio version 1.3.1073, R version 3.3.3 (R Core Team 2020).

## 6.4 Results

### 6.4.1 Questionnaire respondents' characteristics

In total, 2315 people answered the survey. Of these, 823 participants with *relevant expertise* (see Methods) had higher knowledge of the six representative wildflowers (0-6; mean  $\pm$  SD number of correct names given =  $5.46 \pm 0.91$ ) than those with no stated relevant expertise ( $4.80 \pm 1.24$ ,  $n = 1492$ ). This was significant according to a Wilcoxon rank sum test ( $Z = 13.90$ ,  $P < 0.001$ ). Respondents in the '*Relevant expertise*' group also identified fewer of the six wildflowers as weeds, selecting  $0.81 \pm 1.01$  on average ( $n = 822$ ) compared to  $1.00 \pm 0.99$  in the group with no relevant expertise ( $n = 1492$ ; Wilcoxon rank sum test,  $Z = -4.77$ ,  $P < 0.001$ ). Together these confirmed that participants with *relevant expertise* had a higher knowledge of wildflowers and interest

in their ecological value. Finally, a higher proportion selected the highest possible level of interest in nature (10/10; 70%) compared to the group without relevant expertise (43%). Therefore, this group was removed from the dataset to give a sample that was more representative of the wider public.

Of the remaining 1492 participants, a large majority (87.4%) identified as female, 11.9% as male, 0.4% preferred not to say and 0.3% preferred to self-describe. More than half (52.4%) were aged 46-65. Many had a high level of education, with 39.2% and 37.1% holding a Postgraduate or Undergraduate University degree (or equivalent) respectively. Many participants owned or had regular access to a garden (78.8%) or both a garden and allotment (12.7%), while only 3.3% had no regular access to an outside space. Frequency of gardening or growing was high, with 36.3% of participants stating that they partake in these activities daily and 30.3% 2-3 times weekly. Stated level of interest in nature was also high (mean  $\pm$  SD =  $8.75 \pm 1.40$ , median = 9), with most participants selecting 10 (42.5%), 9 (18.1%) or 8 (22.6%) on the 0-10 scale (see Table 6.1 for full details of participant characteristics).

Several of the participant characteristics were associated according to contingency tests. In particular, frequency of growing or gardening was strongly linked to access to outside space ( $\chi^2_{(4)} = 227.81$ ,  $P < 0.001$ ; Freeman's  $\theta = 0.421$ ; Freeman 1976). Access to outside space was also associated with the characteristics of the current area in which participants lived ( $\chi^2_{(16)} = 259.72$ ,  $P < 0.001$ ) with medium strength (Cramer's  $V = 0.209$ ; Cohen 1988): although numbers of participants with gardens and allotments was generally high, lower proportions of those living in city centres (71 of 117 participants, 60.7%) or town centres (55/66, 83.3%) had a garden or allotment or both, compared to 98.3% of those living in a rural area (586/595).

Level of interest in nature was not linked to education level ( $\chi^2_{(3)} = 2.85$ ,  $P = 0.415$ ) but was linked to where participants currently live with a medium level of association ( $\chi^2_{(4)} = 41.43$ ,  $P < 0.001$ , Freeman's  $\theta = 0.142$ ; Freeman 1976). A higher proportion of people living in rural areas selected 10/10 (49.6%) than any other area type, with 35.9% in city centres and the lowest proportion in town centres (25.8%). Interest in nature was weakly positively linked to age ( $Z = 5.95$ ,  $P < 0.001$ , Kendall's tau-b = 0.112), strongly positively associated with growing or gardening frequency ( $Z = 15.67$ ,  $P < 0.001$ ,

Kendall's tau-b = 0.317) and positively associated to access to outside space with medium strength ( $\chi^2_{(4)} = 38.08$ ,  $P < 0.001$ , Freeman's  $\theta = 0.164$ ).

**Table 6.1.** Participant characteristics shown by responses to Questions 1-8.  
Total n participants = 1492

Question	Response	n participants (% of total)
1. What is your age?	18-25	60 (4.0)
	26-35	194 (13.0)
	36-45	200 (13.4)
	46-55	335 (22.4)
	56-65	448 (30.0)
	66-75	224 (15.0)
	76-85	27 (1.8)
	86+	5 (0.3)
2. How would you describe your gender?	Female	1305 (87.4)
	Male	117 (11.9)
	Prefer to self-describe	6 (0.4)
	Prefer not to say	5 (0.3)
3. How would you describe the area where you live now?	City centre	116 (7.8)
	City suburbs	248 (16.6)
	Town centre	66 (4.4)
	Town suburbs	467 (31.3)
	Rural area	595 (39.9)
4. Do you own or have regular access to (select all that apply):	None	49 (3.3)
	Patio	61 (4.1)
	Garden	1176 (78.8)
	Allotment	18 (1.2)
	Garden and allotment	189 (12.7)
5. How often do you partake in gardening or growing, approximately?	Never	49 (3.3)
	Rarely	126 (8.4)
	Monthly	49 (3.3)
	A few times a month	110 (7.4)
	Once a week	164 (11.0)
	2-3 times a week	453 (30.3)
	Daily	542 (36.3)
7. What is your most recent level of education?	Postgraduate University degree or equivalent	585 (39.2)
	Undergraduate University degree or equivalent	554 (37.1)
	College or further education (or equivalent)	87 (5.8)
	School (or equivalent)	266 (17.8)

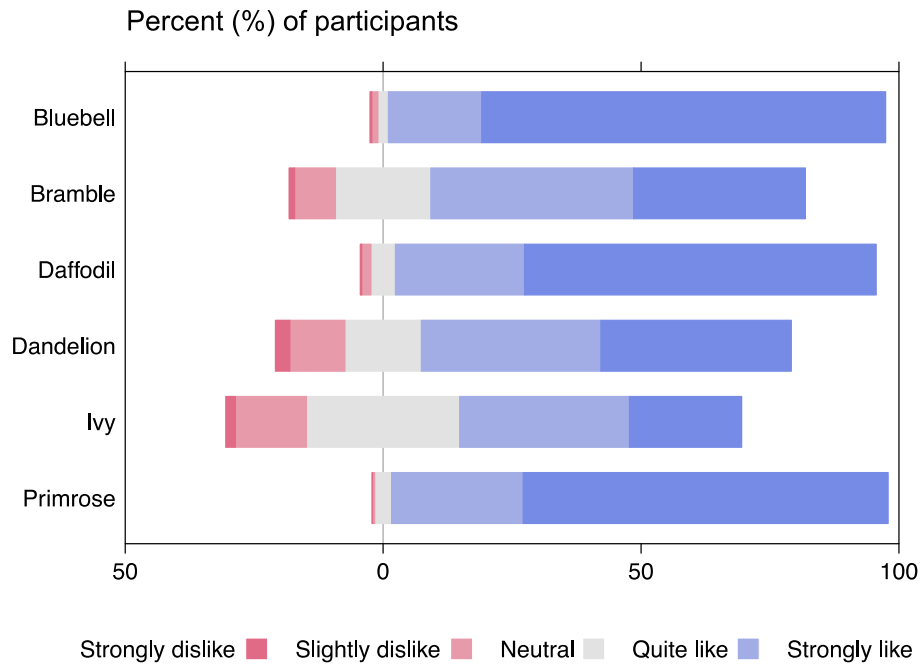
8. How would you rank your personal level of interest in nature, on a scale of 0-10? (0 = no interest, 10 = extremely strong interest)	0	0 (0.0)
	1	1 (0.1)
	2	0 (0.0)
	3	3 (0.2)
	4	13 (0.9)
	5	27 (1.8)
	6	59 (4.0)
	7	148 (9.9)
	8	338 (22.6)
	9	270 (18.1)
	10	634 (42.5)

## 6.4.2 Wildflower perceptions

### 6.4.2.1 Liking rating per wildflower

Ivy was the least liked wildflower, followed by dandelion and bramble (Fig. 6.2). More than 65% of respondents selected ‘5. *Strongly like*’ for bluebell (78.4%), daffodil (68.0%) and primrose (70.9%) compared to less than 40% for bramble (33.4%), dandelion (37.1%) and ivy (21.7%; Fig. 6.2).

Liking rating given by participants was most strongly affected by wildflower species according to a proportional odds logistic regression model. The odds of selecting a higher rating (*i.e.* 2, 3, 4 or 5 versus 1) were 11.2 times greater for bluebell, 9.2 for daffodil, 4.1 for primrose, 2.2 for bramble and 1.7 for dandelion compared to the least liked wildflower, ivy, holding constant all other variables. Age and level of interest in nature also predicted liking ratings: participants with greater nature interest had greater odds of selecting higher ratings than those with lower nature interest, as did older versus younger participants (Table 6.2).



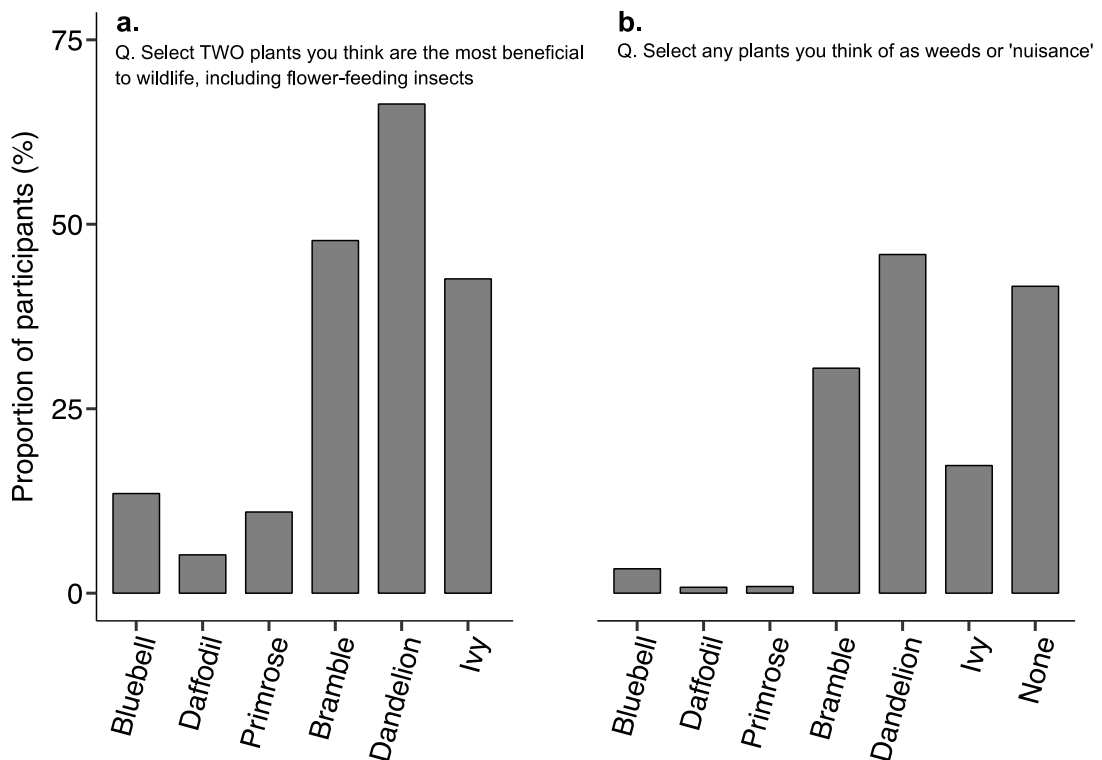
**Figure 6.2.** Proportions (%) of survey respondents' ratings of each wildflower on a 1-5 scale (1 = Strongly dislike, 2 = Slightly dislike, 3 = Neutral, 4 = Quite like, 5 = Strongly like). Plot shows the responses of participants with no stated relevant expertise (n = 1492).

**Table 6.2.** Results of proportional odds logistic regression model testing factors influencing liking ratings for six common wildflower species on a 1-5 Likert-type scale. Odds ratios and 95% confidence intervals are shown for the significant predictor variables Species ( $\chi^2_{(5)} = 2289.19$ ,  $P < 0.001$ ), Age ( $\chi^2_{(6)} = 146.30$ ,  $P < 0.001$ ) and stated level of interest in nature ( $\chi^2_{(6)} = 361.31$ ,  $P < 0.001$ )

Species	Odds ratio (95% CIs)	Age	Odds ratio (95% CIs)	Stated level of interest in nature	Odds ratio (95% CIs)
Ivy	<i>intercept</i>	18-25	<i>intercept</i>	4	<i>intercept</i>
	2.113 (1.848 – 2.417)		0.952 (0.761 – 1.191)		0.941 (0.597 – 1.481)
Dandelion		26-35		5	
	2.021 (1.771 – 2.306)		1.217 (0.970 – 1.525)		1.445 (0.965 – 2.158)
Bramble		36-45		6	
	9.462 (8.160 – 10.982)		1.577 (1.269 – 1.958)		1.656 (1.137 – 2.405)
Daffodil		46-55		7	
	11.420 (9.831 – 13.287)		1.861 (1.504 – 2.300)		2.032 (1.412 – 2.918)
Primrose		56-65		8	
	16.759 (14.275 – 19.717)		1.943 (1.547 – 2.438)		2.722 (1.883 – 4.159)
Bluebell		66-75		9	
			2.073 (1.455 – 2.969)		4.159 (2.896 – 5.960)
		76-85		10	

#### 6.4.2.2 Perceived value to wildlife and 'weed' status

Less than 15% of participants considered each of the more popular flowers to be among the two they considered most beneficial to wildlife (bluebell, 13.5% of participants; primrose, 11.0%; daffodil, 5.2%), while the less well-liked flowers were more commonly considered to be beneficial, particularly dandelion (66.3%) followed by bramble (47.8%) and ivy (42.6%; Fig. 6.3 a). Less than 5% of the 1492 participants considered the more popular flowers to be weeds or a nuisance (bluebell, 3.3% of participants; daffodil, 0.8%; primrose, 0.9%) while the less well-liked flowers were more commonly considered to be weeds, particularly dandelion (45.9%) followed by bramble (30.5%) and ivy (17.3%). 41.6% selected 'None' (Fig. 6.3 b).



**Figure 6.3.** Proportion of participants (%) selecting each wildflower in response to (a) Question 21 (*Select two plants you think are the most beneficial to wildlife, including flower-visiting insects*) and (b) Question 22 (*Select any plants you think of as weeds or a nuisance*). Question response options are given on the x axis, n participants = 1492



Individuals that considered dandelion and ivy to be beneficial to wildlife gave a higher rating on the 1-5 Likert-type response for these flowers on average than those that did not, according to Mann-Whitney-Wilcoxon tests between these groups, however, the effect size was small ( $r = 0.1 - < 0.3$ ) for each species. There was no measurable difference in liking rating among participants that considered bramble, bluebell, daffodil or primrose to be beneficial to wildlife compared to those that did not ( $r < 0.1$ ; Table 6.3). Median response was not different between the groups for any species apart from ivy, which was better-liked on average among participants that considered ivy to be beneficial to wildlife (median liking rating = 4/5) than those that did not (3/5; Table 6.3).

**Table 6.3.** Results of Mann-Whitney-Wilcoxon tests comparing average liking rating given for each wildflower on the 1-5 Likert-type scale (1 = Strongly dislike, 2 = Slightly dislike, 3 = Neutral, 4 = Quite like, 5 = Strongly like) between respondents choosing the flower among the two they selected as the most beneficial to wildlife including FVI, and those that did not (total n participants = 1492). Effect sizes ( $r$ ) were calculated using the formula  $r = Z/\sqrt{N \text{ obs}}$  and interpreted using the standard boundaries: small =  $0.1 - < 0.3$ , medium =  $0.3 - < 0.5$ , large  $\geq 0.5$  (Mangiafico 2020)

Wildflower	Median liking rating given by participants selecting this flower as beneficial to wildlife including FVI (n participants)	Median liking rating given by participants <i>not</i> selecting this flower as beneficial to wildlife including FVI (n participants)	Z, r [95% CI]	Effect size
Bluebell	5 (n=202)	5 (n=1290)	Z = -3.384, r = 0.088, 95% CI [0.03 - 0.15]	None ( $r < 0.1$ )
Bramble	4 (n=933)	4 (n=559)	Z = 2.232, r = 0.058, 95% CI [ $<0.01$ - 0.11];	None ( $r < 0.1$ )
Daffodil	5 (n=78)	5 (n=1414)	Z = 1.490, r = 0.039, 95% CI [ $<0.01$ - 0.09]	None ( $r < 0.1$ )

Dandelion	4, n = 990	4, n = 502	Z = 6.191, r = 0.160, 95% CI [0.11 - 0.21] (small)	Small (r = 0.1 - < 0.3)
Ivy	4 (n=635)	3 (n=857)	Z = 11.082, r = 0.287, 95% CI [0.24 - 0.33]	Small (r = 0.1 - < 0.3)
Primrose	5 (n = 164)	5 (n=1328)	Z = -0.817, r = 0.021, 95% CI [<0.01 - 0.07] (small)	None (r < 0.1)

Participants with the highest level of interest in nature (10/10) selected the lowest number of plants as weeds, on average  $0.80 \pm 0.98$  out of six wildflowers (n = 634 participants) which was significantly fewer than those reporting any lower than 10 on the 0-10 scale ( $P < 0.05$ ). The average number of plants selected as weeds among levels of nature interest did not vary greatly ( $0.80 \pm 0.98$  to  $1.26 \pm 0.81$ ) and all other pairwise comparisons were non-significant. Participants that owned or had regular access to a garden selected a higher number of wildflowers as weeds ( $1.01 \pm 1.00$  wildflowers, n = 1176) with the lowest among those with no garden or other outside space ( $0.735 \pm 0.84$ , n = 49) but there were no significant differences between garden access categories ( $P > 0.05$ ).

