Seasonality of floral resources in relation to bee activity in agroecosystems

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Abstract

The contribution of wild insects to crop pollination is becoming increasingly important as global demand for crops dependent on animal pollination increases. If wild insect populations are to persist in agricultural landscapes, there must be sufficient floral resources (FR) over time and space. The temporal, within-season component of FR availability has rarely been investigated, despite growing recognition of its likely importance for pollinator populations. Here, we examined the visitation rates of common bee genera and the spatiotemporal availability of FR in agroecosystems over one season to determine whether local bee activity was limited by the abundance of landscape FR, and if so, whether it was limited by the present or past abundance of landscape FR. Visitation rates and landscape FR were measured in 27 agricultural sites in Ontario and Québec, Canada, across four time periods and three spatial scales. Landscape FR at varying spatial scales predicted visits for the seven most commonly observed bee genera. *Bombus* visitation rates were higher in landscapes that had greater cumulative seasonal abundance of FR, suggesting the importance of early-season FR for this taxon. Visits from *Halictus* and *Lasioglossum* were higher in landscapes that provided either a stable or increasing amount of FR over the season and were lower in landscapes that experienced a decrease in FR over the course of a season. *Andrena*, *Augochlorella*, *Megachile*, and *Peponapis* visits were not measurably influenced by FR in previous months but were lower in landscapes that had a higher present abundance of FR, perhaps reflecting pollinator movement or dilution. Our research provides insight into how seasonal fluctuations in floral resources affect bee activity, and by examining each bee genus separately, we could observe how differences in foraging periods, foraging ranges, and the number of broods per season influence how bee taxa respond to food availability within agroecosystems.

Keywords

Anthophila, agricultural landscape, floral volume, pollinators, spatiotemporal scale

Introduction

The abundance and accessibility of floral resources (hereafter, 'FR') has been identified as the primary factor limiting wild bee populations globally (Roulston and Goodell 2011). Specifically, if wild bee populations are to persist, there must be sufficient provision of FR over both time and space. However, extensive conversion of natural habitat to arable land to support the growing human population is resulting in the removal of many of the naturally occurring FR on which wild bee populations rely (Kremen et al. 2002, Brosi et al. 2008, Murray et al. 2009). Even if crops themselves provide FR, they do so for only a portion of the growing season, which may be insufficient to support bee populations throughout their activity periods. An abundance of research looking at spatial provisioning of floral resources has generally found that increasing either heterogeneity or abundance of FR will result in increased population sizes or visitation rates of wild bees (synthesized in Kennedy et al. 2013). However, a few recent studies have found the opposite, with certain FR-providing habitats actually distracting bees from visiting crop fields (Nicholson et al. 2019), or causing a dilution of pollinators across landscapes when floral resources are less limited (Kovács-Hostyánszki et al. 2013, Holzschuh et al. 2016).

While the influence of spatial arrangement of FR on bees foraging in agricultural landscapes has been well established, the influence of FR availability over time has been relatively understudied. Much of the existing research on the latter topic has found that in landscapes providing a consistent source of FR over time, wild bees respond positively in terms of their abundance (Mandelik et al. 2012, Mallinger et al. 2016, Martins et al. 2018), density in crops (Kovács-Hostyánszki et al. 2013), colony growth (Westphal et al. 2009, Crone and Williams 2016), and sexual reproduction (Rundlöf et al. 2014). However, most studies examining the effect of temporal and spatial arrangement of FR on bees focus on responses of abundant, social taxa such as honey bees (Lau et al. 2019) and bumble bees (Timberlake et al. 2019), or examine the responses of broad functional groups of bees, often by grouping solitary bees together (Le Féon et al. 2013, Kovács-Hostyánszki et al. 2013). An increase in bee population size or density in landscapes with high FR can only be observed within one season if bees produce multiple broods per season, or if there is immigration from adjacent landscapes. For wild bee species that have limited flight distances and produce a single brood annually—as is the case for most species in temperate regions—we would expect population sizes to remain stable when FR abundance is consistent or increases over a season, and to decrease in response to periods in a season when resources become scarce. Given the differences in brood production, foraging periods, and foraging ranges among bee taxa, fluctuations in FR should produce a diversity of responses (Ogilvie and Forrest 2017). We therefore expect that the spatial and temporal scale of FR that most influences bee population size should be specific to the taxonomic group of bees that is examined. Understanding the responses of specific bee taxa to seasonal FR in agricultural landscapes is important for development of conservation and management strategies that can both enhance pollination services and preserve bee functional diversity.

The objective of this study was to examine the relationship between visitation rates of bees and the amount of FR in agricultural landscapes over one season, to determine at which within-year temporal scale and landscape spatial scale the abundance of FR predicts local bee abundance. We examined visitation rates of the most common genera of bees and the corresponding amount of FR in surrounding agricultural landscapes in four sequential time periods over one season, to assess the relative support for the following hypotheses for each genus (presented in Fig. 1):

H1: Bee visits are only influenced by local FR – for bee populations that are limited by something other than FR (e.g., nesting habitat, pesticides, natural enemies), population sizes should not be correlated with the amount of FR in the broader landscape; instead, we expect that the present abundance of local FR (i.e., within the area in which bee visits are measured) will best predict local visitation rates.

