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

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Abstract. 1. Bramble (*Rubus fruticosus* L. agg.) is a common summer-flowering plant native to the United Kingdom. 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.

2. Regional surveys of insect groups at seven sites across 2 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 flies (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).

3. 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*).

4. 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.

5. Bramble was present in 54 out of 60 200 × 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.

6. 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. Wherever conflicts of interest and management strategies allow, bramble should be maintained and promoted for wildlife and insect conservation.

Key words. *Apis mellifera*, bumblebees, foraging ecology, insect conservation, pollen analysis.

Introduction

Bramble (*Rubus fruticosus* Linnaeus agg.; Rosaceae), also known as blackberry, is an aggregate group of over 300 closely related microspecies (Rose, 1981; Clapham et al., 1987) that are widespread and common throughout the United Kingdom 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 importance.
significance subject to major control efforts (Australian Government Department of the Environment and Heritage & the CRC for Australian Weed Management, 2003).

In the United Kingdom, bramble has cultural value due to the long tradition of collecting the blackberry fruits produced by the plants in early autumn. Nevertheless, 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 12 plant ‘ths’ that thrive in nitrogen-rich road verges and outcompete other native wildflowers (Plantlife, 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. Eastbourne Borough Council, 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 (e.g. RHS, 2019). In contrast, pro-environmental organisations such as the 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, 2020). 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 (NE, 2011; CFE, 2019; DEFRA, 2020).

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 et al., 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 et al., 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; Ballock et al., 2019) including bees (Goulson et al., 2005; Falk & Lewington, 2015), butterflies (Sparks & Parish, 1995; Corbet, 2000; Tudor et al., 2004), hoverflies (Drapple & Drabble, 1927; Lucas et al., 2018) and non-syrphid Diptera (Drapple & Drabble, 1927). Rubus fruticosus has a long flowering period, which typically extends from May to September in the United Kingdom (Streeter et al., 2009; Baude et al., 2016) although flowers can be found into November (V.W. and F.R., 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 et al., 2014; Balfour et al., 2018). Yet, 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 United Kingdom are undergoing widespread declines that are often linked, among other interacting factors, to the loss of flowers on a landscape scale (e.g. 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 United Kingdom 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 (Ballock 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 multidimensional picture of the value of R. fruticosus to summer-flying 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, and regional, group-level, insect surveys that covered a wide area over Sussex. 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 et al., 2014) and can serve as an indicator for surveying foraging conditions for flower-visiting insects more broadly (Balfour et al., 2015).

Materials and methods

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

In each insect survey, we recorded 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°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), could not be reliably separated in the field, so were grouped and recorded as Bombus terrestris/lucorum agg.

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°15′17.8″N, −0°10′20″5W). The rural site was north of Brighton, in a meadow near Falmer village (50°8′70″43″N, −0°8′47″89″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 1 or 2 days in the early, middle and late stages of the main bramble bloom period (rural: 6 June, 21 June and 5 and 6 July; urban: 13 and 15 June, 26 and 27 June and 12 and 13 July). Each rural survey was conducted approximately 1 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 11 am to 12 pm 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-min 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 min 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, 2014a). 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 (Supporting Information Table S1); 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 Supporting Information Tables S1 and S2. Data were pooled across surveys for each site to show the overall range of insects visiting bramble flowers over the main flowering season.

Insects were identified to species where possible by V.W., who is experienced in insect identification and H.N., N.A., A. S. and T.G. who received additional training by V.W. prior to the study. 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 Lasiosglossum were relatively common. Nonetheless, 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 (two to three 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 underestimated the proportion of pollen foragers as some bees may have only just commenced foraging at the time of observation.

We calculated a Shannon–Weiner (H’) diversity index for the early, middle and late stages of blooming in the rural and urban site using the standard equation:

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

where \( p_i/N \) 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–Weiner 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 (Supporting Information Table S2).

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 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°01754′W, rural: 50°97149′W, 0°03299′W).
Lepidoptera are described as butterflies (2014a). No moths were seen in any surveys; therefore, (Lepidoptera), beetles and wasps, following Garbuzov & Ratnieks 2014b. Surveys were made between July and September 2018 in 10 randomly generated squares hereafter. No moths were seen in any surveys; therefore, Lepidoptera are described as butterflies hereafter.

Local R. fruticosus agg. 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, 2014b. Surveys were made between July and September 2018 in 10 randomly generated 200 × 200 m² 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 × 2 km, each with 100 200 × 200 m² (Fig. 1 a, b). In Brighton city, each 4 × 4 km area comprised 400 200 × 200 m² (Fig. 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. 1; Supporting Information Table S3). 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 × 200 m² 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.