The proportion of people that considered bramble to be a weed or nuisance was not significantly different among people that considered it to be beneficial to wildlife (271/934) and those that did not (184/559;  $\chi^2_{(1)} = 2.331$ ,  $P = 0.127$ ). However, a significantly lower proportion of participants considered dandelion to be a weed among those that had selected this flower as beneficial to wildlife, compared to those that had not (381/990 vs 305/503,  $\chi^2_{(1)} = 65.008$ ,  $P < 0.001$ ); the same was true for ivy (85/636 vs 174/857,  $\chi^2_{(1)} = 11.779$ ,  $P < 0.001$ ).

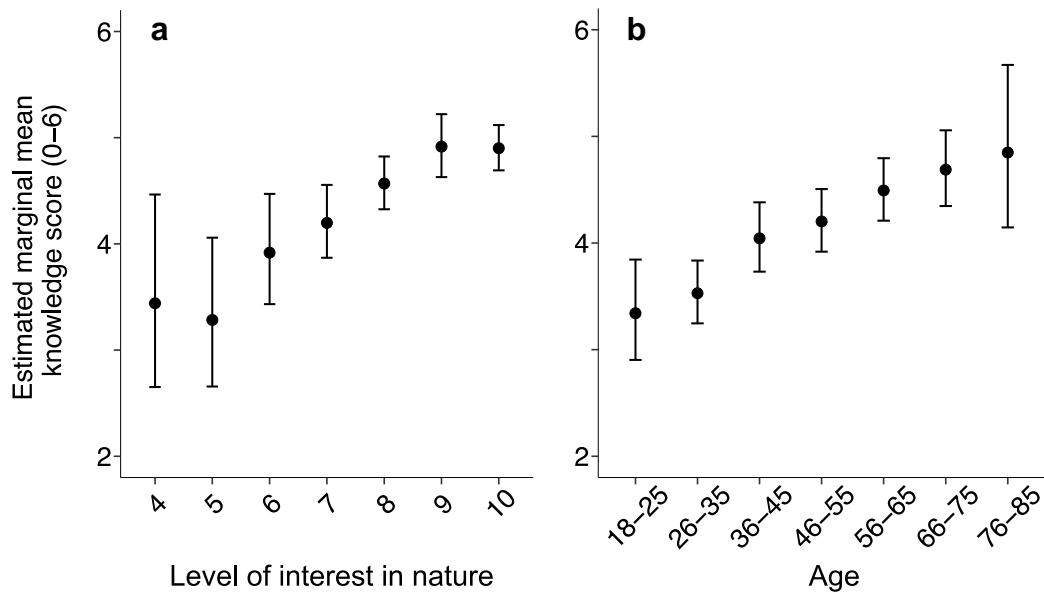
**Figure 6.4.** The most frequent unique words or short phrases used to describe (a) bluebell and (b) bramble (n = 1492 survey respondents). Species names and the words ‘wildflower(s)’ and ‘flower(s)’ and principal colours (*e.g.* ‘pink’, ‘yellow’, ‘blue’) were removed. 75 words are shown per wordcloud. Word size relates to frequency of occurrence from larger (more frequent) to smaller (less frequent). See Appendix E.5 for full figure showing wordclouds for each of the six wildflowers.

### 6.4.3 Wildflower identification

Each wildflower species was named correctly by more than 45% of participants (bluebell 94.6%, bramble 68.8%, daffodil 98.9%, dandelion 97.3%, ivy 49.2%, primrose 71.0%). On average, participants were able to name  $4.80 \pm 1.24$  of the six wildflowers correctly ( $n = 1492$ ), with 38.3% of respondents naming all six species correctly.

Age was a significant predictor of *knowledge score* (number of correctly-named wildflowers, 0-6; GLM,  $\chi^2_{(6)} = 63.19$ ,  $P < 0.001$ ) which increased with each age category from  $3.34 \pm 0.24$  in 18-25 year-olds ( $n = 60$ ) to  $4.85 \pm 0.39$  in 76-85 year-olds ( $n = 32$ ; values given are model estimated marginal means  $\pm 1$  SE; Fig. 6.5 a). Stated level of interest in nature was also a significant predictor of *knowledge score* (GLM,  $\chi^2_{(6)} = 43.33$ ,  $P < 0.001$ ). Participants reporting '9' and '10' had the highest knowledge scores (Fig. 6.5 b). Details of pairwise contrasts are in Table 6.4.

Where participants currently live was not a significant predictor of *knowledge score* and was not included in final regression models. However, knowledge was lowest on average among participants living in city centres (mean  $\pm$  SD,  $4.09 \pm 1.53$ ,  $n = 117$ ) and highest among those living in rural areas ( $5.10 \pm 1.05$ ,  $n = 595$ ).



**Figure 6.5.** Level of interest in nature (a) and age (b) explain participants' *knowledge score*, the ability to correctly identify six common wildflower species (0-6). Estimated marginal means given by a Poisson regression model are plotted as circular points, with errorbars showing 95% confidence intervals.

**Table 6.4.** Results of Poisson regression model testing for differences between participants' ability to correctly identify six common wildflower species, or *knowledge score* (0-6). The model estimated marginal means (EMM)  $\pm$  1 SE for *knowledge score* are given for the significant predictor variables Age (GLM,  $\chi^2_{(6)} = 63.190$ ,  $P < 0.001$ ) and Stated level of interest in nature (0-10;  $\chi^2_{(6)} = 43.329$ ,  $P < 0.001$ ). Results are back-transformed from the model log-scale. Significant pairwise post hoc comparisons with *Bonferonni* adjustment are shown, with all other pairwise comparisons non-significant ( $P > 0.05$ )

Age	<i>Knowledge score</i> EMM $\pm$ 1 SE	Contrast	<i>P</i> value	Stated level of interest in nature	<i>Knowledge score</i> EMM $\pm$ 1 SE	Contrast	<i>P</i> value
18-25	3.34 $\pm$ 0.24	46-55 >	$P =$	4	3.44 $\pm$ 0.46	9 > 5	$P = 0.006$
		18-25	0.037				
26-35	3.53 $\pm$ 0.15	56-65 >	$P <$	5	3.28 $\pm$ 0.36	10 > 5	$P = 0.005$
		18-25	0.001				
36-45	4.04 $\pm$ 0.17	66-75 >	$P <$	6	3.92 $\pm$ 0.26		
		18-25	0.001			9 > 6	$P = 0.037$

46-55	4.20 ± 0.15	76-85 >	$P =$	7	4.20 ± 0.18	10 > 6	$P = 0.027$
		18-25	0.006				
56-65	4.49 ± 0.15	46-55 >	$P =$	8	4.57 ± 0.13	9 > 7	$P = 0.023$
		25-36	0.002				
66-75	4.69 ± 0.18	56-65 >	$P <$	9	4.92 ± 0.15	10 > 7	$P = 0.008$
		25-36	0.001				
76-85	0.39 ± 0.39	66-75 >	$P <$	10	4.90 ± 0.11		
		25-36	0.001				
		76-85 >	$P =$				
		25-36	0.003				
		66-75 >	$P =$				
		36-45	0.017				

## 6.5 Discussion

We anticipated a bias in questionnaire participation, since individuals with an existing interest in wildflowers were more likely to spend time completing a survey on this topic. Confirming this, participants had a clear pre-existing level of interest in wildlife and flowering plants, with high stated levels of interest in nature across age groups (mean ± SD = 8.75 ± 1.40 on a 0-10 scale), strong ability to identify wildflower species (4.80 ± 1.24 of the six wildflowers correctly named on average) and frequent engagement in gardening or growing (66% gardening at least twice weekly, n = 1492 participants). Despite a clear dichotomy in popularity among the wildflower species, the 1-5 liking ratings given for each of the six wildflower species were high overall (Fig. 6.2), which is perhaps also indicative of a high average interest in or appreciation of wild flowering plants among the respondents. Nevertheless, our findings are relevant for understanding how members of the public perceive wildflowers, with practical application for improving vegetation cover and floral resource availability for flower-visiting insects (FVI) in gardens, neighbourhoods, parks and other (non-agricultural) spaces.

### 6.5.1 Dichotomy in popularity among wildflowers

Although the six wildflower species were relatively well-liked by questionnaire respondents in general, the three wildflowers chosen due to their popularity in a nationwide poll by Plantlife in 2015 (bluebell, daffodil and primrose; Trevor Dines Plantlife UK, *personal communication*) were also the most popular in our survey (Fig.

6.2). What is it about these flowers that gives them consistently high popularity among members of the public? This relates to the broader question: what causes some wildflower species to be more popular than others? The quantitative and qualitative data in this study offer some clues.

#### 6.5.1.1 *Aesthetic appeal*

Bluebell, daffodil and primrose each had high perceived aesthetic beauty, described as ‘pretty’ by 122, 42 and 372 participants respectively, and ‘beautiful’ by 100, 38 and 1, with other words such as ‘bright’, ‘colourful’ and ‘delicate’ also common. Species profiles of these wildflowers generally invoked a sense of their positive aesthetic appeal. In comparison, bramble and dandelion were appreciated as aesthetically pleasing to a lesser extent while ivy was considered ‘alien’ and ‘ugly’ (Appendices E.3 & E.5). This is similar to findings by Sumner, Law & Cini (2018) who found that butterflies, which had significantly higher ‘emotive value’ (positive perception) than bees, flies or wasps, were described mostly using words related to aesthetic such as ‘colourful’ and ‘beautiful’ compared to a lower use of such words for the other taxa. ‘*Aesthetic*’ was the most commonly used of nine identified categories when participants were asked to describe the wildflowers, highlighting the importance of this factor.

#### 6.5.1.2 *Charisma*

Aesthetic preference can act in its own right to determine species’ popularity (Landová et al. 2018). However, this quality is also known to interact synergistically with other factors to affect non-human species’ ‘charisma’. Briefly described by Lorimer (2020) as “*familiar, aesthetic organisms that inspire public affection*”, and more extensively discussed elsewhere (Lorimer 2007, Ducarme, Luque & Courchamp 2013, MacDonald et al. 2015), charisma is widely recognised positively to affect an organism’s societal perception. Other common factors known to influence charisma are relevant to our study, chiefly distinctiveness, cultural familiarity and traditional value, and societal reputation (Ducarme, Luque & Courchamp 2013, MacDonald et al. 2015). Plants are usually perceived as being less charismatic than vertebrates and some invertebrates, a potential reason for lower funding of research and conservation for this taxonomic group (Martín-López et al. 2009, Robson Gordon et al. 2019). However, certain plants

can be considered to be charismatic, for example the olive tree (*Olea europaea*) or American Redwood (genera: *Sequoia* and *Sequoiadendron*), or the holoparasitic ‘corpse flower’ (*Rafflesia* spp.). Our findings suggest that there are charismatic species among UK wildflowers, and that non-charismatic species experience lower popularity.

For example, wildflowers have strong cultural familiarity and traditional value in the UK (Mabey 1996). Among our survey responses this seemed to be particularly relevant for daffodil and bluebell. The daffodil is one of two major national emblems of Wales, while a ‘*host of golden daffodils*’ is the subject of the well-known poem “*I Wandered Lonely as a Cloud*”, by English poet William Wordsworth (1804). Both ‘Wales’ and ‘Wordsworth’ were in the top 20 most frequently given words for daffodil. Similarly, ‘woods’, ‘woodland’ and ‘carpet’ were all given by >100 participants to describe bluebell (Fig. 6.4, Appendix E.3), referring to their much-loved and distinctive springtime displays in deciduous woodland (Mabey 1996, Streeter et al. 2009). Interestingly, primroses used to also grow in large numbers, as described in the first line of Wordsworth’s poem ‘Poor Robin’ (1840): ‘*Now when the primrose makes a splendid show*’. This explains the number of ‘Primrose Hills’ in the UK, led to primroses traditionally being used to decorate churches at Easter and being picked in large numbers to sell in bunches (Mabey 1996), and has perhaps contributed to this flower’s positive societal perception.

Positive cultural familiarity and traditional value were also evident for two of the three less well-liked flowers. Bramble’s generous provision of blackberries in late summer and autumn was widely acknowledged, and related culinary traditions such as pies, crumbles, jam, jelly, wine and even gin mentioned by many participants. The tradition of telling the time with dandelion seedheads or ‘clocks’ may add to cultural familiarity with this species, and seemed to invoke personal memories, such as of childhood, for many. However, these qualities were somewhat obscure for ivy, apart from mentions of its use to decorate houses at Christmas (Appendices E.3 & E.5); this flower was also the least known and least liked of the six (Fig. 6.2).

Lorimer (2007) describes the ‘*concurrence of its [a species] ecological rhythms with those of humans*’ as ‘ecological charisma’. This concept rings true for the three well-liked wildflowers in this study, since each of these species blooms soon after winter, giving them a particularly joyous quality for many both now and through past centuries.



This may contribute to their appreciation at both individual and societal level: the word ‘spring’ was given for each of the well-liked flowers by between 480-960 participants, with the specific or closely worded phrase ‘herald of spring’ given for each of bluebell (1 participant), daffodil (13) and primrose (4), but not the other three flowers. It is interesting that a considerably lower number (89) of participants gave the word ‘spring’ to describe dandelion although this flower blooms from March onwards, typically earlier than bluebells. Dandelion has a long flowering period, as do bramble and ivy, compared to relatively short bloom periods for the more popular species (Rose 1981, Streeter et al. 2009). Does ephemerality, as well as phenology, enhance certain wildflowers’ ‘specialness’? This would reflect human’s value of rarity (Angulo & Courchamp 2009, Angulo et al. 2009), which is also known to contribute to non-human charisma (MacDonald et al. 2015). It is also possible that other factors such as the greater aesthetic appeal and distinctiveness of the three more popular species interact with their phenology in a way that is not the case for dandelion, despite this also being an early-flowering species.

Understanding what makes certain species more charismatic could be used to enhance perceptions towards certain undervalued wildflower species, or wildflowers as a group. For example, celebrating species’ particular history and roles within cultures through information provision (Lindon & Root-Bernstein 2015) and via positive marketing and cultural representation (Ducarme, Luque & Courchamp 2013) can also increase their charisma and public support. Education campaigns incorporating per-species cultural memory and value to humans as key components could add to appreciation of common wildflowers; perhaps leading to positive action to grow or tolerate them in personal and public outdoor areas. Encouragingly, this is ongoing among environmental organisations including notably the Wildlife Trusts, and in other varied ways: the eye-catching, building-sized graffiti of common weeds by artist Mona Caron celebrates the beauty and resilience of urban wildflowers <[www.monacaron.com/weeds](http://www.monacaron.com/weeds)>, and the ‘*More than Weeds*’ project inspired by French botanist Sophie Leguil encourages members of the public to notice and appreciate wild ‘pavement plants’ <[www.morethanweeds.co.uk](http://www.morethanweeds.co.uk)>.

#### 6.5.2 ‘Weed’ status and qualities defining species’ ‘nuisance factor’

The perception of certain flowers as ‘weeds’ appears to contribute to the difference in popularity among these representative species. Bramble, dandelion and ivy were considered to be weeds by 31%, 46% and 17% of participants respectively, compared to < 5% for each of the more popular flowers. Notably, this trend is in reverse to the species’ popularity among participants (Figs. 6.2 & 6.3).

The Oxford English Dictionary defines a weed as “*any herbaceous plant not valued for its usefulness or beauty, or regarded as a nuisance in the place where it is growing, esp. when hindering the growth of crops or other cultivated plants*”. It is clear from this research and previous work that some wildflowers are perceived more as a weed while others are perceived more as flowers (Clayton 2007). What qualities make a wildflower a ‘weed’ in a non-agricultural context?