H2: Bee visits are influenced by the present abundance of landscape FR – for bee populations that are influenced by the availability of FR, but that have relatively short foraging periods within a season (overlapping only one time period in which FR were measured), we expect that the present abundance of FR within the landscape will best predict bee visits, and that either **(a)**bees are limited by FR, so that in landscapes with higher FR abundance more bee visits will be observed; or that **(b)** bees are not limited by FR, but instead are "diluted" (dispersed) across landscapes with higher FR abundance, in which case fewer bee visits will be observed at a local flower patch.

H3: Bee visits are influenced by the previous abundance of landscape FR – for bee populations that are influenced by FR and have long foraging periods within a season (overlapping multiple time periods in which FR were measured), we expect that **(a)** for bees producing a single brood per season, both the abundance of FR in the landscape when foraging begins and any decreases in the abundance of FR later in the season will best predict bee visits; or **(b)** for bees producing multiple broods per season, the cumulative abundance of landscape FR from when foraging begins will best predict bee visits.

Materials and methods

Study sites and landscape structure

The study was conducted in 27 farms growing fruit or vegetable crops in Eastern Ontario and the Outaouais region of Québec, Canada. Farms planning to grow cucurbit crops were chosen initially for inclusion because we wished to focus on pollinator-dependent, late-season crops; however, many farms were not able to grow

cucurbits due to drought conditions experienced throughout the region. To maximize independence among farm sites (i.e., to minimize the chance that an individual bee could move between farms), chosen farms were 4–211 km apart. Across all farm sites, 102 locations were sampled for bees and FR abundance (as described below), with one to six locations per farm, depending on the number of distinct land patches in which resource-providing flowers were present, and when permission was given from landowners. Sampling locations within patches of land were selected based on the estimated location of the patch's centre, or, if the patch was over 25 m wide, was located at least 10 m from an edge. In three patches wider than 25 m, sampling locations less than 10 m from the edge were used due to a complete absence of flowers in bloom in the centre. The distance between sampling locations within a farm ranged from 3.8 m to 1040 m. Sites were visited in rotation over four time periods during one season in 2016: the first took place between May 20–June 10 (n = 38 sampling locations), the second from June 10–July 4 (n = 33), the third from July 5–August 1 (n = 37), and the fourth from August 1–September 1 (n = 39). If sampling locations contained open flowers during more than one sampling period, the same location was sampled in multiple time periods.

The composition of the landscape within 250 m, 500 m, and 750 m radii of each sampling location was quantified to estimate landscape-scale FR abundance. The 250–750 m scale has been found in previous studies to be the range at which non-*Apis* bees respond to landscape structure (Steffan-Dewenter et al. 2002), and 500 m was chosen as an intermediate spatial scale. Sampling locations within the same farm site (and with overlapping radii at the 750 m scale) were not treated as independent (see Statistical analysis). Within a 750 m radius around each sampling location, the boundaries between land patches were manually digitized in QGIS version 2.18.7, using both waypoints taken on-site with a Trimble? Juno SD handheld GPS unit (Trimble Navigation Limited, Westminster, CO, USA), and from Google Earth and Bing Aerial satellite imagery.

Each land patch was then categorized by the type of land-use (hereafter, "land type"), through ground-truthing and raster imagery from Agriculture and Agri-Food Canada's (AAFC) 2016 Annual Crop Inventory. Land types fell into three categories: non-resource land, resource-providing land, and unknown land (see Appendix Table A1, Supporting Information, for detailed descriptions of each land type). Non-resource land was defined as any area that did not provide FR, which included crops with exclusively wind-pollinated flowers and crops with anecdotal or no evidence of bees collecting resources from flowers. Urban and developed land was also included in non-resource land; although urban gardens or lawns may provide FR for bees, the amount is inconsistent over time and space, and the number of bee species supported is usually low (Cane 2005, Matteson et al. 2008). Resource-providing land was defined as land areas that provided FR for bees at some point during the season and was categorized into 14 different land types (Appendix Table A1). Sampling locations were located only within resource-providing land, and at least one of each resource-providing land type was sampled during each time period. Unknown land was comprised of areas where we could not determine the crop grown (2.3% of all area surrounding sampling locations); hedgerow (1.8%); or crop land where potentially resource-providing crops were grown, but FR were not measured (0.7%). The total area of each land type was then calculated within radii of 250, 500, and 750 m around each sampling location.

Bee observations

Bee observation methods were adapted from frequently used pollinator surveying designs (Memmott 1999, Alarcon et al. 2008, Gibson et al. 2011). At each sampling location, a transect was set up to survey bee activity within a 30 m x 4 m area (89 transects); a 30 m x 2 m area was surveyed when only one crop row (< 4 m wide) was present (eight transects); and 25 m x 4 m (one transect) or 24 m x 4m areas (four transects) were surveyed when crop rows were shorter than 30 m. Bee observations occurred over one minute per 4 m^2 of transect intervals by slowly walking the length of the transect. The shaded and unshaded temperature, maximum wind speed, and average wind speed were recorded for at least one minute using a Kestrel? 2000 Pocket Weather? Meter (Nielsen-Kellerman, Boothwyn, PA, USA) held at approximately 1.5 m above ground preceding each observation period. If there was a noticeable change in conditions during the observation period, temperature and wind speed were recorded again at the end of the period and averages

were recorded. All bee observations were conducted when shaded temperatures were above 11.9degC, average wind speeds were below 1.9 m/s, and maximum wind speeds were below 4 m/s.