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.

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. Although 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 et al., 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 R. 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).

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°7824’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

Figure 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 × 2 km each with 100 200 × 200 m². In Brighton, grids were 4 × 4 km each with 400 200 × 200 m². The 10 randomly selected squares that were surveyed for the presence or absence of bramble are in black. [Color figure can be viewed at wileyonlinelibrary.com]
have any effect on pollen collection. Hives were in two or three 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 et al., 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 2.5 g from the frozen sample of pellets by shaking this into a new vial, ensuring that the 2.5 g 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, we 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 and 30 μm diameter, and with a smooth non-striate, non-granular surface were defined as R. fruticosus (Sawyer, 2006). Following analysis of 10 grey pellets, if five or more of these were not bramble, we tested 10 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 Supporting Information Methods S2 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 1), it was assumed that there were no false negatives (i.e., non-grey bramble pellets) in our samples.

R. fruticosus (raspberry) pollen grains are very similar to those of R. fruticosus (Sawyer, 2006). Although in our regular transect walks during the study period (see Methods section), 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 × 8 m long) in just two transects compared to R. fruticosus which was abundant in every transect (n = 23 transects, see Results section), suggesting that R. idaeus was extremely uncommon in comparison: false positives from R. idaeus were therefore assumed to be close to 0%.

Statistical analysis

Each low-resolution survey of 100 insects was treated as a ‘community’ for analysis, following Garbuzov & Ratnieks (2014b). 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 (Oksanen et al., 2019). Community similarity (%) was quantified as (1 - Bray–Curtis dissimilarity index)*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 (Brighton, Hailsham, Lewes, Uckfield) using a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017), with the adonis function from the R package vegan (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 R Studio Version 1.1.463. Values are given as mean ± SD unless stated otherwise.

Results

Detailed insect surveys (400 insects)

Honeybees and bumblebees were the most abundant groups in the detailed insect surveys, each comprising 30–40% 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). 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 ± SD, 12.12 ± 19.86 individuals, 1.0%; rural, 14.83 ± 19.84, 1.2%; Fig. 3). The most species-rich genera were
Table 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 and 15 June; 26 and 27 June; 12 and 13 July, \( n = 1168 \) insects in total; rural: 6 June; 21 June; and 5 and 6 July, \( n = 1200 \)). Bees, butterflies, beetles and wasps were identified to species. Hoverflies and non-Syrphid flies were identified to species where possible, and to genus where this was not possible. Proportion (%) is given for both the overall genus and species within genera where both data are shown.