We hypothesise that, consistent with the OED definition, this is affected by aesthetic preference but also largely influenced by the nuisance caused to individuals by certain flowers, since this is likely to contribute to low appreciation or dislike on both an individual and societal level. The qualitative information in this survey indicates that certain practical and ecological characteristics determine a species’ ‘nuisance factor’, with the following commonly mentioned for the three ‘weedier’ species:

- i) being difficult to remove or control (bramble, dandelion, ivy)
- ii) having vigorous growth and pervasiveness (bramble, dandelion, ivy)
- iii) efficient self-propagation and/or dispersal (bramble, dandelion, ivy)
- iv) causing pain or physical irritation (bramble, dandelion)
- v) being thought to cause damage to other plants (ivy)

These qualities, in particular (i), (ii) and (iii), are also likely to interact with a contemporary preference for a ‘tidy’ aesthetic (Gobster et al. 2007). This is a known sociocultural driver for removing certain plants in domestic gardens, both due to individual preference and due to perceived neighbourhood expectations (Clayton 2007, Loram et al. 2011, Blaine et al. 2012).

The nuisance characteristics identified here are likely to relate to wild flowering plants more broadly and may need to be considered in management strategies promoting wild

flowering plants in public spaces. However, since many of the participants in this survey owned or had regular access to a garden (91.5%) and engaged in gardening either daily or 2-3 times weekly (66.3%), it is likely that their perceptions of bramble, dandelion and ivy related particularly to their undesirability in this context. Perceptions may be more positive for these and other similar flowers in public parks and other greenspace, where the nuisance caused to an individual is likely to be reduced; however, it is also possible that the individual and societal dislike linked to a species' 'weed' status extends to any situational context. Further research should specifically assess perceptions of these and other insect-attractive wildflowers in other spaces such as road verges and public parks, for example through enquiry of lived experiences (Özgüner & Kendle 2006) or using edited photo montages which can successfully assess human perceptions of species in different scenarios (Lindon & Root-Bernstein 2015).

#### 6.5.3 Ecological value influences species popularity on an individual, but not societal, level

Popularity of the six species was in reverse to perceived ecological value, which was considerably higher for the less well-liked flowers: bramble, dandelion and ivy were each considered to be beneficial for wildlife by >40% of participants, compared to <15% for the three more popular flowers. This suggests that even among a participant sample with a clear pre-existing interest in ecology, factors other than ecological function are more important in defining wildflower species' popularity.

However, on an individual level, participants that selected dandelion and ivy (but not bramble) as beneficial for wildlife gave them a higher liking rating on average, although the magnitude of this effect was small. The proportion of participants who selected dandelion and ivy (but not bramble) as weeds or a 'nuisance' was also significantly lower among those that thought of these species as beneficial to wildlife compared to those that did not recognise their ecological value. These findings may be magnified among a more representative sample of the wider public: since many of the participants in this survey are likely to have a pre-existing interest in wildflowers, perceptions were generally likely to be higher than a population average meaning that any positive effect of perceived ecological value on liking and/or 'weed' status may be muted in this sample.

The qualitative data revealed a clear conflict among some participants between wildflowers' perceived ecological value and 'nuisance factor', with descriptions including: '*bee food –dilemma –weed*' and '*bees, spreading, unpopular with neighbours!*' (dandelion); '*good for pollinators but wouldn't want it in the garden*' and '*bees, prickly, untidy*' (bramble); '*pollinators, climbing, weed*' and '*butterfly, nectar, nuisance*' (ivy).

#### 6.5.4 Personal attributes affecting wildflower knowledge and liking rating

Due to a high knowledge of wildflowers among survey participants, who named  $4.80 \pm 1.24$  of the six wildflowers correctly on average, our analysis of personal attributes contributing to wildflower knowledge, *i.e.* ability to correctly name the six representative wildflower species, is limited since this was high across most grouping factors.

Nevertheless, greater knowledge was positively associated with both age and level of interest in nature. The positive effect of age on wildflower identification is consistent with a YouGov poll commissioned by the UK plant conservation charity Plantlife in 2017, in which 2132 participants were asked to name three wildflowers from photographs. Just 4% of 16-24 year olds were able to name *Trifolium pratense* as 'clover', compared to 45% of those aged 55 or above (Trevor Dines Plantlife UK, *personal communication*). Possible factors influencing the positive effect of age could include simply more years of interaction with wildflowers, through observing such plants and also through garden ownership and/or time spent gardening or growing. It is possible that the lower knowledge among younger age groups is symptomatic of an ongoing loss of personal interaction with nature in modern and increasingly urbanised societies (Miller 2005, Soga & Gaston 2016). This effect may contribute to the lowest level of wildflower knowledge among participants living in city centres ( $4.09 \pm 1.53$  of six flowers correctly identified), with the highest knowledge in rural areas ( $5.10 \pm 1.05$ ); however, neither association can be definitively concluded from our study.

A positive effect of stated level of interest in nature on participants' ability to name wildflowers is somewhat self-explanatory, since greater interest may lead to more time

spent actively learning about and interacting with nature, including common wild flowering plants. Participants with the highest stated level of interest in nature (10/10) also selected fewer flowers as ‘weeds’, in line with studies linking felt nature connection to pro-environmental knowledge, attitudes and behaviour (*e.g.* Davis, Green & Reed 2009). Similarly, participants in older age groups and with higher stated nature interest had greater odds of selecting higher liking ratings on the 1-5 Likert-type scale. However, these factors had a small effect compared to that of species, suggesting that species-specific qualities, such as charisma and ‘weed’ status and resulting societal reputation may have a greater effect on how much wildflowers are liked by individuals than those individuals’ personal attributes.

Although many studies have found a link between education level and pro-environmental knowledge, attitudes and behaviour (Gifford & Nilsson 2014, Wilson Wilson, Forister & Carril 2017, Sumner, Law & Cini 2018), here we found no link between education level and stated nature interest, and education level did not predict wildflower identification or liking rating. This may be because any effect is masked due to a high average education level among participants (76.3% having an Undergraduate University degree or above).

#### 6.5.5 Practical steps: education and awareness

It is a paradox that many wild flowering plants with the potential to provide a common and widely available source of nectar and pollen for FVI (Baldock et al. 2019) seem to be undesirable in part to the very qualities that make them common, namely their resilience and ability to proliferate (section 6.5.2). Removing such plants from both private and public green spaces in order to achieve a ‘tidy’ aesthetic is still seemingly ingrained in the social psyche in the UK and elsewhere (Clayton 2007, Gobster et al. 2007, Loram et al. 2011, Blaine et al. 2012, Baldock et al. 2019, this study) despite increased climate and ecological awareness due to recent breakthrough of these topics into the ‘Overton window’ of public consciousness (Thackeray et al. 2020).

However, our findings show that individual-level awareness of wildflowers’ ecological value leads to a higher liking rating for species considered to be weeds or a ‘nuisance’ (despite a small effect size; section 6.5.3). This suggests that it would be worthwhile

and effective to improve public perceptions of wild flowering plants through education and awareness programmes highlighting their ecological function. Various means of communication can successfully achieve this and garner public support for ‘less managed’ landscapes, preventing public anger and concern at perceived neglect (Coupey et al. 2015). These include the use of information pamphlets, webpages, posters and signposts, workshops with local residents and local decision makers, themed events and activities, and local press (Coupey et al. 2015).

In France, a nationwide ban on the use of the herbicide glyphosate in public spaces in early 2019 (Nature 2020) led to the adoption of more labour-intensive methods of weed control and a proliferation of spontaneously-growing vegetation in urban areas. Positive communication by local authorities has led to widespread acceptance of such management changes and greater ecological awareness among citizens (Richard et al. 2019), with the Vice-President of Lyon describing this as a ‘cultural shift’ towards accepting spontaneous vegetation and allowing nature to coexist with humans in urban spaces: “*Il y a un changement culturel: on accepte la végétation spontanée... On laisse la nature reprendre sa place dans la ville*” (Bruno Charles in *Les Echos* 2017). This points to a role of proactive communication alongside practical management changes as an effective and efficient method of improving attitudes towards common wild flowering plants, as well as perhaps shifting attitudes more broadly towards a normative ‘ecological aesthetic’ (Gobster et al. 2007).

#### 6.5.6 Limitations and further research

The findings in this study relate most strongly to members of the public with a high average level of interest in nature and knowledge of wildflowers. While this created interesting conclusions in itself, it is also limiting. It would be useful to repeat the study among a larger sample of participants that are more representative of the wider public in terms of pre-existing interest in this topic. Further studies of wildflower perceptions within landscape management contexts should also include more equal representation across age groups and an education level closer to the national average.

In this survey participants were not directly asked about their perceptions of common wildflowers in different contexts. A natural next step would be to investigate

specifically whether perceptions of certain wildflowers that are often considered to be ‘weeds’ or have a high objective ‘nuisance factor’ vary between different land use types where they could be a valuable source of nectar and pollen for FVI if allowed to grow (Baldock et al. 2019), for example domestic gardens, urban streets, public parks and in road verges. Our findings suggested that perceived ecological value can lead to higher liking of wildflowers and reduce their status as a ‘weed’ or ‘nuisance’ for an individual. It would be interesting to test this experimentally, for example using measurements of individuals’ perceptions and practice before and after information provision regarding species’ ecological value and associated environmental context.

## Chapter Seven: Final Discussion, Future Directions and Practical Actions

### 7.1 Resource competition mediated by eusocial bees

Several previous studies have demonstrated that honeybees can displace non-*Apis* bees from preferred foraging resources (*e.g.* bumblebees: Thomson 2004, Herbertsson et al. 2016, Lindström et al. 2016; non-*Apis/Bombus* ('solitary') bees: Dupont et al. 2004, Hudewenz & Klein 2015, Lindström et al. 2016). The findings in this thesis add to this body of research, showing a significant increase in bumblebee and solitary bee foraging on *Rubus fruticosus*, a common and abundant wildflower (Chapter Two) following honeybee exclusion (Chapter Four). The data presented here also add to scarcer research demonstrating that wild (*i.e.* not commercially managed) bumblebees can displace honeybees (Chapter Three) and also solitary bees (Chapter Four) from preferred flowers. In the latter chapter, smaller-bodied ( $FW \leq 5.5$  mm) solitary bees did not show any evidence of resource competition exerted by eusocial bees. However, larger-bodied ( $FW > 5.5$  mm) solitary bees were depressed to the largest extent when both *Apis* and *Bombus* were present: at a peri-urban site, the number of larger-bodied solitary bees foraging on patches of bramble flowers increased by 447%, 287% and 202% following removal of *Apis* and *Bombus*, *Bombus* only and *Apis* only, respectively. Therefore, it is clear that despite a large majority of studies exploring floral resource competition between insect groups focusing on the role of managed bees, primarily the honeybee (see two recent systematic reviews: Mallinger, Gaines-Day & Gratton 2017, Wojcik et al. 2018), that of wild bumblebees should not be overlooked.

A substantial body of evidence to date shows that exploitative competition can have measurable impacts on the fitness of displaced FVI species (Thomson 2004, Goulson & Sparrow 2009, Elbgami et al. 2014, Hudewenz & Klein 2015). Therefore, a precautionary approach based on the accumulating evidence, added to by this thesis, that eusocial bees can and do displace wild insects from preferred sources of forage is advisable. Recent research using data from the Bees, Wasps and Ants Recording Society (BWARS) revealed a 32% decline in 1 km<sup>2</sup> grid cell occupancy for non-eusocial solitary bees in Britain from 1980 to 2013 (Powney et al. 2019), suggesting that measures to reduce the negative effects of competition should particularly consider



this group, given this alarming trend alongside apparent vulnerability to competitive displacement by eusocial foraging bees (Chapter Four). In particular, it is necessary to ensure that honeybee stocking densities take into account surrounding floral resource availability (Cane & Tepedino 2017) in order to safeguard the health and wellbeing not only of *A. mellifera* colonies themselves, but also the wild insects with which they coexist (Henry & Rodet 2018) and the complex interaction networks between plants and their wild native pollinators (Dupont et al. 2004). A step towards more informed honeybee husbandry in the UK would be to introduce formal registration of colonies, currently undertaken on a voluntary basis only (Steele et al. 2019). Looking beyond this, introducing integrated assessments of floral and bee abundances within a meaningful distance around apiaries could help beekeepers to gauge the extent of any potential impacts of honeybee-mediated competition on wild bee communities (Cane & Tepedino 2017), enabling beekeepers (particularly in commercial contexts) to make informed stocking decisions or undertake mitigation schemes such as local flower planting. Understanding the feasibility of such a scheme at a policy level could involve participatory research with professional beekeepers, a useful method to understand any barriers or facilitating factors, to optimise success through integrating local knowledge, and to maximise participation at a wider level (Kouchner et al. 2018).

Competition between organisms with dietary overlap is expected to be highest when resources are limited. The data presented here are consistent with this theory, with stronger competitive pressure recorded when floral resource availability was known to be lowest. In Chapter Three, the stronger competitive pressure observed between honeybees and bumblebees in July and August supports previous research identifying late summer as a seasonal gap in floral availability for FVI (Couvillon, Schürch & Ratnieks 2014, Timberlake, Vaughan & Memmott 2019), when phenological flowering patterns coincide with larger numbers of foraging FVI to create low per-insect resource availability (Balfour et al. 2018). In practical terms, these findings add to knowledge that can be applied to improve current measures taken to enhance floral resources. These include nectar- and pollen-rich wildflower strips planted under Agri-Environment Schemes (Pywell et al. 2012, Williams et al. 2015, Wood, Holland & Goulson 2017, Steele et al. 2019) and wildflower ‘meadows’ planted in urban areas to support pollinators (Hicks et al. 2016). Planting additional resources for FVI in spring and early summer when flowering trees and shrubs are in bloom (Balfour et al. 2018), nectar

availability is seasonally high (Couvillon et al. 2014) and competition between insects is relatively weak (Chapter Three), may be less effective than if these measures were applied in late summer. Although subject to geographical variation, the principle of integrating floral and FVI abundances to guide wildflower planting and restoration measures is likely to be a useful tool for reducing the strength and associated negative effects of exploitative competition between co-foraging FVI, thereby maximising both the benefits and efficiency of conservation resources.

## 7.2 Human dimensions

In a recent review, Amel and coauthors (2017) highlight the simple fact that present, large-scale ecosystem disruption is at its core a result of human behaviour, meaning that conservation cannot ignore human dimensions including internal but also influential social factors affecting behaviour (Gifford & Nilsson 2014, Amel et al. 2017). This is relevant to improving floral resource provision for FVI, since factors depleting flowering plant availability are largely human-driven, in particular, land management (comprising both action and inaction) within agricultural systems (Robinson & Sutherland 2002, Ollerton 2014) and in non-agricultural urban and rural contexts (Loram et al. 2011, Goddard, Dougill & Benton 2013, Baldock et al. 2019, Baldock 2020). Decision-making in agricultural systems is outside the scope of thesis (but see *e.g.* Brodt, Klonsky & Tourte 2006, Sutherland 2013, Lamarque et al. 2014). Chapters Five and Six explore human dimensions of the management of private and public greenspaces in non-agricultural areas, through qualitative and quantitative surveys of members of the public.

Citizens are a core stakeholder in FVI conservation since they are affected by and may also effect any changes in how greenspaces are managed (Defra 2014, Coupey et al. 2015), while public support is crucial for sustainable, longer term improvements in floral resource availability for FVI (Coupey et al. 2015). This is reflected in the National Pollinator Strategy (NPS) for England, which includes “*Supporting pollinators across towns, cities and the countryside* [separate to farmland]” and “*Raising awareness of what pollinators need to survive and thrive*” among its five key strategy areas. The NPS aims to engage members of the public in planting for pollinators, and to

disseminate science-based advice and information through the Defra-led outreach programme 'Bees' Needs'. This programme encourages gardeners, farmers and managers of urban or amenity spaces to grow more flowers, shrubs and trees, leave patches of land to grow wild, cut grass less often, avoid disturbing or destroying nesting or hibernating insects and think carefully about whether to use pesticides (adapted from Defra 2014).

Chapters Five and Six hint at a paradox within public engagement with these goals. In Chapter Five, members of the public visiting garden centres showed a strong positive interest in FVI and inclination to purchase 'pollinator-friendly' ornamental plants. Many, 77% of participants, were already growing pollinator-friendly plants in their garden or outside space, although it was not clear whether this was a deliberate action or whether attracting FVI was a secondary result of plants grown for other reasons. Meanwhile the online survey presented in Chapter Six reveals mixed public attitudes towards common wild flowering plants. In a dichotomy among six representative wildflowers, three less well-liked species were those most commonly considered to be 'weeds' and perceived as having a lower aesthetic appeal, compared to three more popular species that were not considered to be weeds and were commonly described as aesthetically pleasing. Despite a high average self-reported level of interest in nature among participants (mean  $\pm$  SD:  $8.75 \pm 1.40$  on a 0-10 scale,  $n = 1492$ ), the three least popular species were also those most frequently considered to be beneficial to wildlife.