During observation periods, all occurrences of bees visiting open flowers were recorded by two observers, standing on either side of the transect width, and recording all visits within 2 m each. A visit was counted when a bee was seen contacting sexual organs of an entomophilous flower or was probing a flower for nectar. All visited flowers were identified to genus (9 out of 77 taxa) or species (68 out of 77 taxa), and bees were identified on the wing to genus or species. When identification was not possible on the wing, the observations were paused and both observers attempted to catch the bee to take a photograph from inside a glass vial or to collect as a voucher (79 specimens total). Vouchers were then identified to species or genus and are stored in the Forrest lab's collection at the University of Ottawa (Ottawa, ON, Canada). Overall, 82% of bees were identified to species, 17% to genus, 0.1% to family, and 1% as Anthophila.

Floral resources

Floral density was recorded at each sampling location, using three quadrats of 1.5 m x 1.5 m. Quadrats were placed in random locations within the same transect used for bee observations, immediately following the observation period. If no open flowers were present in all three quadrat locations, an additional location was randomly selected and the mean count across the four quadrats was recorded. Within a quadrat, the number of open flowers was counted for each non-graminoid species encountered; for species with many-flowered inflorescences, five individuals were haphazardly selected, and the number of flowers was counted on a randomly selected inflorescence. The mean number of flowers per inflorescence for many-flowered species was then multiplied by the number of inflorescences in a quadrat to obtain the number of flowers per quadrat. In members of the Asteraceae family, capitula were treated as single flowers (see Appendix Table A2 for descriptions of floral units used for counts of each species). For 29 out of 96 species encountered, the number of flowers per inflorescence was obtained from either literature sources or digital images of herbarium specimens due to the large number of flowers encountered in the field, and for a few species that inadvertently were not measured in the field (see Appendix Table A2 for literature values for each species).

To estimate the amount of FR (nectar and pollen) provided by a species, floral dimensions were measured on five haphazardly selected individuals of each species. The length and width of the receptacle (or capitulum in Asteraceae species) were measured at right angles to each other, as well as the height from the receptacle to the end of the longest sexual organ (stamen or pistil); in species with sexual organs completely hidden within a corolla, height was measured from the receptacle to the end of the corolla. Measurements were made using calipers and were rounded to the nearest 1 mm. Thirty-one of 96 species were not measured in the field, and floral measurements were instead obtained from literature sources or digital images of herbarium specimens (see Appendix Table A2 for measurements and literature sources for each species). Floral measurements were used to calculate both the surface area (A) of flowers:

$$A = \pi ab \quad (1)$$

and the volume (V) of flowers:

$$V = \pi abh \quad (2)$$

where a is the semi-major axis, or half the length or width (whichever was longest) of a flower's receptacle or capitulum, b is the semi-minor axis, or half the length or width (whichever was shortest) of a flower's receptacle or capitulum, and h is the height of a flower or inflorescence (Fig 2c and Appendix Table A2).

To determine which measurement of floral dimensions was the best proxy for FR amount, literature searches for daily nectar sugar mass (µg/day) and pollen volume (in µl/flower) were conducted for all flowering species encountered; these measurements have been previously used to assess FR available to pollinators (Hicks et

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al. 2016, Baude et al. 2016). Literature sources that provided counts of pollen grains per flower and volumes of individual pollen grains were used to calculate an estimate of pollen volume per flower for species for which we could not find measurements of total pollen volume. Nectar sugar mass was obtained for 46 species and pollen volume for 33 species of the 96 encountered (see Appendix Tables A3–A4 for full species lists). Pearson correlations between nectar sugar mass or pollen volume and the length, width, height, surface area, and volume measurements of each species (all variables log-transformed to approximate normal distributions) were used to determine which floral dimension could best estimate the amount of FR.

For all bee genera other than *Peponapis* , the abundance of FR in the landscape surrounding each sampling location was calculated by determining the mean FR value per flower of each species and multiplying this value by the count of each flower in a quadrat. In the genus *Peponapis* , pollen is collected exclusively from *Cucurbita* spp. (Hurd et al. 1974). Therefore, in models of *Peponapis* visits, the abundance of FR in the landscape surrounding each sampling location was calculated from the mean FR value per squash (*Cucurbita* spp.) or cucumber (*Cucumis sativus*) flower, since 99.7% of all visits observed were to squash and 0.3% were to cucumber. While the other bee genera we considered include some oligolectic (pollen-specialist) species in our study area, they are not uniformly specialized on a single plant taxon, so all rewarding plant taxa were included in calculations of FR for these bees. The mean abundance of FR per 1 m^2 was then calculated across quadrats for each transect, and the median of the transect-level values was calculated for each land type during each time period. This number was then multiplied by the total area of each land type within 250 m, 500 m, and 750 m around a sampling location to obtain an estimate of the total FR at a given spatial scale during a given time period.

Statistical analysis

All statistical analyses were performed in R version 3.6.1 (R Core Team 2019). Analyses of bee visitation rate per transect were conducted on bee genera that were present in at least four out of 27 sites during a given time period. Spatial autocorrelation among sites in the number of visits by each genus in a given time period was assessed using Moran's I (Paradis et al. 2004). Visits from *Apis mellifera* were found to be spatially autocorrelated across all time periods (p = 0.02, Moran's I |observed – expected| = 0.14), likely due to the presence of hives on certain farms, so were not analyzed.