| Group          | Genus and Species                  | Brighton urban | Brighton rural |
|----------------|------------------------------------|----------------|---------------|
|                |                                    | Count | Proportion (%) | Count | Proportion (%) |
| *Apis mellifera* L. | 409 [177] 35 | 406 [67] 33.8 |
| *Bombus* spp.   |                                    | 456 39 | 364 30.3 |
| *B. hortorum* (L.) | 1 0.1 | 10 0.8 |
| *B. humilis Illiger* | 7 0.6 | 0 0 |
| *B. hypnorum* (L.) | 17 (4) 1.5 | 53 (2) 4.4 |
| *B. lapidarius* (L.) | 32 (1) 2.7 | 34 (1) 2.8 |
| *B. pascuorum* (Scopoli) | 113 9.7 | 83(1) 6.9 |
| *B. pratorum* (L.) | 1 0.1 | 70 5.8 |
| *B. terrestris/lucorum agg.* | 282 (2) 24.1 | 113 (6) 9.4 |
| Bee: Other      |                                    | 5 0.4 | 0 0 |
| *Megachile* centuncularis (L.) | 3 0.3 | 0 0 |
| *Megachile willughbiella* (Kirby) | 2 0.2 | 0 0 |
| *Andrena*      | 78 6.7 | 25 2.1 |
| *Andrena bicolor* Fabricius | 1 0.1 | 0 0 |
| *Andrena cineraria* (L.) | 0 0 | 1 0.1 |
| *Andrena dorsata* (Kirby) | 41 3.5 | 18 1.5 |
| *Andrena flavipes* Panzer | 11 0.9 | 0 0 |
| *Andrena fucata* Smith | 6 0.5 | 0 0 |
| *Andrena haemorrhoea* (Fab.) | 10 0.9 | 5 0.4 |
| *Andrena minutula* (Kirby) | 1 0.1 | 0 0 |
| *Andrena scotica* Perkins | 1 0.1 | 0 0 |
| *Andrena subopaca* Nylander | 0 0 | 1 0.1 |
| *Andrena* (unknown) | 7 0.6 | 0 0 |
| *Lastoglossum* | 70 6.0 | 38 3.2 |
| *Lastoglossum calceatum* (Scop.) | 6* | 2* |
| *Lastoglossum fulvicorne* (Kirby) | 1* | 2* |
| *Lastoglossum malachurum* (Kirby) | 0 | 1* |
| *Lastoglossum morio* (Fab.) | 0 | 1* |
| *Lastoglossum pauxillum* (Schenck) | 1* | 1* |
| *Halictus tumulorum* (L.) | 1 0.1 | 2 0.2 |
| Diptera: Syrphidae |                                    | 1 0.1 | 1 0.1 |
| *Criorhina* | 21 1.8 | 28 2.3 |
| *Episyrphus balteatus* (De Geer) | 11 0.9 | 18 1.5 |
| *Eristalis* horticola (De G.) | 1 0.1 | 0 0 |
| *Eristalis nemorum* (L.) | 0 0 | 1 0.1 |
| *Eristalis tenax* (L.) | 10 0.8 | 17 1.4 |
| *Eupeodes* | 0 0 | 2 0.2 |
| *Helophilus pendulus* (L.) | 0 0 | 1 0.1 |
| *Myathropa florea* (L.) | 5 0.4 | 0 0 |
| *Platycheirus* | 1 0.1 | 2 0.2 |
| *Syrphus* | 23 2.0 | 94 7.8 |
| *Volucella* | 2 0.2 | 10 0.8 |
| *Volucella bombylans* (L.) | 2 0.2 | 3 0.3 |
| *Volucella pellucens* (L.) | 0 0 | 6 0.5 |
| *Volucella zonaria* (Poda) | 0 0 | 1 0.1 |
| *Xanthogramma pedissequum* (Harris) | 2 0.2 | 0 0 |
| Diptera: Other |                                    | 6 0.5 | 3 0.3 |
| *Calliphora* | 15 1.3 | 2 0.2 |
| *Chlororhyncha formosa* (Scop.) | 0 0 | 18 1.5 |
| *Empis* | 0 0 | 18 1.5 |
| *Lucilia sericata* (Meigen) | 1 0.1 | 20 1.7 |

(continued)
**Table 1.** (continued)

| Group | Genus and Species | Brighton urban | | | | Brighton rural | | |
|-------|------------------|---------------|---|---|---|----------------|---|
|       | Count | Proportion (%) | | |   | Count | Proportion (%) | | |
| Butterfly | Aglais io (L.) | 0 | 0 | | | 3 | 0.3 | | |
|         | Aphantopus hyperantus (L.) | 0 | 0 | | | 13 | 1.1 | | |
|         | Coenonympha pamphilus (L.) | 0 | 0 | | | 4 | 0.3 | | |
|         | Limenitis camilla (L.) | 9 | 0.8 | | | 43 | 3.6 | | |
|         | Maniola jurtina (L.) | 1 | 0.1 | | | 7 | 0.6 | | |
|         | Melanargia galathea (L.) | 0 | 0 | | | 1 | 0.1 | | |
|         | Ochloides sylvanus (Esper) | 0 | 0 | | | 7 | 0.6 | | |
|         | Pieris | 10 | 0.9 | | | 7 | 0.6 | | |
|         | Pieris brassicae (L.) | 6 | 0.5 | | | 3 | 0.3 | | |
|         | Pieris napi (L.) | 0 | 0 | | | 3 | 0.3 | | |
|         | Pieris rapae (L.) | 4 | 0.3 | | | 1 | 0.1 | | |
|         | Polyommatinae c-album (L.) | 2 | 0.2 | | | 5 | 0.4 | | |
|         | Polyommatus icarus (Rottemburg) | 0 | 0 | | | 2 | 0.2 | | |
|         | Pyronia tithonus (L.) | 3 | 0.3 | | | 18 | 1.5 | | |
|         | Thymelicus sylvestris (Poda) | 1 | 0.1 | | | 0 | 0 | | |
|         | Vanessa atalanta (L.) | 1 | 0.1 | | | 0 | 0 | | |
| Wasp | Cerceris rybeyensis (L.) | 1 | 0.1 | | | 0 | 0 | | |
|         | Vespula vulgaris (L.) | 0 | 0 | | | 12 | 1.0 | | |
| Beetle | Oedemera nobilis (Scop.) | 16 | 1.4 | | | 43 | 3.6 | | |
|         | Oedemera lutea (Scop.) | 17 | 1.5 | | | 7 | 0.6 | | |

Species in bold are listed as priority species in the UK biodiversity action plan (UK BAP, 2007). 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.