This is reminiscent of an apparent knowledge-action gap in conservation more broadly. Although members of the public cite high levels of awareness and concern regarding biodiversity losses, this has not translated into widespread pro-environmental behaviour (Amel et al. 2017). Members of the public seem to be aware of and concerned about reported declines in FVI (Chapter Five, Wilson, Forister & Carril 2017). However, pro-biodiversity action to support insects through improving floral resources can be selective, ineffective (Alton & Ratnieks 2020) and highly influenced by sociocultural norms and ideals, aesthetic preferences and a pervasive convention of 'neat' landscapes (Clayton 2007, Goddard, Dougill & Benton 2013, Hoyle et al. 2017, Hoyle et al. 2018). In particular, despite the potential for common insect-attractive wild flowering plants to be used as a cost-effective tool for resource enrichment for FVI in towns, cities and along transport highways (Noordijk et al. 2009, Baldock 2020, Chapter Two), these

plants are routinely removed through intensive mowing, strimming and herbicide use in both domestic and public greenspaces (Loram et al. 2011, Larson, Kesheimer & Potter 2014, Baldock 2020) while financial and other resources are simultaneously channelled into planting wildflower meadows or purchasing pollinator-friendly ornamental plant varieties. What causes this apparent paradox?

Previous work has addressed this question through assessments of public attitudes towards landscapes managed with varying levels of intensity (*e.g.* Özgüner & Kendle 2006, Weber, Kowarik & Säumel 2014, Garbuzov, Fensome & Ratnieks 2015, Nam & Dempsey 2019), socio-economic and demographic factors predicting urban wildlife gardening behaviours (Gaston et al. 2007) and motivations and drivers behind garden management style including pro-biodiversity approaches (Clayton 2007, Loram et al. 2011, Freeman et al. 2012). Chapter Six adds to this body of research at a finer resolution, showing that public attitudes towards wildflowers can vary on a species-by-species basis and identifying features that add to or subtract from species' popularity. This suggests that initiatives aiming to improve floral resource provision for FVI through growing or tolerating wild flowering plants should not only consider macro-scale perceptions but also the acceptability of plant species within enhancement measures. Providing on-site and off-site information where public spaces are managed for FVI and other wildlife helps to maximise acceptability and long-term public support (Coupey et al. 2015, Hoyle et al. 2017). The data in Chapter Six suggest that integrating information about wildflower species' value for FVI, wider ecological function and even cultural history could be important components within this information provision.

Looking forwards, it would be interesting to extend the social research in this thesis to understand more about public engagement with FVI conservation. The findings in Chapter Five suggest that working with garden centres to achieve outcomes for FVI, for example under the remit of the National Pollinator Strategy's outreach body *Bees' Needs* (Defra 2014), could be a win-win for garden centres, pollinators and the garden retail industry. However, to further such a partnership, research is needed to quantitatively test whether the positive public attitudes identified in this research translate into consumer choice, for example through experimental studies of actual purchase behaviour. Further research should also explore whether education and information provision regarding the ecological and cultural value of wildflower species

directly improves their liking rating among members of the public, and whether this translates to tolerating and/or encouraging their growth in different land-use types. Given the urgent need to increase the abundance and quality of floral resources for FVI (Vanbergen et al. 2013), as well as multiple co-benefits of enhancing wild vegetation cover for biodiversity and public health (Wu 2014), it may be most efficient simultaneously to make management changes alongside comprehensive information provision. This method has been shown to be effective in France (Coupey et al. 2015), however, a thorough research study of such a programme would be beneficial.

Since mid-2018, global movements drawing attention to environmental and ecological breakdown have resulted in greater penetration of these issues into the public consciousness (Thackeray et al. 2020), meaning that current societal perceptions of wildlife may currently be undergoing rapid change. Meanwhile, members of the public report greater awareness of and concern for pollinating insects, linked to a perceived increase in mainstream media focus on threats facing FVI in recent years (Chapter Five). There is also evidence to suggest that public awareness of the ecological value of wild vegetation for pollinators is becoming more widespread (Hoyle et al. 2017), alongside greater acceptance of more naturalistic landscapes with greater value to FVI (Weber, Kowarik & Säumel 2014, Hoyle et al. 2017, Nam & Dempsey 2019). Overall, it may be a particularly opportune time for practical action to improve floral resources for FVI, for example through land management, corporate engagement and supporting national and regional policy, with a need to consider both ecological factors and human dimensions to meet this goal successfully and sustainably.

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## Appendix A

**A.1.** Foraging activity of insect groups visiting *Rubus fruticosus* flowers in detailed insect transect walks in two locations in Brighton, East Sussex, 2018. Counts and proportions are pooled over the three surveys made during the early, middle and late stages of bramble bloom (urban: 13 & 15 June, 26 & 27 June, 12 & 13 July; rural: 6 June, 21 June and 5 & 6 July). For each location, data shown firstly include all transect walks per survey, and secondly include only the first transect walk per survey.

Group	Brighton urban				Brighton rural			
	All walks per survey	Proportion (%)	One walk per survey	Proportion (%)	All walks per survey	Proportion (%)	One walk per survey	Proportion (%)
Honeybee	409	35.0	110	39.9	406	33.8	103	36.4
Bumblebee	456	39.0	107	38.8	364	30.3	87	30.7
Bee: Other	154	13.2	27	9.8	65	5.4	22	7.8
Diptera: Syrphidae	66	5.7	13	4.7	156	13.0	28	9.9
Diptera: Other	22	1.9	3	1.1	43	3.6	8	2.8
Butterfly	27	2.3	8	2.9	104	8.7	21	7.4
Wasp	1	0.1	0	0.0	12	1.0	2	0.7
Beetle	33	2.8	8	2.9	50	4.2	12	4.2
Total insects	1168		276		1200		283	



**A.2.** Foraging activity of insects visiting *Rubus fruticosus* flowers in detailed insect transect walks in two locations in Brighton, East Sussex, 2018. Counts of insects visiting bramble flowers are shown for the first transect walk for each of three surveys made during the early, middle and late stages of bramble bloom (urban: 13 June, 27 June, 12 July,  $n = 276$  insects in total; rural: 6 June, 21 June, 5 July,  $n = 283$ ). Genus-level richness  $S_{(G)}$ , Shannon-Weiner diversity ( $H'$ ) and Pielou's measure of evenness ( $J$ ) are given for each individual transect.

Group	Genus	Brighton urban			Brighton rural		
		13 June	27 June	12 July	6 June	21 June	5 July
<i>Apis mellifera</i>	<i>Apis</i>	51	34	25	36	41	26
<i>Bombus</i> spp.	<i>Bombus</i>	67	19	21	44	17	26
Bee: Other	<i>Andrena</i>	0	3	10	0	0	8
	<i>Lasioglossum</i>	2	6	4	0	2	12
	<i>Megachile</i>	2	0	0	0	0	0
Diptera: Syrphidae	<i>Criorhina</i>	0	0	0	1	0	0
	<i>Episyrphus</i>	4	4	0	2	1	0
	<i>Eristalis</i>	0	0	0	0	2	1
	<i>Rhingia</i>	1	0	0	5	0	0
	<i>Syrphus</i>	0	1	2	1	11	0
	<i>Volucella</i>	1	0	0	1	2	1
Diptera: Other	<i>Calliphora</i>	2	0	0	0	0	0
	<i>Chloromyia</i>	0	1	0	0	0	0
	<i>Empis</i>	0	0	0	1	1	0
	<i>Lucilia</i>	0	0	0	0	6	0
Butterfly	<i>Aglais</i>	0	0	0	0	0	1
	<i>Aphantopus</i>	0	0	0	0	0	6
	<i>Maniola</i>	0	4	0	0	1	5
	<i>Melanargia</i>	0	0	0	0	0	1
	<i>Ochlodes</i>	0	0	0	0	1	0
	<i>Pieris</i>	0	0	4	0	0	1
	<i>Polygonia</i>	0	0	0	0	0	1
	<i>Pyronia</i>	0	0	0	0	0	4
Wasp	<i>Vespula</i>	0	0	0	0	0	2
Beetle	<i>Oedemera</i>	1	0	2	6	4	0
	<i>Rhagonycha</i>	0	0	5	0	0	2
n insects		131	72	73	97	89	97
$S_{(G)}$		9	8	8	9	12	15
$H'$		1.12	1.49	1.70	1.32	1.71	2.07
$J$		0.51	0.71	0.82	0.60	0.69	0.76

**A.3.** Dates of regional surveys of 100 insects carried out in seven locations across Sussex in 2018 and 2019. One survey was carried out in June and one in July in each survey year.

Main site	Urban or rural	Survey number	Survey date
Hailsham	Rural	1	15/06/2018
Hailsham	Rural	2	09/07/2018
Hailsham	Rural	3	17/06/2019
Hailsham	Rural	4	11/07/2019
Hailsham	Urban	1	21/06/2018
Hailsham	Urban	2	09/07/2018
Hailsham	Urban	3	17/06/2019
Hailsham	Urban	4	16/07/2019
Lewes	Rural	1	21/06/2018
Lewes	Rural	2	10/07/2018
Lewes	Rural	3	20/06/2019
Lewes	Rural	4	15/07/2019
Lewes	Urban	1	18/06/2018
Lewes	Urban	2	10/07/2018
Lewes	Urban	3	20/06/2019
Lewes	Urban	4	17/07/2019
Uckfield	Rural	1	22/06/2018
Uckfield	Rural	2	10/07/2018
Uckfield	Rural	3	20/06/2019
Uckfield	Rural	4	17/07/2019
Uckfield	Urban	1	21/06/2018
Uckfield	Urban	2	10/07/2018
Uckfield	Urban	3	20/06/2019
Uckfield	Urban	4	11/07/2019
Pevensey	Rural	1	22/06/2018
Pevensey	Rural	2	22/07/2018
Pevensey	Rural	3	17/06/2019
Pevensey	Rural	4	16/07/2019

**A.4.** Bramble presence or absence in randomly generated grid squares in and near to Brighton, Ferring and Lewes towns, Sussex.

Site	Brambles present? (Y/N)	Coordinates of brambles within square	Habitat category
Brighton urban	N	-	Urban residential
	Y	530727, 107589	Urban residential
	Y	532288, 106774	Urban residential
	Y	529435, 105980	Urban residential
	Y	528924, 108686	Woodland
	N	-	Urban residential
	Y	532487, 108167	Urban park
	N	-	Urban residential
	Y	531283, 108406	Urban residential
	Y	530705, 107414	Urban school field
Brighton rural	Y	534968, 107401	Agricultural field margin
	Y	535978, 110284	Bridlepath
	Y	535703, 109762	Bridlepath
	Y	534931, 108289	Bridlepath
	Y	533377, 108456	Urban residential
	Y	535205, 110522	Agricultural field margin
	Y	533420, 107877	Urban residential
	Y	534666, 110768	Rural out-building
	Y	534384, 110496	Agricultural field margin
	Y	534192, 110624	Agricultural field margin
Ferring urban	Y	508957, 102285	Rural riverbank
	Y	509317, 102615	Urban residential
	N	-	Agricultural field
	Y	508499, 101633	Urban residential
	Y	508902, 102403	Rural riverbank
	Y	508906, 102589	Rural riverbank
	Y	508682, 101623	Urban residential
	Y	509280, 103376	Urban riverbank
	Y	510066, 103177	Railway
	Y	509288, 102371	Urban residential
Ferring rural	Y	508329, 104438	Agricultural field margin
	Y	509319, 105776	Woodland
	Y	508813, 105722	Agricultural field margin
	Y	509127, 104373	Bridlepath
	Y	508271, 105661	Agricultural field margin
	Y	509734, 105362	Woodland
	Y	509611, 105904	Woodland

	Y	509250, 105280	Agricultural field margin
	Y	509589, 104345	Agricultural field margin
	Y	509336, 105253	Rural out-building
Lewes urban	Y	541909, 110703	Urban carpark
	N	-	Urban residential
	Y	540939, 110738	Industrial estate
	N	-	Urban residential
	Y	540780, 110377	Urban residential
	Y	540765, 110939	Urban residential
	Y	540513, 109266	Urban residential
	Y	541924, 110273	Urban riverbank
	N	-	Urban riverbank
	Y	540712, 109687	Urban park
Lewes rural	Y	543347, 111411	Agricultural field margin
	Y	543061, 110889	Woodland
	Y	543382, 112371	Agricultural field margin
	Y	542551, 110769	Agricultural field margin
	Y	542398, 111894	Agricultural field margin
	Y	542201, 110773	Industrial estate
	Y	542188, 111761	Agricultural field margin
	Y	542628, 112294	Agricultural field margin
	Y	543053, 111302	Agricultural field margin
	Y	543004, 111169	Nature reserve field

## A.5 Calculating the proportion of bramble pellets using a correction for false positives.

### *Summary*

Bramble is a grey pollen colour, which is rare. However, pollen pellets from certain other plant species (for example, field bean *Vicia faba*) is also grey. Therefore, after counting the grey pellets in each pollen sample, we needed to apply a correction procedure to account for any false positives (non-bramble grey pellets) and estimate the proportion that were bramble. To do this we used data from our microscopic analysis of grey pellets from each sample (see Methods in main text) in the following *Correction procedure*, which accounted for temporal variation in the proportion of false positives per location. This is demonstrated in a *Worked example*, see below.

### *Correction procedure*

It was not appropriate to make a false positives correction per hive as this would have introduced a large binomial sampling error. Instead, we corrected for false positives in a way that was both ecologically relevant and would not introduce any overall bias in the data by over- or underestimating the proportion of bramble in the samples.

First, we calculated the proportion of false positives (pfpos) in each sample using the proportions of bramble and non-bramble in the tested grey pellets. Then, in each location, we divided the sampling period into three 3-week periods, to account for the fact that the proportion of false positives in the samples changed over the sampling period, which was likely to be due to the flowering of nearby plants visited by honey bees that also have grey pollen, although this is a rare colour. For example, in one of the rural locations (Magham Down village), the proportion of false positives in samples collected in mid-June to mid-July was much higher on average than those collected in late May – mid-June. This was likely to be due to the flowering of bean crops in nearby fields, since grey pellets identified as *Vicia faba* pollen were commonly present in the samples from 15 June – 2 July. It was not possible to divide the sampling period according to the specific occurrence of false positives from certain species of flowering plant, since these overlapped and would have led to too many permutations; however,

arbitrary division into three three-week periods gave finer resolution and was more ecologically relevant than an overall average per location.

We calculated the average proportion of false positives in the samples collected over each 3-week period within each location ( $\bar{x}(\text{pfpos})$ ; see below for worked example). To calculate the number of bramble pellets in each sample, using this correction for false positives, the number of grey pellets in the sample was multiplied by the average proportion of confirmed true bramble in the respective 3-week period ( $1 - \bar{x}(\text{pfpos})$ ):

$$\begin{aligned} \text{n bramble pellets (corrected for false positives using 3 – week average)} \\ = \text{n grey pellets} * (1 - \bar{x}(\text{pfpos})) \end{aligned}$$

This was converted into a proportion in order to account for different numbers of pellets in the samples:

$$\text{proportion bramble pellets} = (\text{n bramble pellets} / \text{n total pellets}) * 100$$

*Worked example: of one sample collected in a rural location, Ashcombe farm*

27 samples were collected from Ashcombe farm over the sampling period from 30 May – 3 August 2018. This was divided into three 3-week periods: 30 May – 20 June (n=10 samples); 21 June – 12 July (n=9) and 13 July – 3 August (n=8).

Sample X was collected on 04/07/2018 from hive Y at Ashcombe farm.

Sample X has 291 pellets in total, 280 of which are grey. We analysed 10 grey pellets, of which 8 were confirmed to be *R. fruticosus*.

The results of pollen pellet analysis were then used to calculate the proportion of false positives (*pfpos*) for each sample:  $\text{pfpos} = (10 \text{ tested grey pellets} - 4 \text{ confirmed bramble}) / 10 \text{ tested grey pellets} = 0.6$

For each 3-week period we then calculated the average proportion of false positives ( $\bar{x}(\text{pfpos})$ ):

$$\bar{x}(\text{pfpos}) = \frac{1}{n} \sum_{i=1}^n \text{pfpos}_i$$

The average proportion of false positives during the 3-week period in which sample X was collected (21 June – 12 July (n=9)) at Ashcombe farm was 25.0% (n=9 samples; see A.5. Supporting Table 1).