Generalized linear mixed models were run with a zero-inflated negative binomial distribution and log link function, using the glmmTMB package (Brooks et al. 2017). Models treated the total number of bee visits observed within a transect as the response variable and were run separately for each genus; all models included a log offset to account for varying lengths of observation time based on transect sizes, and the crossed random effects of time period and site. For genera that were present in at least four sites in only a subset of the time periods, only models including data for those time periods were run. The model for the null hypothesis was of the form

$$\text{Visits}_{ijk} = 1 + \text{Site}_j + \text{Time}_k + \log(\text{Obs}_{ijk})$$
$$\text{Site}_j \sim N\left(0, \sigma^2_{\text{site}}\right)$$
$$\text{Time}_k \sim N\left(0, \sigma^2_{\text{time}}\right) \tag{3}$$

where Visits_{ijk} is the number of bee visits observed in the i th transect in site j during time period k , and Obs_{ijk} is the length of the observation time in the i th transect in site j during time period k . All of the following models included the same random intercept terms and offset but differed from equation (3) in the fixed effects included. The model for H1 was of the form

$$\text{Visits}_{ijk} = T_{ijk} + \text{Site}_j + \text{Time}_k + \log(\text{Obs}_{ijk}) \tag{4}$$

where T_{ijk} is the transect FR volume (cube-root transformed) within the i th transect in site j during time

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period k ; i.e., this model includes a term for local but not landscape-level FR. The model for H2a and H2b, which also includes landscape-level FR, was of the form

$$\text{Visits}_{ijk} = T_{ijk} + L_{ijk} + \text{Site}_j + \text{Time}_k + \log(\text{Obs}_{ijk}) \quad (5)$$

where L_{ijk} is the landscape FR volume (cube-root transformed) within either a 250, 500, or 750 m radius (each spatial scale was run in separate models) surrounding the i th transect in site j during time period k ; models were run both including and excluding the T_{ijk} term. The model for H3a was of the form

$$\text{Visits}_{ijk} = T_{ijk} + L_{ij(1)} + \sum_{k=1}^{k} \Delta L_{ijk} + \text{Site}_j + \text{Time}_k + \log(\text{Obs}_{ijk})$$
$$\Delta L_{ijk} = (L_{ijk} \geq L_{ij(k1)} \rightarrow 0) \bigwedge (L_{ijk} < L_{ij(k1)} \rightarrow L_{ijk}\ L_{ij(k1)}) \quad (6)$$

where $L_{ij\ (1)}$ is the landscape FR volume (cube-root transformed) within either a 250, 500, or 750 m radius (each spatial scale was run in separate models) surrounding the i th transect in site j during the first time period (1) that bees were observed visiting flowers, and ΔL_{ijk} is the non-positive change (positive changes were equivalent to no change, i.e. equalling zero) in the landscape FR volume (cube-root transformed), within the same radius as the $L_{ij\ (1)}$ term, surrounding the i th transect in site j from the previous time period ($k - 1$) to the current time period k , from which was calculated the cumulative sum of ΔL_{ijk} across all time periods since bees were first observed visiting flowers; models were run both including and excluding the T_{ijk} term. Finally, the model for H3b was of the form

$$\text{Visits}_{ijk} = T_{ijk} + \sum_{k=1}^{k} L_{ijk} + \text{Site}_j + \text{Time}_k + \log(\text{Obs}_{ijk}) \quad (7)$$

where the cumulative sum of L_{ijk} was calculated across all time periods since bees first were observed visiting flowers (including the present time period) and was run both including and excluding the T_{ijk} term. Models for H3b were only run for bee genera that might produce multiple broods per season (*Augochlorella* , *Bombus* , *Halictus* ,*Lasioglossum* ; Packer et al. 2007).

Model selection with the MuMIn package (Bartoń 2019) was used to determine which models best predicted bee visits, considering all models with ΔAICc < 2. Model selection was run in two iterations, with unknown land area assigned either the median FR value calculated from all land types within a specific radius during a given time period ('median models'), or the minimum FR value calculated from all land types within a specific radius during a given time period, which was always zero ('minimum models'). This was done to test the sensitivity of our conclusions to the presence of unknown areas; we found no differences between the identities of models with ΔAICc < 2 when unknown areas were assigned either minimum or median FR values, and we have presented the results from both iterations.

Results

Floral resources

Floral volume was the best predictor of both daily nectar sugar mass (µg/day; $R^2 = 0.39$, p $= 3.6 \times 10^{-6}$, n = 46, Fig. 2a), and pollen volume (µl/flower; $R^2 = 0.40$, p $= 6.0 \times 10^{-5}$, n = 33, Fig. 2b), and therefore was used to represent FR in all subsequent analyses. Flower length, width, height, and surface area were also significantly correlated with nectar and pollen volume, but to a lesser degree (R^2 [?] 0.34). Floral measurements, pollen volumes, and nectar sugar mass for individual species can be found in Appendix, Table A2–A4.