*Counts indicate the representative sample of bees identified using a microscope for *Lasioglossum* bee species.

**Figure 2.** Foraging activity of insect groups recorded in three pooled 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.

*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 1.

Diversity (Shannon–Weiner $H'$) 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). Fewer genera were recorded at the urban site ($S_{(G)} = 31$) than rural site ($S_{(G)} = 25$) overall. These trends were similar for the first transect walks per survey period (Supporting Information Table S2).

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.

**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 ± SD across all sites and survey years: 60.2 ± 15.5). Bumblebees (*Bombus spp.*) were again the second most abundant on average, ranging from 1 to 48% (17.4 ± 12.1). Other taxa were: hoverflies, 7.9 ± 6.9 individuals...
per survey; butterflies, 6.4 ± 5.1; other (non-Apis/Bombus) bees, 2.8 ± 3.0; beetles, 4.4 ± 4.7, other Diptera, 0.6 ± 1.3 and wasps, 0.4 ± 1.25 (Fig. 4).

On average, across all sites over 2018 and 2019, honeybees were proportionally 31.5% more abundant in July (68.4 ± 14.2 bees per survey, n = 100 insects per survey) than June (52.0 ± 12.5). Bumblebees were 64% less abundant in July (9.1 ± 4.5) than June (25.6 ± 11.8; Fig. 4).

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/

Local R. fruticosus agg. abundance and habitat

Bramble plants were present in 54 of the 60 randomly selected 200 × 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 Supporting Information Table S3). The only surveyed habitat in which no bramble was present was in the middle of an agricultural field.

Table 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.

| Bramble bloom stage | Brighton urban | Brighton rural |
|---------------------|---------------|---------------|
|                     | Early         | Middle        | Late          | Early         | Middle        | Late          |
| 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         |

Data are from surveys of approximately 400 insects carried out during the early, middle and late stages of bramble bloom (urban: Early = 13 and 15 June, middle = 26 and 27 June, late = 12 and 13 July, n = 1168 insects in total; rural: 6 June; 21 June; and 5 and 6 July, n = 1200). Genus-level richness $S_{(G)}$, Shannon-Weiner diversity ($H'$) and Pielou’s measure of evenness (J) are given for each survey period per location.
Figure 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). [Color figure can be viewed at wileyonlinelibrary.com]

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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 × 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 (Supporting Information Table S4). 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 of 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 ≥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. (Supporting Information Table S5).

We recorded one patch, roughly 6 × 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.

**Honeybee pollen trapping**

Overall, we analysed 1184 grey pollen pellets from the four locations where samples were collected in 2018 (Falmer village, n = 503; Ashcombe Farm, n = 273; and Magham Down village, n = 472; Brighton city, n = 120). R. 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. 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. 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 3).

**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 and 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 33–89% 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. Nevertheless, a wide range of other foraging insect species were recorded (Fig. 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 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, 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 Harelequin sponshyludium L. (240); data from studies using
insect-flower transect data rather than observations 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. 5; Table 3), bramble is an important pollen source for many other insects, including bumblebees (Gyan & Woodell, 1987c; Kleijn & Raemakers, 2008).

Table 3. Proportion of bramble pellets in honeybee pollen samples in four locations in East Sussex, 2018, corrected for false positives (see Methods and Supporting Information Methods S2).

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

Pollen was collected in three rural (R) locations (30 May to 3 August) and one urban (U) location (30 May to 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.

Figure 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 to 3 August) and one urban (U) location (30 May to 6 July).

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., 2018). 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 et al., 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 & Wooddell, 1987b; Baude et al., 2016; Fowler et al., 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 and 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 et al., 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, 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 and 4). Bramble is common in hedgerows bordering agricultural fields, public footpaths and bridleways in rural areas (Williams & Carreck, 1994; Hanley & Wilkins, 2015; this study). It is also commonly found growing along linear transportation infrastructure including railways (NERC, 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). Yet, bramble is often removed from urban greenspace (e.g. Eastbourne Borough Council, 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, 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 United Kingdom, 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 United Kingdom (e.g. bumblebees: Carvell et al., 2006; butterflies: 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). 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.

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Conflicts of Interest

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available on request.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1: Supporting information
Appendix S2: Supporting information

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