The number of bramble pellets in sample X, after correcting for false positives, is therefore:

$$n \text{ grey pellets} * (1 - \bar{x}(pfp_{pos})) = 280 * (1 - 0.25) = 210$$

The percent of grey pellets in sample X, which had a total of 291 pellets, is:

$$210/291 * 100 = 72.5\%$$

**A.5. Supporting Table 1.** Average proportion (%) of grey, non-bramble, pellets (false positives) in pollen samples collected from honey bee hives in one urban (U) and three rural (R) locations across Sussex in 2018. For each location the average proportion of false positives in the samples was calculated for the full sampling period (final column), and over three 3-week periods in each location (30/05-20/06, 21/06-12/07, 13/07-03/08). These are shown, with the number of pollen samples tested for false positives in parentheses. These data were used to correct for false positives in calculating the proportion of bramble pellets in the pollen samples (Appendix A.5 main).

Location	Average proportion of false positives over three-week period (n samples tested)			Average proportion of false positives over sampling period (n)
	30/05 - 20/06	21/06 - 12/07	13/07 - 03/08	30/05 – 12/07 or 03/08
Ashcombe farm (R)	0.1700 (10)	0.2500 (9)	0.1125 (8)	0.1792 (27)
Magham Down village (R)	0.1656 (16)	0.3928 (12)	0.2789 (9)	0.2669 (37)
Onion Field (R)	0.0250 (12)	0.0300 (10)	0.1330 (9)	0.0581 (31)
Brighton city (U)	0.1367 (10)	0.1500 (6)	na	0.1417 (16)

**A.6.** Abundance, floral bloom intensity and *overall availability* (abundance x bloom intensity) of flowering bramble from 15 May to 30 July 2018. Plants were recorded on three fixed transect routes in northeast, northwest and southwest directions within a 2 km radius from the Laboratory of Apiculture and Social Insects. Abundance and bloom intensity were recorded using a modified 5-point DAFOR scale, with 5 being the maximum (Kent and Coker, 1992).

Date	Transect direction	Flowering <i>R. fruticosus</i> abundance (0-5)	Flowering <i>R. fruticosus</i> bloom intensity (0-5)	Availability (abundance * bloom)
15.05.2018	NE	na	na	0
23.05.2018		1	1	1
05.06.2018		3	2	6
15.06.2018		3	3	9
20.06.2018		5	5	25
27.06.2018		4	3	12
06.07.2018		4	3	12
13.07.2018		4	2	8
30.07.2018		3	2	6
14.05.2018	NW	na	na	0
23.05.2018		1	1	1
04.06.2018		4	3	12
22.06.2018		5	4	20
29.06.2018		5	3	15
05.07.2018		5	3	15
13.07.2018		3	3.5	10.5
25.07.2018		3	2	6
15.05.2018	SW	na	na	0
23.05.2018		2	1	2
05.06.2018		3	2	6
13.06.2018		3	3	9
20.06.2018		3	4	12
26.06.2018		2	3	6
09.07.2018		3	1	3
13.07.2018		3	2	6
25.07.2018		2	3	6



**A.7.** Abundance, floral bloom intensity and *overall availability* (abundance x bloom intensity) of flowering forb, shrub and tree species from 15 May to 30 July 2018. Plants were recorded on three fixed transect routes in northeast, northwest and southwest directions within a 2 km radius from the Laboratory of Apiculture and Social Insects. Abundance and bloom intensity were recorded using a modified 5-point DAFOR scale, with 5 being the maximum (Kent and Coker, 1992). Data for the flowering plant species with 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> highest *overall availability* of flowers are shown for each transect. Per-transect species richness of flowering plants is shown in the final column.

Date	Transect direction	Flowering plant species with 1 <sup>st</sup> , 2 <sup>nd</sup> and 3 <sup>rd</sup> highest per-transect availability	Abundance (1-5)	Bloom level (1-5)	Availability (abundance * bloom; 1-25)	Species richness per transect ( <i>S<sub>T</sub></i> )
15.05.2018	NE	<i>Brassica napus napus</i>	3	5	15	n = 20
		<i>Anthriscus sylvestris</i>	5	4	18	
		<i>Crataegus monogyna</i>	5	5	23	
23.05.2018	NE	<i>Anthriscus sylvestris</i>	3	4	12	n = 25
		<i>Ranunculus repens</i>	4	4	16	
		<i>Bellis perennis</i>	4	4	16	
		<i>Crataegus monogyna</i>	4	5	20	
05.06.2018	NE	<i>Brassica nigra</i>	2	4	8	n = 31
		<i>Rosa canina</i>	2	4	8	
		<i>Sambucus nigra</i>	2	4	8	
		<i>Leucanthemum vulgare</i>	3	3	9	
		<i>Bellis perennis</i>	3	3	9	
		<i>Ranunculus repens</i>	4	3	12	
15.06.2018	NE	<i>Ranunculus repens</i>	2	2	4	
		<i>Rosa canina</i>	2	2	4	
		<i>Sambucus nigra</i>	2	2	4	
		<i>Papaver rhoeas</i>	2	2	4	
		<i>Aruncus dioica</i>	2	2	4	
		<i>Silene dioica</i>	2	2	4	
		<i>Trifolium pratense</i>	2	2	4	
		<i>Trifolium repens</i>	2	2	4	
		<i>Veronica chamaedrys</i>	2	2	4	
		<i>Calystegia silvatica</i>	3	2	6	
		<i>Lotus corniculata</i>	3	2	6	
		<i>Glechoma hederaceae</i>	2	3	6	
		<i>Senecio jacobaea</i>	3	2	6	
		<i>Carduus crispus</i>	3	2	6	

		<i><b>Rubus fruticosus</b></i>	3	3	9	
		<i>Anthriscus sylvestris</i>	3	3	9	
		<i>Medicago lupulina</i>	3	3	9	
		<i>Trifolium dubium</i>	3	3	9	
		<i>Leucanthemum vulgare</i>	3	3	9	n = 34
20.06.2018	NE	<i>Lotus corniculata</i>	3	4	12	
		<i>Trifolium campestre</i>	3	4	12	
		<i>Matricaria chamomilla</i>	3	4	12	
		<i>Medicago lupulina</i>	4	4	16	
		<i>Trifolium repens</i>	4	4	16	
		<i><b>Rubus fruticosus</b></i>	5	5	25	n = 54
27.06.2018	NE	<i>Trifolium pratense</i>	2	4	8	
		<i>Chamaenerion angustifolium</i>	2	4	8	
		<i>Convolvulus arvensis</i>	3	3	9	
		<i>Leontodon</i> spp.	3	3	9	
		<i>Heracleum sphondylium</i>	3	3	9	
		<i>Galium album</i>	3	3	9	
		<i>Leucanthemum vulgare</i>	3	3	9	
		<i>Trifolium repens</i>	3	4	12	
		<i><b>Rubus fruticosus</b></i>	4	3	12	n = 38
06.07.2018	NE	<i><b>Rubus fruticosus</b></i>	4	3	12	
		<i>Cirsium arvense</i>	4	3	12	
		<i>Convolvulus arvensis</i>	4	3	12	
		<i>Centaurea scabiosa</i>	4	3	12	
		<i>Matricaria chamomilla</i>	3	4	12	
		<i>Epilobium hirsutum</i>	4	4	12	
		<i>Chamaenerion angustifolium</i>	4	4	16	
		<i>Phacelia tanacetifolia</i>	4	5	20	
		<i>Heracleum sphondylium</i>	4	5	20	
		<i>Clematis vitalba</i>	4	5	20	n = 38
13.07.2018	NE	<i>Convolvulus arvensis</i>	4	3	12	
		<i>Cirsium arvense</i>	4	3	12	
		<i>Chamaenerion angustifolium</i>	3	4	12	
		<i>Matricaria chamomilla</i>	4	3	12	
		<i>Phacelia tanacetifolia</i>	4	4	16	
		<i>Clematis vitalba</i>	4	5	20	n = 46
30.07.2018	NE	<i>Senecio jacobaea</i>	4	2	8	

		<i>Knautia arvensis</i>	3	3	9	
		<i>Centaurea scabiosa</i>	3	3	9	
		<i>Chamaenerion angustifolium</i>	4.5	2	9	
		<i>Thymus serpyllum</i>	3	3	9	
		<i>Heracleum sphondylium</i>	5	2	10	n = 25
14.05.2018	NW	<i>Aesculus hippocastanum</i>	2	5	10	
		<i>Ranunculus repens</i>	4	3	12	
		<i>Anthriscus sylvestris</i>	5	5	25	
		<i>Crataegus monogyna</i>	5	5	25	n = 22
04.06.2018	NW	<i>Rosa canina</i>	3	3	9	
		<i>Veronica persica</i>	3	3	9	
		<b><i>Rubus fruticosus</i></b>	4	3	12	
		<i>Bellis perennis</i>	3	4	12	
		<i>Glechoma hederaceae</i>	3	4	12	
		<i>Trifolium repens</i>	4	3	12	
		<i>Ranunculus repens</i>	5	3	15	
		<i>Sambucus nigra</i>	3	5	15	n = 30
22.06.2018	NW	<i>Lotus corniculata</i>	3	3	9	
		<i>Papaver rhoeas</i>	3	3	9	
		<i>Heracleum sphondylium</i>	3	3	9	
		<i>Medicago lupulina</i>	3	4	12	
		<i>Cirsium arvense</i>	3	4	12	
		<i>Vicia cracca</i>	3	4	12	
		<i>Trifolium repens</i>	4	5	20	
		<b><i>Rubus fruticosus</i></b>	5	4	20	n = 32
29.06.2018	NW	<i>Heracleum sphondylium</i>	4	3	12	
		<i>Senecio jacobaea</i>	4	3	12	
		<i>Galium verum</i>	3	4	12	
		<i>Vicia cracca</i>	3	4	12	
		<i>Ligustrum vulgare</i>	3	4	12	
		<b><i>Rubus fruticosus</i></b>	5	3	15	
		<i>Cirsium arvense</i>	4	4	16	
		<i>Trifolium repens</i>	4	4	16	n = 29
05.07.2018	NW	<b><i>Rubus fruticosus</i></b>	5	3	15	
		<i>Calystegia silvatica</i>	3	5	15	
		<i>Senecio jacobaea</i>	4	4	16	
		<i>Ononis repens</i>	4	4	16	
		<i>Vicia cracca</i>	4	4	16	
		<i>Cirsium arvense</i>	5	4	20	

		<i>Vicia cracca</i>	4	5	20	
		<i>Galium verum</i>	4	5	20	n = 31
13.07.2018	NW	<i>Calystegia silvatica</i>	3	5	15	
		<i>Cirsium arvense</i>	4	4	16	
		<i>Clematis vitalba</i>	4	4	16	
		<i>Vicia cracca</i>	4	4	16	
		<i>Senecio jacobaea</i>	4	5	20	
		<i>Heracleum sphondylium</i>	5	4	20	n = 27
25.07.2018	NW	<i>Centaurea nigra</i>	3	3	9	
		<i>Ononis repens</i>	3	3	9	
		<i>Knautia arvensis</i>	3	3	9	
		<i>Convolvulus arvensis</i>	4	3	12	
		<i>Senecio jacobaea</i>	3	4	12	
		<i>Vicia cracca</i>	4	3	12	
		<i>Clematis vitalba</i>	4	5	20	n = 29
15.05.2018	SW	<i>Ranunculus repens</i>	5	3	15	
		<i>Bellis perennis</i>	5	3	15	
		<i>Aesculus hippocastanum</i>	3	5	15	
		<i>Acer spp.</i>	3	5	15	
		<i>Anthriscus sylvestris</i>	4	4	16	
		<i>Crataegus monogyna</i>	4	5	20	n = 19
05.06.2018	SW	<i>Rosa canina</i>	3	4	12	
		<i>Bellis perennis</i>	4	4	16	
		<i>Trifolium dubium</i>	4	4	16	
		<i>Veronica chamaedrys</i>	4	4	16	
		<i>Trifolium repens</i>	4	4	16	
		<i>Ranunculus acris</i>	5	4	20	n = 33
13.06.2018	SW	<i>Lotus corniculata</i>	3	3	9	
		<b><i>Rubus fruticosus</i></b>	3	3	9	
		<i>Trifolium dubium</i>	3	3	9	
		<i>Veronica chamaedrys</i>	3	3	9	
		<i>Sambucus nigra</i>	3	4	12	
		<i>Ranunculus acris</i>	5	3	15	
		<i>Trifolium repens</i>	5	3	15	n = 33
20.06.2018	SW	<i>Calystegia sepium</i>	3	2	6	
		<i>Bellis perennis</i>	2	3	6	
		<i>Rosa canina</i>	2	3	6	
		<i>Sambucus nigra</i>	2	3	6	

		<i>Convolvulus arvensis</i>	2	3	6	
		<i>Glechoma hederaceae</i>	3	2	6	
		<i>Ligustrum vulgare</i>	2	3	6	
		<b><i>Rubus fruticosus</i></b>	3	3	9	
		<i>Trifolium repens</i>	3	4	12	
		<i>Trifolium dubium</i>	4	3	12	n = 36
26.06.2018	SW	<b><i>Rubus fruticosus</i></b>	2	3	6	
		<i>Malva sylvestris</i>	3	2	6	
		<i>Calystegia silvatica</i>				
		<i>Cirsium arvense</i>	3	2	6	
		<i>Sambucus nigra</i>	2	3	6	
		<i>Trifolium pratense</i>	2	3	6	
		<i>Ligustrum vulgare</i>	2	3	6	
		<i>Convolvulus arvensis</i>	3	3	9	
		<i>Trifolium repens</i>	3	4	12	n = 33
09.07.2018	SW	<i>Clematis vitalba</i>	3	4	12	
		<i>Tilia</i> spp.	3	4	12	
		<i>Senecio jacobaea</i>	5	3	15	
		<i>Calystegia sepium</i>	4	4	16	
		<i>Calystegia silvatica</i>	4	4	16	
		<i>Cirsium arvense</i>	4	4	16	n = 34
13.07.2018	SW	<i>Convolvulus arvensis</i>	4	3	12	
		<i>Calystegia silvatica</i>	3	4	12	
		<i>Clematis vitalba</i>	4	5	20	
		<i>Senecio jacobaea</i>	5	5	25	n = 34
25.07.2018	SW	<i>Buddleja davidii</i>	2	5	10	
		<i>Crepis</i> spp.	5	2	10	
		<i>Matricaria discoidea</i>	4	3	12	
		<i>Senecio jacobaea</i>	4	3	12	
		<i>Matricaria chamomilla</i>	4	3	12	
		<i>Daucus carota</i>	3	5	15	n = 28

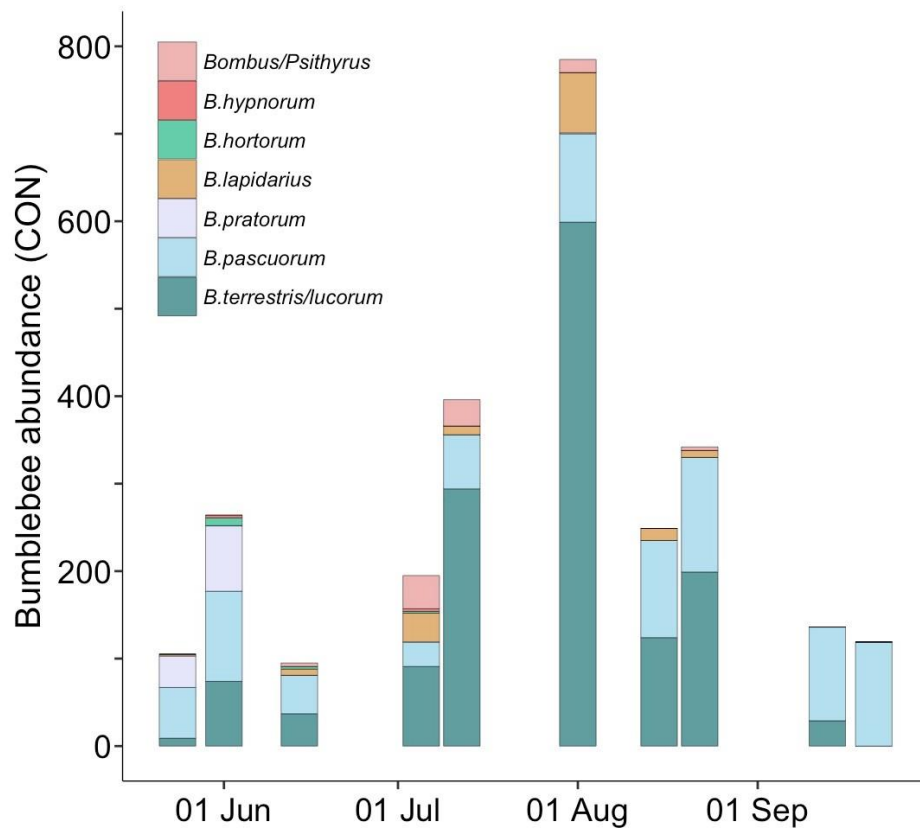
## Appendix B

**B.1.** Mean per-trial nectar standing crop volume ( $\mu\text{L}$ ) and concentration (% sugar) extracted from flowers in lavender patches from which bumble bees have been excluded (BBE), honey bees have been excluded (HBE), and unmanipulated control patches (CON), across ten bee-exclusion trials in early summer (<sup>a</sup>), late summer (<sup>b</sup>) and autumn (<sup>c</sup>) from May to September 2017. Standing crop nectar data for each trial are averaged over trial days 2 and 3 ( $n = 20$  flowers), except Trial 1 in which nectar was extracted only on day 2 ( $n = 10$  flowers). Concentration data are from extracted standing crop samples that were large enough such that it was possible to measure concentration using a refractometer; number of samples is shown as [n]. Kruskal Wallis  $\chi^2$  and  $P$  value for significant difference in nectar volume between patches per trial are given with Bonferroni adjustment of  $P$  values. *Post hoc* Dunn's test results for pairwise comparison are also calculated with Bonferroni adjustment. Asterisk \* denotes significance at  $P < 0.05$ .