Across many of the landscapes sampled in this study, there was a high degree of correlation between the FR at each spatial scale within a given time period, particularly between the 500 m and 750 m spatial scales

(Fig. 3). In most landscapes, the fourth (last) time period had the lowest FR, and the highest FR abundance generally was seen in either in the second or third time period, with a few landscapes having the highest FR of the season in the first time period (Fig. 3).

Most common bee genera

Over the season, 8422 bee visits were observed across all sites, with 1647 visits observed in the first time period, 1946 in the second, 2211 in the third, and 2618 in the fourth. Bees in the genera *Andrena*(mining bees), *Apis* (*A. mellifera* ; Western honey bee),*Bombus* (bumble bees), *Halictus* (furrow bees), and*Lasioglossum* (sweat bees) were observed visiting flowers in at least four of the 27 sites surveyed during all time periods. Bees in the genus *Augochlorella* (*A. aurata* ; golden green sweat bee) were observed during just the first and second time periods in at least four sites, while *Megachile* (leafcutter bees) were observed in the second and third, and *Peponapis* (*P. pruinosa* ; hoary squash bee) in the third and fourth. All other bee genera found in at least four sites were only observed during one time period.

H1: Bee visits are only influenced by local FR

No models for any genera supported the hypothesis that bee visits were influenced only by local FR (Table 1). Several taxa did, however, show a positive relationship with the abundance of FR within transects based on the best models which also included landscape FR abundance as a predictor (Table 1; Fig, 4 for *Halictus* and *Peponapis*).

H2: Bee visits are influenced by the present abundance of landscape FR

The number of visits observed from *Andrena* , *Augochlorella* ,*Megachile* , and *Peponapis* supported hypothesis H2b, that bee visits were negatively associated with the present abundance of landscape FR (Fig. 4; Table 1). The number of bee visits was best predicted by models of present landscape FR at a 250 m scale for*Megachile* (ΔAICc = 0), and at a 750 m scale for*Augochlorella* (ΔAICc = 0) and *Peponapis* (ΔAICc = 0).*Andrena* visits were best predicted by models of the present landscape FR at a 250 m scale (ΔAICc [?] 1.00) but showed some support for hypothesis H3a (Table 1), described in the following section.

H3: Bee visits are influenced by the previous abundance of landscape FR

For *Halictus* and *Lasioglossum* , hypothesis H3a—that bee visits were influenced by the previous abundance of landscape FR within a season—was best supported (Table 1; Fig. 4). *Halictus* and*Lasioglossum* visits were best predicted from models including landscape FR abundance during the first time period, and the non-positive change in the abundance of landscape FR since the first time period within 750 m of sampling locations (both ΔAICc = 0). For both genera, bee visits were negatively associated with landscape FR during the first time period and were also lower in landscapes that experienced greater decreases in landscape FR over the season (Table 1; Fig. 4). *Andrena* visits also showed some support for hypothesis H3a, with bee visits predicted by the previous abundance of landscape FR at the 250 m scale (ΔAICc [?] 1.81), but in this genus, greater decreases in FR over the season were associated with a higher number of bee visits. However, hypothesis H2b had slightly better support in*Andrena* (Table 1), as described in the previous section.

Bombus visitation rates best supported hypothesis H3b, that bee visits are influenced by the cumulative abundance of landscape FR since the first time period (Table 1; Fig 4). Landscape FR was a predictor of*Bombus* visits at all spatial scales over which it was measured, but the 250 m scale was the strongest predictor (ΔAICc = 0). Visits from*Bombus* were positively associated with the cumulative abundance of landscape FR at all spatial scales.

Discussion

We found that FR in the landscape over preceding months was an important predictor of bee activity for most bees that were foraging over the entire season. High FR abundance in previous months was positively related to the number of visits for bees that were more social and produced multiple broods per season (*Bombus*) , while stable FR abundance over previous months positively influenced the number of visits for genera that were less social and produced fewer broods per season (*Halictus* and *Lasioglossum*). For all other

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bees, including solitary bees (*Andrena* , *Megachile* , and *Peponapis*) and bees with shorter observed foraging periods (*Augochlorella* , *Megachile* , and *Peponapis*), the present abundance of FR in the landscape was the best predictor of bee visits. However, the present abundance of FR was negatively related to local bee visits, possibly because of a dilution of pollinators across high-FR landscapes. Individual bee taxa exhibit unique combinations of foraging distances, foraging periods, and numbers of brood produced per season, all of which can influence how bees respond to changes in landscape FR abundance over a season. Our research acknowledged these taxonomic differences by assuming each bee genus observed would respond at different spatial and temporal scales to the abundance of FR in a landscape. By doing this, we were able to document important differences in the ways in which each genus was influenced by the spatial and temporal availability of FR.

Much of the previous research on wild bees responding to FR in agricultural landscapes has found that a higher abundance of FR is associated with larger populations, higher densities, or greater numbers of visits (Mandelik et al. 2012, Kovács-Hostyánszki et al. 2013, Mallinger et al. 2016, Martins et al. 2018). In our study, the number of visits by *Bombus* was positively related to cumulative landscape FR, in line with the hypothesis that bees producing multiple broods in a season can increase population sizes within one season with access to more FR through time. This finding agrees with previous research examining *B. vosnesenskii* colony responses to FR in agricultural landscapes, which found that the production of males and workers was more positively related to high early-season FR abundance in the surrounding landscape than to late-season FR (Williams et al. 2012). Bumble bees represent some of the most common and important pollinators for both wildflowers and crops in the Northern Hemisphere, but many species are facing declines (Goulson et al. 2008). Our results suggest that early-season FR in agricultural landscapes could promote high bumble bee visitation rates later in the season, and potentially maintain or increase colony sizes over a season.