Trial	Patch treatment	Mean nectar standing crop ( $\mu\text{L}$ )	Mean nectar standing crop concentration (% sugar) [n flowers]	Per-trial KW test for differences in standing crop volume between patch treatments; $\chi^2$ (DF), $P$ value	Per-trial <i>post hoc</i> Dunn's test for pairwise comparison of standing crop volume between patch treatments; Z and ( $P$ ) values
1 <sup>a</sup>	BBE	$0.178 \pm 0.035$	$33.5 \pm 0.5$ [3]	2.34 <sub>(2)</sub> , $P = 0.311$	BBE – CON: 1.49 ( $P = 0.203$ )
1 <sup>a</sup>	HBE	$0.103 \pm 0.013$	$33.0 \pm 2.8$ [2]		BBE – HBE: 0.46 ( $P = 0.969$ )
1 <sup>a</sup>	CON	$0.076 \pm 0.010$	$31.8 \pm 2.2$ [4]		CON – HBE: -1.03 ( $P = 0.452$ )
2 <sup>a</sup>	BBE	$0.427 \pm 0.046$	$36.6 \pm 4.6$ [19]	40.44 <sub>(2)</sub> , $P < 0.001^*$	BBE – CON: 5.76 ( $P < 0.001$ )*
2 <sup>a</sup>	HBE	$0.033 \pm 0.007$	$30.4 \pm 2.6$ [4]		BBE – HBE: 5.21 ( $P < 0.001$ )*
2 <sup>a</sup>	CON	$0.027 \pm 0.009$	$32.5 \pm 0.7$ [2]		CON – HBE: -0.56 ( $P = 0.870$ )
3 <sup>a</sup>	BBE	$0.506 \pm 0.072$	$41.4 \pm 6.7$ [17]	18.30 <sub>(2)</sub> , $P < 0.001^*$	BBE – CON: 3.23 ( $P = 0.002$ )*
3 <sup>a</sup>	HBE	$0.160 \pm 0.050$	$33.7 \pm 4.5$ [8]		BBE – HBE: 4.04 ( $P < 0.001$ )*
3 <sup>a</sup>	CON	$0.182 \pm 0.033$	$32.2 \pm 5.5$ [9]		CON – HBE: 0.81 ( $P = 0.630$ )
4 <sup>b</sup>	BBE	$0.102 \pm 0.033$	$42.8 \pm 10.3$ (2)	2.98 <sub>(2)</sub> , $P = 0.225$	BBE – CON: 0.85 ( $P = 0.594$ )
4 <sup>b</sup>	HBE	$0.043 \pm 0.011$	$41.2 \pm 1.6$ [3]		BBE – HBE: 1.73 ( $P = 0.127$ )
4 <sup>b</sup>	CON	$0.068 \pm 0.019$	$40.5 \pm \text{na}$ [1]		CON – HBE: 0.88 ( $P = 0.571$ )
5 <sup>b</sup>	BBE	$0.066 \pm 0.012$	na	11.36 <sub>(2)</sub> , $P < 0.001^*$	BBE – CON: 3.37 ( $P = 0.001$ )*
5 <sup>b</sup>	HBE	$0.033 \pm 0.008$	$29.0 \pm \text{na}$ [1]		BBE – HBE: 1.71 ( $P = 0.129$ )
5 <sup>b</sup>	CON	$0.020 \pm 0.006$	$21.0 \pm \text{na}$ [1]		CON – HBE: -1.66 ( $P = 0.146$ )
6 <sup>b</sup>	BBE	$0.054 \pm 0.017$	$30.3 \pm 2.5$ [2]	11.37 <sub>(2)</sub> , $P < 0.001^*$	BBE – CON: 2.86 ( $P = 0.006$ )*
6 <sup>b</sup>	HBE	$0.009 \pm 0.003$	na		BBE – HBE: 3.51 ( $P < 0.001$ )*
6 <sup>b</sup>	CON	$0.011 \pm 0.004$	na		CON – HBE: 0.65 ( $P = 0.771$ )
7 <sup>b</sup>	BBE	$0.037 \pm 0.009$	na	8.78 <sub>(2)</sub> , $P = 0.012^*$	BBE – CON: 2.92 ( $P = 0.005$ )*
7 <sup>b</sup>	HBE	$0.019 \pm 0.008$	na		BBE – HBE: 1.91 ( $P = 0.084$ )
7 <sup>b</sup>	CON	$0.006 \pm 0.002$	na		CON – HBE: -1.01 ( $P = 0.472$ )
8 <sup>b</sup>	BBE	$0.071 \pm 0.013$	$21.5 \pm 4.2$ [4]		BBE – CON: 3.80 ( $P < 0.001$ )*

8 <sup>b</sup>	HBE	0.018 ± 0.006	na	16.12 <sub>(2)</sub> , P < 0.001*	BBE - HBE: 3.02 (P = 0.004)*
8 <sup>b</sup>	CON	0.013 ± 0.005	24.0 ± na [1]		CON - HBE: -0.79 (P = 0.648)
9 <sup>c</sup>	BBE	0.404 ± 0.098	32.8 ± 5.9 [17]		BBE - CON: 5.02 (P < 0.001)*
9 <sup>c</sup>	HBE	0.015 ± 0.004	na	40.60 <sub>(2)</sub> , P < 0.001*	BBE - HBE: 5.42 (P < 0.001)*
9 <sup>c</sup>	CON	0.018 ± 0.005	28.5 ± 2.1 [2]		CON - HBE: 0.39 (P = 1.000)
10 <sup>c</sup>	BBE	0.238 ± 0.056	27.9 ± 6.1 [14]		BBE - CON: 4.34 (P < 0.001)*
10 <sup>c</sup>	HBE	0.032 ± 0.011	27.7 ± 3.8 [3]	21.49 <sub>(2)</sub> , P < 0.001*	BBE - HBE: 3.98 (P < 0.001)*
10 <sup>c</sup>	CON	0.017 ± 0.004	28.8 ± 3.9 [4]		CON - HBE: -0.36 (P = 1.000)

**B.2. Bumblebee (*Bombus* spp.) abundance and species composition on the control (CON) patch in ten trials from May – September 2017.** Each bar represents the total number of bumblebee visits per species over trial days 2 and 3 of each trial (n = 36 = 2 days x 18 counts per day from 09:00-17:30). Species names are shown in the key. *Bombus terrestris* and *Bombus lucorum* are grouped due to the difficulty of separating these species in the field, see Methods, Chapter Three, section 3.3.



## Appendix C

**C.1.** Raw counts of insect species or group foraging on patches of *Rubus fruticosus* flowers with four bee exclusion treatments (no bees excluded (Control), honeybees excluded (HBE), bumblebees excluded (BBE) and both honey and bumblebees excluded (HB&BBE)) at Site 1, which was carried out in a semi-rural location north of Brighton city, UK, 20 June – 02 July 2019. The mean  $\pm$  SD and sum of half-hourly counts from 10:00 – 17:00 on all exclusion days (n = 8 trial days) are shown for each treatment patch. Insects were identified to species where possible. *Bombus terrestris* (L.) and the *B. lucorum* complex, comprising cryptic species *B. lucorum* (L.), *B. magnus* Vogt and *B. cryptarum* (Fabricius) (McKendrick et al. 2017), are grouped as *Bombus terrestris/lucorum* agg. since these could not be reliably separated in the field (Fussell & Corbet 1992). Group-level totals for each treatment are shown at the base of the table.

Group	Species	CON		HBE		BBE		HB&BBE	
		Mean $\pm$ SD	Sum	Mean $\pm$ SD	Sum	Mean $\pm$ SD	Sum	Mean $\pm$ SD	Sum
<b>Honey bee</b>	<i>Apis mellifera</i>	2.957 $\pm$ 1.733	352	0.176 $\pm$ 0.444	21	2.827 $\pm$ 1.720	328	0.367 $\pm$ 0.702	43
<b>Bumble bee (<i>Bombus</i> spp.)</b>	<i>B. hypnorum</i>	0.058 $\pm$ 0.236	7	0.151 $\pm$ 0.359	18	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0
	<i>B. lapidarius</i>	0.050 $\pm$ 0.219	6	0.344 $\pm$ 0.681	41	0.008 $\pm$ 0.092	1	0.008 $\pm$ 0.092	1
	<i>B. pascuorum</i>	0.151 $\pm$ 0.359	18	0.235 $\pm$ 0.464	28	0.043 $\pm$ 0.203	5	0.034 $\pm$ 0.182	4
	<i>B. pratorum</i>	0.008 $\pm$ 0.091	1	0.042 $\pm$ 0.201	5	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0
	<i>B. terrestris/lucorum</i> agg.	0.840 $\pm$ 0.833	100	1.142 $\pm$ 1.385	136	0.017 $\pm$ 0.130	2	0.059 $\pm$ 0.238	7
	<i>B. vestalis</i>	0.016 $\pm$ 0.129	2	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0
<b>Solitary (non-<i>Apis</i>/<i>Bombus</i>) bee</b>	<i>Andrena</i> (species unknown)	0.025 $\pm$ 0.156	3	0.008 $\pm$ 0.091	1	0.000 $\pm$ 0.000	0	0.016 $\pm$ 0.128	2
	<i>Andrena dorsata</i>	0.000 $\pm$ 0.000	0	0.033 $\pm$ 0.180	4	0.137 $\pm$ 0.414	16	0.017 $\pm$ 0.130	2
	<i>Andrena flavipes</i>	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0	0.008 $\pm$ 0.092	1	0.000 $\pm$ 0.000	0
	<i>Andrena fucata</i>	0.008 $\pm$ 0.091	1	0.000 $\pm$ 0.000	0	0.008 $\pm$ 0.092	1	0.000 $\pm$ 0.000	0
	<i>Andrena haemorrhoa</i>	0.016 $\pm$ 0.129	2	0.025 $\pm$ 0.157	3	0.008 $\pm$ 0.092	1	0.017 $\pm$ 0.184	2
	<i>Andrena nigroaenea</i>	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0	0.008 $\pm$ 0.092	1	0.000 $\pm$ 0.000	0
	<i>Andrena semilaevis</i>	0.008 $\pm$ 0.091	1	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0
	<i>Halictus tumulorum</i>	0.000 $\pm$ 0.000	0	0.000 $\pm$ 0.000	0	0.034 $\pm$ 0.183	4	0.017 $\pm$ 0.130	2



Hoverfly	<i>Lasioglossum (species unknown)</i>	0.041±0.200	5	0.066±0.250	8	0.083±0.277	10	0.150±0.358	18
	<i>Lasioglossum calceatum</i>	0.008±0.091	1	0.000±0.000	0	0.008±0.092	1	0.000±0.000	0
	<i>Lasioglossum fulvicorne</i>	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0	0.025±0.158	3
	<i>Lasioglossum morio</i>	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1	0.008±0.092	1
	<i>Osmia (species unknown)</i>	0.000±0.000	0	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0
	<i>Nomada ruficornis</i>	0.016±0.129	2	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0
	<i>Sphecodes monilicornis</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1
	<i>Hoverfly (species unknown)</i>	0.016±0.128	2	0.050±0.254	6	0.041±0.200	5	0.050±0.254	6
	<i>Chrysotoxum bicintum</i>	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0
	<i>Chrysotoxum festivum</i>	0.008±0.091	1	0.008±0.091	1	0.017±0.130	2	0.025±0.158	3
	<i>Episyrphus balteatus</i>	0.184±0.468	22	0.310±0.563	37	0.198±0.421	23	0.205±0.483	24
	<i>Eristalis tenax</i>	0.025±0.157	3	0.033±0.18	4	0.086±0.281	10	0.068±0.253	8
	<i>Eueodes corollae</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1
	<i>Eupeodes luniger</i>	0.093±0.291	11	0.252±0.555	30	0.301±0.675	35	0.324±0.569	38
	<i>Helophilus pendulus</i>	0.000±0.000	0	0.016±0.129	2	0.000±0.000	0	0.000±0.000	0
	<i>Myathropa florea</i>	0.008±0.091	1	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0
	<i>Platycherius albimanus</i>	0.050±0.219	6	0.117±0.372	14	0.043±0.203	5	0.051±0.257	6
	<i>Scaeva pyrastris</i>	0.033±0.180	4	0.025±0.157	3	0.043±0.203	5	0.017±0.130	2
	<i>Scaeva selenitica</i>	0.091±0.317	11	0.083±0.332	10	0.083±0.306	10	0.058±0.268	7
	<i>Sphaephoria scripta</i>	0.225±0.541	27	0.175±0.423	21	0.058±0.235	7	0.216±0.537	26
	<i>Sphaerophoria interrupta</i>	0.033±0.180	4	0.033±0.180	4	0.051±0.222	6	0.025±0.206	3
	<i>Syrphus ribesii</i>	0.241±0.608	29	0.416±0.784	50	0.175±0.496	21	0.341±0.692	41
	<i>Syrphus vitripennis</i>	0.000±0.000	0	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0
	<i>Volucella bombylans (b/y morph)</i>	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0
	<i>Volucella bombylans (red morph)</i>	0.000±0.000	0	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0
	<i>Volucella inflata</i>	0.000±0.000	0	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0
Non-Syrphidae fly	<i>Large fly</i>	0.025±0.156	3	0.016±0.128	2	0.008±0.091	1	0.041±0.200	5

<b>Butterfly</b>	<i>Medium fly</i>	0.100±0.327	12	0.133±0.387	16	0.066±0.282	8	0.166±0.416	20
	<i>Small fly</i>	0.033±0.180	4	0.058±0.235	7	0.058±0.235	7	0.066±0.250	8
	<i>Very small fly</i>	0.000±0.000	0	0.016±0.129	2	0.034±0.225	4	0.034±0.182	4
	<i>Aglaia urticae</i>	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1	0.000±0.000	0
	<i>Macroglossum stellatarum</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1
	<i>Maniola jurtina</i>	0.075±0.295	9	0.050±0.255	6	0.051±0.222	6	0.042±0.203	5
	<i>Satyrion w-album</i>	0.000±0.000	0	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0
	<i>Thymelicus sylvestris</i>	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1	0.000±0.000	0
	<i>Vanessa atalanta</i>	0.000±0.000	0	0.033±0.180	4	0.008±0.092	1	0.000±0.000	0
	<i>Vanessa cardui</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1
<b>Wasp</b>	<i>Vespula vulgaris</i>	0.117±0.348	14	0.243±0.450	29	0.206±0.447	24	0.273±0.519	32
	<i>Wasp (species unknown A)</i>	0.000±0.000	0	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0
	<i>Wasp (species unknown B)</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1
	<i>Wasp (species unknown C)</i>	0.000±0.000	0	0.000±0.000	0	0.008±0.092	1	0.000±0.000	0
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Honeybee		2.96±1.73	352	0.18±0.44	21	2.83±1.72	328	0.37±0.70	43
Bumblebee: all		1.13±1.03	134	1.92±1.85	228	0.07±0.25	8	0.10±0.36	12
Solitary bee: all		0.13±0.39	16	0.14±0.40	17	0.31±0.53	36	0.26±0.52	31
Hoverfly: all		1.03±1.13	123	1.56±1.32	186	1.11±1.12	129	1.41±1.45	165
Other fly: all		0.16±0.45	19	0.23±0.46	27	0.17±0.48	20	0.32±0.58	37
Butterfly/Moth: all		0.08±0.30	9	0.09±0.32	11	0.08±0.27	9	0.06±0.24	7
Wasp: all		0.12±0.35	14	0.25±0.47	30	0.22±0.45	25	0.28±0.52	33



<b>Hoverfly</b>	<i>Lasioglossum pauxillum</i>	0.025±0.204	3	0.016±0.129	4	0.016±0.128	2	0.038±0.239	3
	<i>Megachile centuncularis</i>	0.000±0.000	0	0.025±0.157	3	0.050±0.254	6	0.019±0.138	2
	<i>Megachile leachella</i>	0.008±0.091	1	0.109±0.363	13	0.433±0.817	52	0.854±1.013	88
	<i>Megachile maritima</i>	0.000±0.000	0	0.084±0.278	10	0.050±0.254	6	0.233±0.489	24
	<i>Megachile willughbiella</i>	0.075±0.295	9	0.285±0.584	34	0.166±0.436	20	0.310±0.626	32
	<i>Osmia caerulescens</i>	0.000±0.000	0	0.016±0.129	2	0.008±0.091	1	0.009±0.098	1
	<i>Chrysotoxum festivum</i>	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0	0.019±0.138	2
	<i>Episyrphus balteatus</i>	0.344±0.669	41	0.344±0.752	41	0.375±0.674	45	0.466±0.777	48
	<i>Eristalis tenax</i>	0.008±0.091	1	0.000±0.000	0	0.025±0.156	3	0.000±0.000	0
	<i>Eupeodes luniger</i>	0.033±0.180	4	0.075±0.295	9	0.041±0.200	5	0.048±0.215	5
	<i>Helophilus pendulus</i>	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0
	<i>Myathropa florea</i>	0.008±0.091	1	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0
	<i>Platycheirus albimanus</i>	0.033±0.180	4	0.000±0.000	0	0.016±0.128	2	0.019±0.138	2
	<i>Platycheirus succutus</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.009±0.098	1
	<i>Pyronia tithonus</i>	0.016±0.129	2	0.016±0.129	2	0.033±0.180	4	0.019±0.138	2
	<i>Scaeva pyrastris</i>	0.008±0.091	1	0.033±0.180	4	0.008±0.091	1	0.019±0.138	2
	<i>Scaeva selentrica</i>	0.000±0.000	0	0.033±0.180	4	0.000±0.000	0	0.019±0.138	2
	<i>Sphaerophoria scripta</i>	0.033±0.180	4	0.058±0.236	7	0.008±0.091	1	0.038±0.194	4
	<i>Syrirta pipens</i>	0.008±0.091	1	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0
	<i>Syrphus ribesii</i>	0.033±0.180	4	0.016±0.129	2	0.041±0.238	5	0.009±0.098	1
	<i>Volucella bombylans (by)</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.009±0.098	1
	<i>Volucella bombylans (r)</i>	0.016±0.129	2	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0
<b>Non-Syrphidae fly</b>	<i>Large fly</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.009±0.098	1
	<i>Medium fly</i>	0.000±0.000	0	0.016±0.129	2	0.025±0.156	3	0.016±0.129	2
	<i>Small fly</i>	0.000±0.000	0	0.000±0.000	0	0.008±0.091	1	0.048±0.215	5
	<i>Very small fly</i>	0.000±0.000	0	0.000±0.000	0	0.008±0.091	1	0.009±0.098	1
<b>Butterfly</b>	<i>Aphantopus hyperantus</i>	0.000±0.000	0	0.008±0.091	1	0.008±0.091	1	0.000±0.000	0
	<i>Pieris.rapae</i>	0.000±0.000	0	0.016±0.129	2	0.016±0.128	2	0.000±0.000	0

	<i>Pyronia tithonus</i>	0.017±0.129	2	0.033±0.180	4	0.017±0.129	2	0.019±0.139	2
	<i>Thymelicus.lineola</i>	0.000±0.000	0	0.000±0.000	0	0.000±0.000	0	0.009±0.098	1
<b>Wasp</b>	<i>Vespula vulgaris</i>	0.050±0.219	6	0.067±0.311	8	0.125±0.332	15	0.223±0.462	23
	<i>Solitary wasp</i>	0.000±0.000	0	0.000±0.000	0	0.008±0.091	1	0.000±0.000	0
Honeybee		2.60±1.45	310	0.08±0.27	9	3.79±1.50	455	0.19±0.44	20
Bumblebee: all		2.47±1.48	294	3.62±1.98	431	0.03±0.18	4	0.04±0.19	4
Solitary bee: all		1.12±1.33	133	2.20±1.92	262	2.56±1.95	307	3.22±2.16	333
Solitary bee: <i>larger-bodied</i>		0.45±0.77	54	1.37±1.43	163	1.76±1.48	211	2.40±1.56	247
Solitary bee: <i>smaller-bodied</i>		0.66±0.93	79	0.83±1.67	99	0.80±1.03	96	0.85±1.09	85
Hoverfly: all		0.55±0.88	65	0.57±1.00	68	0.52±0.83	62	0.66±1.02	68
Other fly: all		0.00±0.00	0	0.02±0.13	2	0.04±0.20	5	0.09±0.28	9
Butterfly/Moth: all		0.02±0.13	2	0.04±0.20	5	0.06±0.30	7	0.03±0.17	3
Wasp: all		0.05±0.22	6	0.07±0.31	8	0.13±0.34	16	0.22±0.46	23

**C.3.** Mean petal area and diversity indices of flower-rich habitat types within a 500 m radius area surrounding the trial sites. Habitat types shown were verified to have flowers present and are shown as a percent of the overall *flowers available* area within each site. *Flowers available* habitat comprised 74.7% of the 500 m radius area surrounding Site 1 and 22.9% at Site 2. Using quadrat data, mean petal area (mm<sup>2</sup>) per 1 m<sup>2</sup> quadrat, Shannon-Wiener H' diversity, species richness (S<sub>Q</sub>) and Pielou's evenness index (*J'*) are shown for habitat types that were possible to survey. Overall species richness per habitat type (using transect data) is also shown (S<sub>T</sub>). Where "na" is written, flower surveys were not possible due to access restrictions. The final column shows the three species with the greatest petal area within surveyed habitats.

Trial	Habitat type (% <i>flowers available</i> area)	Mean petal area (mm <sup>2</sup> )/1m <sup>2</sup> quadrat (n quadrats)	Diversity (H')	Species richness (quadrats; S <sub>Q</sub> )	Species richness (transects; S <sub>T</sub> )	Species evenness ( <i>J'</i> )	Species with greatest proportion of petal area (%)
Trial 1	Field margin (2.8%)	5723.6 (40)	1.415	25	69	0.440	<i>Rubus fruticosus</i> L. agg. (67.6) <i>Trifolium repens</i> L. (7.8) <i>Ranunculus repens</i> L. (6.6)
	Unimproved grassland (57.9%)	9279.5 (40)	0.640	16	21	0.231	<i>Trifolium repens</i> L. (85.7) <i>Lotus corniculatus</i> L. (7.5) <i>Lotus pedunculatus</i> Cav. (2.6)
	Site field (4.4%)	7981.9 (25)	0.684	24	53	0.215	<i>Leontodon hispidus</i> L. (38.2) <i>Lotus corniculatus</i> L. (17.7) <i>Rubus fruticosus</i> L. agg. (14.3)
	Woodland (28.9%)	1447.5 (40)	1.422	5	11	0.884	<i>Sanicula europaea</i> L. (52.3) <i>Geranium robertianum</i> L. (46.6) <i>Geum urbanum</i> L. (0.7)
	Residential gardens (6.1%)	na	na	na	na	na	na
Trial 2	Field margin (2.1%)	1160.0 (20)	1.725	11	29	0.719	<i>Rubus fruticosus</i> L. agg. (46.2) <i>Senecio jacobaea</i> L. (12.2) <i>Achillea millefolium</i> L. (12.2)
	Site field [urban greenfield] (6.6%)	15208.9 (20)	1.926	14	42	0.730	<i>Daucus carota</i> L. (32.3) <i>Calystegia sepium</i> L. (19.2)

Woodland (12.7%)	82.8 (20)	0.841	3	8	0.765	<i>Galium verum</i> L. (16.2) <i>Convolvulus arvensis</i> L. (56.9) <i>Cirsium arvense</i> L. (38.0) <i>Senecio jacobaea</i> L. (5.1)
Nature Reserve (6.1%)	12847.1 (15)	1.963	17	27	0.693	<i>Trifolium pratense</i> L. (28.7) <i>Crepis vesicaria</i> L. (18.6) <i>Ononis repens</i> L. (9.9)
Flowery road verge (8.3%)	17926.3 (15)	2.286	20	53	0.763	<i>Lotus corniculatus</i> L. (22.0) <i>Trifolium repens</i> L. (20.5) <i>Trifolium pratense</i> L. (16.0)
Residential gardens (32.4%)	na	na	na	na	na	na
Other urban greenspace (15.5%)	na	na	na	na	na	na
Urban greenfield (10.3%)	na	na	na	na	na	na
Cliff face (6.1%)	na	na	na	na	na	na

## Appendix D

**D.1.** Garden centre customer questionnaire results. Proportions of all (n = 150) participants answering each question are shown, as well as proportions of Male (n = 32) and Female (n = 118) shown separately in the final two columns.

Question	Answer	% overall (n=150 unless otherwise stated)	% Male (n=32)	% Female (n=118)
1. What is your age?	16-25	2.0	0.7	1.3
	26-35	2.7	1.3	1.3
	36-45	2.7	0	2.7
	46-55	14.7	1.3	13.3
	56-65	26.7	4.0	22.7
	66+	51.3	14.0	37.4
2. What is your gender?	Male	21.3	-	-
	Female	78.7	-	-
	Prefer not to say	0	-	-
3. Do you have an outside space in which to grow plants? <i>Please tick <b>all that apply</b>.</i>	Yes, a garden	94.7	20.0	74.7
	Yes, an outside space ( <i>eg. communal space, allotment, window boxes, pots</i> )	8.0	2.0	6.0
	No	0.7	0	0.7
4. What is the purpose of your visit today?	By plants or seeds/bulbs	56.7	11.3	45.3
	Buy other gardening items ( <i>eg. tools, fertiliser, garden furniture</i> )	22.0	4.7	17.3
	Buy other items not connected to gardening/gardens ( <i>eg. a gift, food items</i> )	16.0	3.3	12.7
	Leisure ( <i>eg. having a browse, meeting at the café</i> )	52.0	9.3	42.7
5. When you are buying plants do you most often look for: <i>Tick <b>one box</b> (n=138)</i>	Ornamental plants with flowers ( <i>e.g. bedding plants/perennials</i> )	68.1 (n=138)		
	Vegetable/fruit plants	7.2		
	Trees or shrubs	19.6		
	Indoor plants	5.1		
6. When you are buying flowering plants, what do you generally consider the <b>three</b> most important features <b>apart from price</b> ? <i>Tick <b>three boxes</b> (n=145)</i>	Length of flowering	55.1 (n=145)		
	Hardiness/low level of maintenance	55.9		
	Attractiveness to humans	22.8		
	Bee- or Pollinator-friendly	53.1		
	Specific colour	26.9		
	Size	21.4		



	Time of year when it blooms	43.4		
7. Does the decline of wildlife in Britain concern you?	Yes	97.3		
	No	1.3		
	I didn't know that our wildlife was in decline	1.3		
8. Do you do anything in your garden or outside space to help wildlife?	Yes	96.7		
	No	3.3		
9. Thinking about bees and other pollinators, do you think they are beneficial to your garden or outside area?	Yes	97.3		
	No	1.3		
	I don't know	1.3		
10. How do you help bees and other pollinators in your outdoor area? <i>Tick all that apply to you</i>	Put up 'bee hotels'	19.3		
	Use limited or no pesticides	64.0		
	Grow bee-friendly and pollinator-friendly plants	77.3		
	Provide flowers throughout the year	57.3		
	Leave some areas unmown/unmanaged	37.3		
	I don't currently help bees/pollinators	2.7		
11. Do you know that some flowers are much more attractive to bees than others?	Yes	98.7		
	No	1.3		
12. Are you familiar with 'pollinator-friendly' labels, such as the RHS "Perfect for Pollinators"?	Yes	59.3		
	No	40.7		
12(i). Are you familiar with 'pollinator-friendly' labels, such as the RHS "Perfect for Pollinators"? (n=53, subset of 53 people who thought garden centres offer enough information about which plants are good for pollinators [Q16: Yes])	Yes	71.7 (n=53)		
	No	28.3		
13. Do you think these labels are reliable sources of information	Yes	70.7		
	No	2.7		
	I don't know	26.7		
13(i). Do you think these labels are reliable sources of information (n=89; subset of 89 people who were familiar with pollinator-friendly labels [Q12: Yes])	Yes	87.6 (n=89)		

	No	1.1		
	I don't know	11.2		
14. If a plant has a 'pollinator-friendly' label would you be more inclined to buy that plant?	Yes	64.0		
	No	4.0		
	Maybe	32.0		
15. Do you think the labels are visible enough?	Yes	51.3		
	No	48.7		
15(i). Do you think the labels are visible enough? (n=89; subset of 89 people who were familiar with pollinator-friendly labels [Q12: Yes])	Yes	74.2 (n=89)		
	No	25.8		
16. Do you think garden centres offer enough information about which plants are good for bees and other pollinators?	Yes	35.3	8.7	26.7
	No, and it would be useful to have more information	50.0	10.0	40.0
	No, but I don't mind	2.0	-	2.0
	I don't know	12.7	2.7	10.0
17. Do you ever ask the staff for advice about suitable plants for bees and other pollinators?	Yes	23.3	4.7	18.7
	No	76.7	16.7	60.0
18. Any further comments about pollinator-friendly plants	.....	...	...	...

- |                      |       |       |       |       |       |     |
|----------------------|-------|-------|-------|-------|-------|-----|
| 1) What is your age? | 16-25 | 26-35 | 36-45 | 46-55 | 56-65 | 66+ |
|----------------------|-------|-------|-------|-------|-------|-----|

2) What is your gender?	Male	Female	Prefer not to say
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3) Do you have an outside space in which to grow plants? *Please tick **all that apply**.*

Yes, a garden

Yes, an outside space (eg. communal space, allotment, window boxes, pots)

No

4) What is the purpose of your visit today? *Please tick **all that apply***

Buy plants or seeds/bulbs

Buy other gardening items (eg. tools, fertiliser, garden furniture)

Buy other items not connected to gardening/gardens (eg. a gift, food items)

Leisure (eg. having a browse, meeting at the café)

5) When you are buying plants do you most often look for: *Tick **one box***

Ornamental plants with flowers (e.g. bedding plants/perennials)

Vegetable/fruit plants

Trees or shrubs

Indoor plants

6) When you are buying flowering plants, what do you generally consider the **three** most important features **apart from price**? *Tick **three boxes***

Length of flowering

Hardiness/low level of maintenance

Attractiveness to humans

Bee- or Pollinator-friendly

Specific colour

Size

Time of year when it blooms

7) Does the decline of wildlife in Britain concern you?

Yes

No

I didn't know that our wildlife is in decline

8) Do you do anything in your garden or outside space to help wildlife?

Yes

No

9) Thinking about bees and other pollinators, do you think they are beneficial to your garden or other outdoor area?

Yes	No	I don't know
-----	----	--------------

- 10) How do you help bees and other pollinators in your outdoor area? *Tick **all that apply to you***

Put up 'bee hotels'  
 Use limited or no pesticides  
 Grow bee-friendly and pollinator-friendly plants  
 Provide flowers throughout the year  
 Leave some areas unmown/unmanaged  
 I don't currently help bees/pollinators

- 11) Do you know that some flowers are much more attractive to bees than others?

Yes  
 No

- 12) Are you familiar with 'pollinator-friendly' labels, such as the RHS "Perfect for Pollinators"?

Yes  
 No

- 13) Do you think these labels are reliable sources of information?

Yes  
 No  
 I don't know



- 14) If a plant has a 'pollinator-friendly' label would you be more inclined to buy that plant?

Yes  
 No  
 Maybe

- 15) Do you think the labels are visible enough?

Yes  
 No

- 16) Do you think garden centres offer enough information about which plants are good for bees and other pollinators?

Yes  
 No, and it would be useful to have more information  
 No, but I don't mind  
 I don't know

- 17) Do you ever ask the staff for advice about suitable plants for bees and other pollinators?

Yes  
 No

- 18) Any further comments about pollinator-friendly plants:

.....

.....

.....

.....

### D.3. Customer information sheet, given to each participant in questionnaires and interviews.



#### Surveys and interviews of Garden Centre customers: what are we doing and why?

This document provides further information about a research study conducted by the Laboratory of Apiculture and Social Insects (LASI) (<http://www.sussex.ac.uk/lasi/>) in the School of Life Sciences at the University of Sussex. The project is part of the research of PhD student Veronica Wignall, whose PhD is supervised by Professor Francis Ratnieks.