For *Halictus* and *Lasioglossum* , our findings best supported the hypothesis that these bees were producing a single brood per season, and therefore were able to maintain (but not increase) their population sizes when FR was consistent or increased over time. However, in the region this study was conducted, both *Halictus* and*Lasioglossum* include eusocial species that produce multiple broods per season and solitary species that only produce a single brood (Mitchell 1960, Packer et al. 2007). Given the stronger support for the hypothesis that these genera responded as expected for single-brood-producing bees, our results indicate either that more solitary species were present in our study locations, or that the more social species in this region were producing too few brood per season to exhibit a strong response to the cumulative abundance of FR. Geographic variations can influence both the degree of sociality and the number of broods produced within single species of *Halictus* and*Lasioglossum* , with a general pattern of more solitary bees and fewer broods being produced at higher elevations and latitudes (Richards and Packer 1995, Wcislo 1997, Davison and Field 2016). In our study locations, most *Halictus* and *Lasioglossum* species are closer to their northern range limit (Mitchell 1960), which should increase the prevalence of populations in this region that produce fewer broods per season and exhibit less social behaviours.

The remaining bee genera (*Andrena* , *Augochlorella* ,*Megachile* , and *Peponapis*) were all most influenced by the present abundance of FR in the landscape. These genera include both eusocial (*Augochlorella*) and solitary bees (*Andrena* ,*Megachile* , and *Peponapis*). Although *Augochlorella*visits were primarily observed during the first and second sampling periods, the only species of *Augochlorella* in eastern Canada,*A* . *aurata* (Packer et al. 2007), is in flight for the entire growing season (Mitchell 1960). Similar to *Halictus* and*Lasioglossum* , some *A. aurata* populations are solitary, while others produce just two broods (one worker and one reproductive brood) per season (Packer et al. 1989). If only two broods were produced over the entire season by *A. aurata* populations, we might have been unable to observe any influence of cumulative FR abundance by the second time period (only the first and second time periods were analyzed for this genus). The fact that visits from the solitary bee genera*Andrena* , *Megachile* , and *Peponapis* were apparently unaffected by past FR makes sense in light of the short flight periods of individual species within these genera. Although *Andrena* were found foraging over the entire season, this genus comprises 75 species in eastern Canada (Packer et al. 2007), many of which are active as adults for just one or two months (LaBerge 1986, Larkin et al. 2008).*Megachile* were observed foraging during the second, third, and fourth time periods, but

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a number of the species in this region have more restricted foraging periods (Mitchell 1962, Sheffield et al. 2011). The single local species of *Peponapis* , *P. pruinosa* , is a specialist on pollen in the Cucurbitaceae family and has a foraging period synchronized with its flowering in southern Ontario (Willis and Kevan 1995). Given the prevalence of species with short flight periods in our study area, the foraging periods of many individual species were likely too short to respond to fluctuations in FR at the roughly monthly scale we considered. Future research should focus on examining how fluctuations in FR over shorter temporal scales (e.g., weekly) influence bee activity, which would allow for development of agricultural landscapes that specifically benefit those species with short flight periods.

Despite the variety of life-history traits represented by *Andrena* , *Augochlorella* , *Megachile* , and *Peponapis* , all four genera responded similarly to the present abundance of FR; visits were generally fewer in landscapes that had a high abundance of FR. Several studies have previously found that abundant FR can decrease bee density on crops, either through dilution of pollinators across a landscape (Kovács-Hostyánszki et al. 2013, Holzschuh et al. 2016), or through distraction of pollinators from crops to other resource-rich areas (Lander et al. 2011, Nicholson et al. 2019). This may indicate that the landscapes used in our study generally provided a high amount of FR outside the local sampling areas, perhaps because we selected sampling locations based on their proximity to farms growing fruit or vegetables. Population sizes for solitary bees that produce a single brood per season (*Andrena* , *Megachile* , and *Peponapis*) should also be strongly limited by the amount of FR available in the previous year, which would be used to produce the generation foraging in the current year. Since we did not know the relative abundance of FR in the previous year, this may have been the primary factor limiting bee populations, especially for species that only forage for a few weeks in a season.

Differences in body size can contribute to differences in the maximum foraging ranges of bee taxa (Greenleaf et al. 2007) and thus to availability of FR to bees within the landscape surrounding sampling locations. For most genera, we found that the number of bee visits observed within a transect was best predicted by landscape FR at a consistent spatial scale. Within genera like *Andrena* ,*Halictus* , and *Lasioglossum* , individual species can vary greatly in body size (Mitchell 1960), but the average body size across a genus did not seem to correlate with the spatial scale at which landscape FR was most relevant. Visits for *Andrena* , a relatively small-bodied bee (body length ranges from 4–15 mm; Mitchell 1960) were best predicted by FR at 250 m, the smallest spatial scale we measured, while visits from other small-bodied bees like *Augochlorella*(average body length of *A. aurata* is 5.25 mm; Mitchell 1960),*Halictus* (body length 7–13 mm; Mitchell 1960) and *Lasioglossum* (body length 3.5–10 mm; Mitchell 1960) were best predicted by FR at 750 m, the largest spatial scale measured. On the other hand, visits from the relatively large-bodied *Bombus* (body length 5–28 mm; Laverty and Harder 1988) and *Megachile* (body length 6–25 mm; Sheffield et al. 2011) were best predicted by the abundance of FR within just 250 m around a sampling location. The spatial arrangement of both FR and nesting habitat in a landscape are likely the more relevant predictors of how far most bees are actually foraging (Zurbuchen et al. 2010). The spatial scales we have determined as the best predictor of bee visits may therefore represent the upper end of foraging areas used by bees in the majority of landscapes that we examined, with many bees actually foraging in smaller areas of landscapes with more densely packed resources.

By teasing apart the responses of individual genera, we discovered a diversity of responses among taxonomic groups, highlighting potential problems with lumping all non-*Bombus* bees into a single functional group, or with examining responses of the entire bee community to FR. Our research highlights the importance— particularly for social taxa—of not only the current floral resource landscape but also the FR present earlier in the season. This information can help determine how to configure agricultural landscapes in a way that promotes bee population persistence and growth, and thus, increases the pollination services crops receive. Our findings suggest that bees with longer flight periods likely benefit from continuous, consistent provision of FR throughout a single season, and high FR abundance early in the season. However, the number of bee visits observed may not be a good proxy for bee population sizes. An important next step will be to determine how across-year patterns in visitation rates change with spatiotemporal fluctuations in FR, particularly for single-brood species which can only respond positively to FR availability over this timescale. Though we observed fewer visits by bees with short foraging periods in landscapes with a high present abundance of FR,

this pattern should not hold across years: if other factors are not limiting, more abundant floral resources in landscapes should yield higher bee abundances in subsequent years.

Acknowledgements

Conflict of Interest

None declared.

Data Accessibility Statement

Data for this study will be archived in Dryad upon acceptance.

Author Contributions

JG and JF originally formulated the idea and developed methodology. JG conducted fieldwork and analyzed the data. JG wrote the manuscript; JF provided editorial advice.

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Tables

Table 1 Models of bee visits and corresponding hypotheses with the landscape scale within which FR were measured (radius in metres around a sampling location), where 'FR' = floral resources, and hypotheses are as follows: 'H_0' = bee visits are not limited by FR; 'H_1' = bee visits are limited only by the present abundance of local FR; 'H_{2a}' = bee visits are best predicted by the present abundance of landscape FR, and will increase with increasing FR; 'H_{2b}' = bee visits are best predicted by the present abundance of landscape FR, and decrease with increasing FR; 'H_{3a}' = bee visits are best predicted by the abundance of landscape FR when foraging is first observed and any non-positive changes in abundance in subsequent time periods; and 'H_{3b}' = bee visits are limited by the cumulative abundance of landscape FR from when foraging is first observed. Models shown are those with ΔAICc values < 2 when all unknown areas in a spatial scale were assigned either the median ('Med') or minimum ('Min') volume of FR measured across all resource-providing land types during a given time period.

Hypotheses for bee visits and landscape scale of FR	Hypotheses for bee visits and landscape scale of FR	Hypotheses for
Andrena	H2b	250m
	H3a	250m
Augochlorella	H2b	750m
Bombus	H3b	250m
	H3b	750m
	H3b	250m
	H3b	500m
	H3b	750m
Halictus	H3a	750m
	H2a	250m
	H2a	250m
Lasioglossum	H3a	750m
Megachile	H2b	250m
	H2b	250m
Peponapis	H2b	750m

* All FR values input for this term were negative or 0 (non-positive change in FR), so a negative coefficient means that the number of visits were negatively related to smaller decreases in FR, while a positive coefficient means that the number of visits were positively related to smaller decreases in FR