The aim of this study is to understand the role of garden centres in providing 'pollinator-friendly' plants, as well as advice and information about helping bees and other pollinators in gardens.

Bees in our urban and rural areas need flowers to survive, since nectar and pollen are their main food supply. However, our previous research has shown that flowers can vary 100-fold in the number of pollinators they attract (1). Furthermore, many ornamental plants with flowers are actually not attractive to bees and other pollinating insects.

At LASI we have shown that there is great potential for urban gardens and parks to support pollinators through planting plant varieties that are attractive to bees and other insects. Garden centres could play a key role in this by selling such varieties, and by providing advice and information to customers who wish to help our urban spaces become more pollinator-friendly.

As the first step in this project, we want to quantify customer demand for pollinator-friendly plants, via a questionnaire survey of approximately 150 people visiting garden centres in Sussex. We then hope to deepen our understanding of peoples' attitudes towards pollinators and pollinator-friendly plants through approximately 20 face-to-face interviews of regular visitors to garden centres.

We then hope to work with centres to provide science-based advice for providing pollinator-friendly plants and evidence-based information to customers. In the long term, this information could enable garden centres throughout the UK to help the public make their gardens more bee- and pollinator-friendly.

**\*\* This research project has been approved by the Sciences & Technology Cross-Schools Research Ethics Committee (C-REC) - [crecsitec@sussex.ac.uk](mailto:crecsitec@sussex.ac.uk) \*\***

Should you wish to contact LASI for further information, please contact Veronica Wignall, [v.wignall@sussex.ac.uk](mailto:v.wignall@sussex.ac.uk) or tel: 01273 872587

Thank you for your time.

1) Garbuzov M and Ratnieks FLW (2013) *Functional Ecology* 28(2): 364-374.

**D.4.** Semi-structured interview format in three sections. Researcher questions are in italics and prefixed with ‘*Researcher:*’.

-----  
-----  
**Semi-structured interview – Garden Centre customers**

*Researcher:* Before starting this interview, I’d like to make it clear that I will be recording our conversation. Is that ok?

-----  
-----

**Section 1:** *Preamble and survey*

[A]

- i) Roughly how often do you visit garden centres?
- ii) Would you say this is the centre you normally visit?

[B] *Customer Survey*

*Researcher:* Please answer the Customer Survey with no input from me/the researcher. This should take roughly 3-5 minutes.

-----  
-----

**Section 2:** *Based on questions from customer survey*

*Researcher:* Looking at your responses to the Customer Survey, there are a few questions I’d like to explore in more detail.

6) When you are buying flowering plants, what do you generally consider the **three** most important features **apart from price**?

*Researcher:* Could you tell me a little about why you selected these options?

8) Do you do anything in your garden or outside space to help wildlife?

*Researcher:* Could you tell me in brief how you help wildlife in your outside area? Is there any specific wildlife you particularly like to encourage - why?

9) Thinking about bees and other pollinators, do you think they are beneficial to your garden or other outdoor area?

*Researcher:* [If yes] Why/how? [If no] Why not?

11) Do you know that some flowers are much more attractive to bees than others?

*Researcher:* [If yes] Do you know why this is?

12) Are you familiar with ‘pollinator-friendly’ labels, such as the RHS “Perfect for Pollinators”?

*Researcher:* I’ve got a sheet here with some labels on [see supplementary materials]. Could you tick the boxes next to all the logos you recognise or are familiar with?

13) Do you think these labels are reliable sources of information?

*Researcher:* Any further comments about your answer to this question?

14) If a plant has a ‘pollinator-friendly’ label would you be more inclined to buy that plant?

*Researcher:* Why have you answered yes/no/maybe?

15) Do you think the labels are visible enough?

*Researcher:* Any further comments about your answer to this question?

16) Do you think garden centres offer enough information about which plants are good for bees and other pollinators?

*Researcher:* Regarding your answer to this question, why have you responded with XXX?

-----  
-----

### **Section 3:** *Exploring further topics*

*Researcher:* Following on from the Customer Survey, there are a couple of related questions I'd like to ask.

1. Has your awareness of/interest in bees and other pollinators/pollinator-friendly plants changed over time? If so, could you tell me a little more about this?
2. Where do you think you receive most information about pollinators?

## Appendix E

### E.1 Survey information and consent to participate.

Title of Project: Underappreciated British flowering plants for flower-visiting insects

Name of Researcher and School: Veronica Wignall, Life Sciences

C-REC Ref no: ER/VW58/6

This online survey asks questions about British wildflowers. Participation time is approx. 15 minutes. Thank you for your participation.

Information: You are being invited to take part in a research study to further our understanding of perceptions of wild plants and pollinators. Thank you for carefully reading this information. This study is being conducted by student researcher Veronica Wignall from the School of Life Sciences, University of Sussex, who is happy to be contacted (v.wignall@sussex.ac.uk) if you have any questions.

This research has been approved ([ER/VW58/6]) by the Sciences & Technology Cross-Schools Research Ethics Committee (C-REC). If you have any ethical concerns, please contact the ethics chair (crecscitec@sussex.ac.uk).

The University of Sussex has insurance in place to cover its legal liabilities in respect of this study

- ☐ I am over 18 years of age
- ☐ I consent to completing an online questionnaire
- ☐ I understand that the answers I provide will be used in a PhD thesis chapter and possibly a published article
- ☐ I consent to the use of anonymised quotes in publications from the research
- ☐ I understand that any information I provide is confidential, and that no information that I disclose will lead to the identification of any individual in the reports on the project, either by the researcher or by any other party
- ☐ I consent to the processing of my personal information and data for the purposes of this research study. I understand that such information will be treated as strictly confidential and handled in accordance with the General Data Protection Regulation (GDPR) 2016.
- ☐ I understand that my participation is voluntary, that I can choose not to complete the survey without being penalised or disadvantaged in any way nor do I have to give reasons for this. I understand that the survey is anonymous and therefore it will be impossible to withdraw my data once I have submitted the survey.
- ☐ I consent to my data being deposited in the UK Data Archive for re-use in future research and analysis. I understand that it will be fully anonymised before deposit.
- ☐ I agree to take part in the above University of Sussex research project

Please write your name to confirm that you consent to participating in the survey:

.....



## E.2 Survey questions and response options, Sections 1-3.

### Section 1. About you (pre-lockdown!)

*This part of the survey asks questions about you. Please give answers that relate to your life \*as normal\*, not during Covid-19 lockdown.*

1. What is your age?	18-25; 26-35; 36-45; 46-55; 56-65; 66-75; 76-85; 86+
2. How would you describe your gender?	Female; Male; Prefer to self-describe; Prefer not to say
3. How would you describe the area where you live now?	City centre; City suburbs; Town centre; Town suburbs; Rural area
4. Do you own or have regular access to (select all that apply):	none; patio; garden; allotment; garden and allotment
5. How often do you partake in gardening or growing, approximately?	Never; Rarely; Monthly; A few times a month; Once a week; 2-3 times a week; Daily
6. Have you ever worked in a role with an environmental or horticultural focus, for example: Landscape design, garden centres, farming, greenspace management, wildlife conservation, natural sciences researcher, ecological consultancy, environmental education?	Yes; No; Other (...)
7. What is your most recent level of education?	Postgraduate University degree or equivalent; Undergraduate University degree or equivalent; College or further education; School; Other (...)
8. How would you rank your personal level of interest in nature, on a scale of 0-10? (0 = no interest, 10 = extremely strong interest)	0, 1, 2, 3, 4, 5, 6, 7, 8, 9, 10

### Section 2.

9. How much do you like this flowering plant? [primrose]	1. I strongly dislike it; 2. I somewhat dislike it; 3. Neutral, neither like nor dislike; 4. I quite like it; 5. I strongly like it
10. Without taking too long, write down up to three words that come to mind to describe this plant? (Not the name!) [primrose]	..., ..., ...
11-20. Questions 9 & 10 Repeated for (11-12) bramble, (13-14) bluebell, (15-16) ivy, (17-18) dandelion and (19-20) daffodil	
21. Select TWO plants you think are the most beneficial to wildlife, including flower-feeding insects: (please select TWO options)	Primrose; Bramble, Bluebell, Ivy, Dandelion; Daffodil
22. Select any plants you think of as weeds or 'nuisance': (select as many options as you like)	Primrose; Bramble, Bluebell, Ivy, Dandelion; Daffodil

### Section 3.

23. Write the name of this flowering plant in the space below the photo: (or write e.g. 'not sure').	...
24-28. Question 23 Repeated for (24) bramble, (25) bluebell, (26) ivy, (27) dandelion and (28) daffodil	

**E.3.** Species profiles for bluebell, bramble, daffodil, dandelion, ivy and primrose. Profiles are made up of the 20 words most commonly given by participants in response to the question: *‘Without taking too long, write down up to three words that come to mind to describe this plant? (Not the name)’*. The frequency of occurrence for each word is given in parentheses. Words are grouped into one or more of ten categories representing key factors involved in wildflower perception (see Appendix E.5), shown in the final column. Species names, prominent colours (*e.g.* for bluebell: blue and purple) and the word ‘flower(s)’ and ‘wildflower(s)’ were removed.

Species	Word	Perception root category
Bluebell	Spring (483)	Other
	Woodland (376)	Other
	Woods (202)	Other
	Pretty (122)	Aesthetic
	Beautiful (100)	Aesthetic
	Carpet (100)	Aesthetic
	Scent (92)	Sensory
	Colour (84)	Aesthetic
	Delicate (84)	Aesthetic
	Colourful (77)	Aesthetic
	Native (64)	Ecological
	Wild (56)	Ecological
	English (39)	Ecological/Traditional
	Childhood (38)	Personal
	Scented (37)	Sensory
	Springtime (36)	Other
	Walks (35)	Personal/Other
	Fragrant (34)	Sensory
	Bees (33)	Ecological
	Fairies (31)	Culture
Bramble	Prickly (261)	Practical
	Fruit (234)	Food, foraging and health (human)
	Wild (207)	Ecological
	Bees (116)	Ecological
	Thorns (109)	Practical
	Thorny (100)	Practical
	Pretty (94)	Aesthetic
	Berries (85)	Food, foraging and health (human)
	Invasive (77)	Practical
	Hedgerows (71)	Other
	Summer (68)	Other
	Blackberries (67)	Food, foraging and health (human)
	Autumn (61)	Other
	Spiky (58)	Practical
	Delicate (54)	Aesthetic
	Natural (52)	Ecological
	Prickles (49)	Practical
	Jam (47)	Food, foraging and health (human)

	Blossom (46)	Other
	Food (44)	Food, foraging and health (human)
Daffodil	Spring (961)	Other
	Bright (173)	Aesthetic
	Bulb (132)	Other/Practical
	Cheerful (122)	Psychological
	Happy (118)	Psychological
	Easter (116)	Traditional/Cultural/Personal
	Trumpet (115)	Other
	Wales (99)	Traditional
	Garden (59)	Personal/Practical
	Springtime (57)	Other
	Wordsworth (48)	Cultural
	Sunshine (46)	Other
	Hope (42)	Psychological
	Pretty (42)	Aesthetic
	Colourful (41)	Aesthetic
	Sunny (39)	Aesthetic
	Beautiful (38)	Aesthetic
	Colour (37)	Aesthetic
	Early (37)	Other
	Fresh (23)	Other
Dandelion	Bees (368)	Ecological
	Weed (305)	Practical
	Bright (199)	Aesthetic
	Clock (147)	Other/Traditional
	Spring (89)	Other
	Lawn (78)	Practical
	Wild (72)	Ecological
	Food (66)	Food, foraging and health (human)
	Sunny (63)	Other
	Cheerful (59)	Psychological
	Sunshine (59)	Other
	Colourful (56)	Aesthetic
	Happy (56)	Psychological
	Childhood (55)	Personal
	Seeds (52)	Other
	Common (49)	Practical/Other
	Pretty (45)	Aesthetic
	Edible (40)	Food, foraging and health (human)
	Invasive (39)	Practical
	Insects (37)	Ecological
Ivy	Bees (160)	Ecological
	Spiky (94)	Aesthetic
	Interesting (93)	Aesthetic
	Unusual (73)	Aesthetic

	Alien (70)	Aesthetic
	Insects (64)	Ecological
	Christmas (62)	Traditional/Cultural
	Invasive (61)	Practical
	Climbing (57)	Practical
	Birds (55)	Ecological
	Boring (49)	Aesthetic
	Winter (43)	Other
	Autumn (41)	Other
	Berries (40)	Ecological
	Nectar (38)	Ecological
	Food (37)	Ecological
	Waxy (37)	Aesthetic
	Ugly (33)	Aesthetic
	Glossy (32)	Aesthetic
	Shiny (31)	Aesthetic
Primrose	Spring (678)	Other
	Pretty (363)	Aesthetic
	Delicate (141)	Aesthetic
	Fresh (134)	Aesthetic
	Bright (121)	Aesthetic
	Cheerful (97)	Psychological
	Happy (73)	Psychological
	Beautiful (68)	Aesthetic
	Small (67)	Other
	Woodland (61)	Other
	Sunshine (51)	Other
	Springtime (48)	Other
	Sunny (47)	Aesthetic
	Wild (44)	Ecological
	Colourful (44)	Aesthetic
	Bees (41)	Ecological
	Early (37)	Other
	Pale (36)	Other
	Colour (32)	Aesthetic
	Garden (29)	Personal/Practical

**E.4.** Categories showing underlying factors involved in perception of wildflowers, identified through 235 unique words and short phrases given by 10 or more respondents in response to the question: ‘*Without taking too long, write down up to three words that come to mind to describe this plant? (Not the name)*’. Examples are given for each category. Words may be associated with several categories simultaneously. Common overlaps between categories are mentioned.

<b><i>Perception root category</i></b>	<b>Description</b>
<i>Aesthetic</i>	Words describing visual appearance ( <i>e.g.</i> ‘pretty’, ‘attractive’, ‘ugly’, ‘colourful’, ‘messy’)
<i>Cultural and socio-cultural</i>	Words referring to beliefs ( <i>e.g.</i> religious festivals such as ‘Easter’), values, customs, or other cultural references such as the arts ( <i>e.g.</i> poetry) or folklore ( <i>e.g.</i> ‘magical’, ‘fairy’). Also included are any mentions of organisations that use the wildflowers as emblems, for example ‘Marie Curie’ for daffodil; these may overlap with <i>Personal</i> <i>Sociocultural</i> words are included here that refer to societal norms ( <i>e.g.</i> ‘neighbours’)
<i>Food, foraging and health (human)</i>	Words relating to plants used for (human) food ( <i>e.g.</i> ‘berries’, ‘[dandelion] coffee’, ‘fruit’) and health-related words linked to consuming or exposure to parts of the plant ( <i>e.g.</i> ‘Vitamin C’, ‘allergic’) Some overlap with <i>Cultural</i> ( <i>e.g.</i> cuisine such as ‘crumble’), <i>Traditional</i> ( <i>e.g.</i> foraging traditions such as ‘blackberrying’) and <i>Sensory</i> ( <i>e.g.</i> ‘tasty’, ‘delicious’)
<i>Ecological</i>	Words related to ecology or ecological value ( <i>e.g.</i> ‘natural’, ‘bees’, ‘nectar’, ‘wild’, ‘birds’, ‘bee-friendly’)
<i>Personal</i>	Including any mention of memories, personal experience ( <i>e.g.</i> ‘childhood’), a relationship such as ‘friends’ or ‘mum’, or a specific person or place
<i>Practical</i>	Relating to practical or functional considerations, for example terminology relating to garden or gardening ( <i>e.g.</i> ‘lawn’, ‘invasive’, ‘weed’, ‘climber’), and references to plant qualities that have practical consequences ( <i>e.g.</i> ‘thorny’, ‘strangling’, ‘pervasive’, ‘taproot’)
<i>Psychological</i>	Incorporating words linked to mental or emotional state, such as ‘happy’, ‘sad’, ‘hope’, and including phobias ( <i>e.g.</i> ‘tryptophobia’)
<i>Sensory</i>	Including any reference to senses (other than visual, incorporated in <i>Aesthetic</i> ), for example ‘smell’, ‘fragrance’. There is overlap with <i>Food, foraging and health (human)</i> ( <i>e.g.</i> ‘tasty’, ‘delicious’)

<i>Traditional</i>	Including references to traditions, including behaviours such as time-telling with dandelion clocks. Also including older traditional names for wildflowers such as ‘wet-the-bed’ for dandelion and ‘fairy bonnets’ for bluebell. Often linked to or synonymous with <i>Culture</i> (e.g. ‘Christmas’)
<i>Other</i>	Any associative words not considered to affect perceptions (e.g. ‘pale’, ‘small’, ‘bell-shaped’)