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Figures
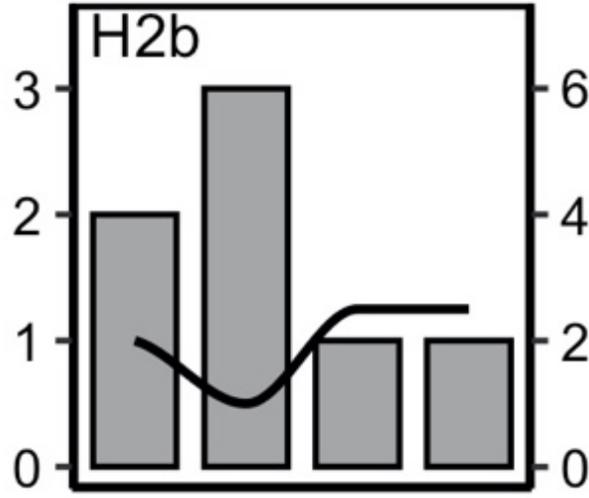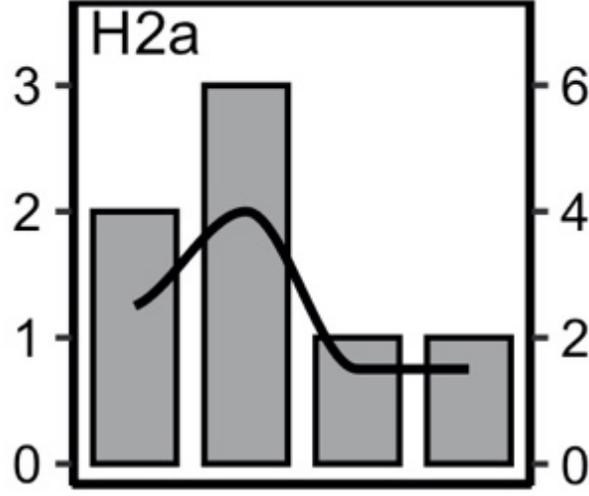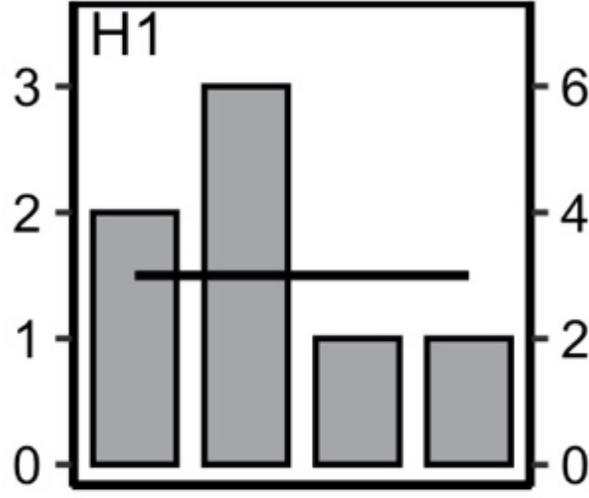
Fig. 1 Hypothetical responses of bee visits (in transects) to the amount of floral resources (FR) in the surrounding landscape in four time periods over one season, with FR represented as grey bars, and bee visits represented as black lines, with hypotheses depicted as follows: H1 = bee visits are not influenced by the abundance of landscape FR; H2a = bee visits are limited by the abundance of FR in the landscape during the present time period, and are higher in time periods with higher FR; H2b = bee visits are influenced by the abundance of FR in the landscape during the present time period, but are lower in time periods with high FR due to dilution of bees across the landscape; H3a = bee visits are limited by the abundance of FR in a landscape in the first time period (when foraging hypothetically begins), and by non-positive changes in FR abundance in subsequent time periods relative to the first time period; and H3b = bee visits in a given time period are limited by the cumulative abundance of landscape FR over all previous time periods, from when foraging began.
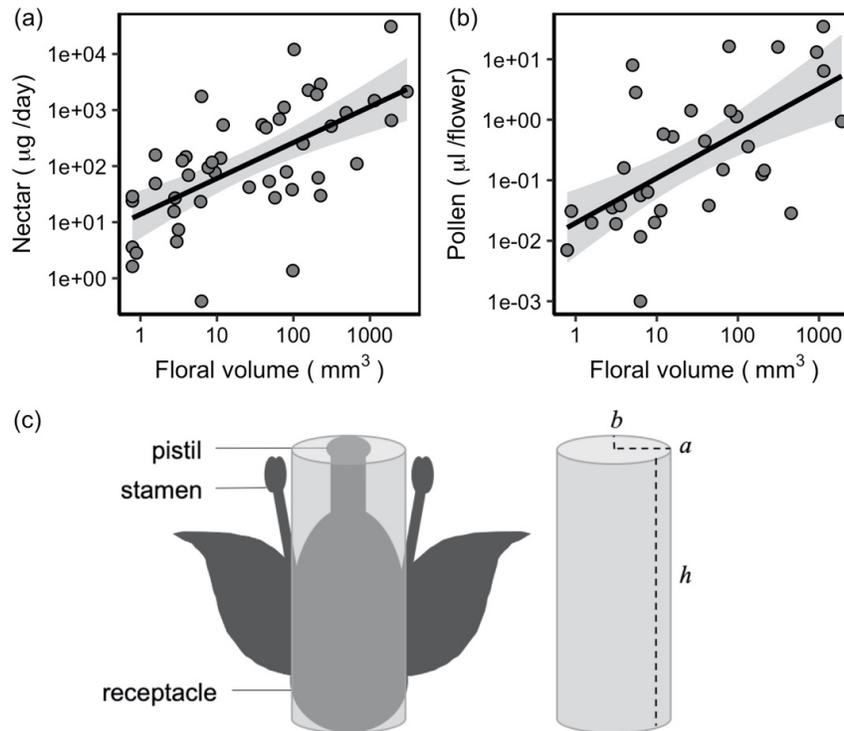
Fig. 2 Correlations between floral volume and (a) daily nectar sugar mass in 46 flowering species, and (b) pollen volume in 33 flowering species; with (c) a diagram of floral volume measurements using the volume of an elliptic cylinder ($V = \pi abh$). Black lines in (a) and (b) represent linear model estimates of nectar mass or pollen volume by floral volume; shaded areas are 95% confidence intervals. Note logarithmic axes.

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Fig. 3 Median volumes of floral resources ('FR') per square metre within each landscape spatial scale (250 m, 500 m, and 750 m radii around sampling locations) across all time periods in one season, with panels showing trends within each site (n = 27). Floral resources were calculated with any unknown areas assigned the median floral resource volume from all resource-providing land types in a given spatial scale and time period.

H2b:

H3a:

H3b:

Time period
- T1
- T2
- T3
- T4
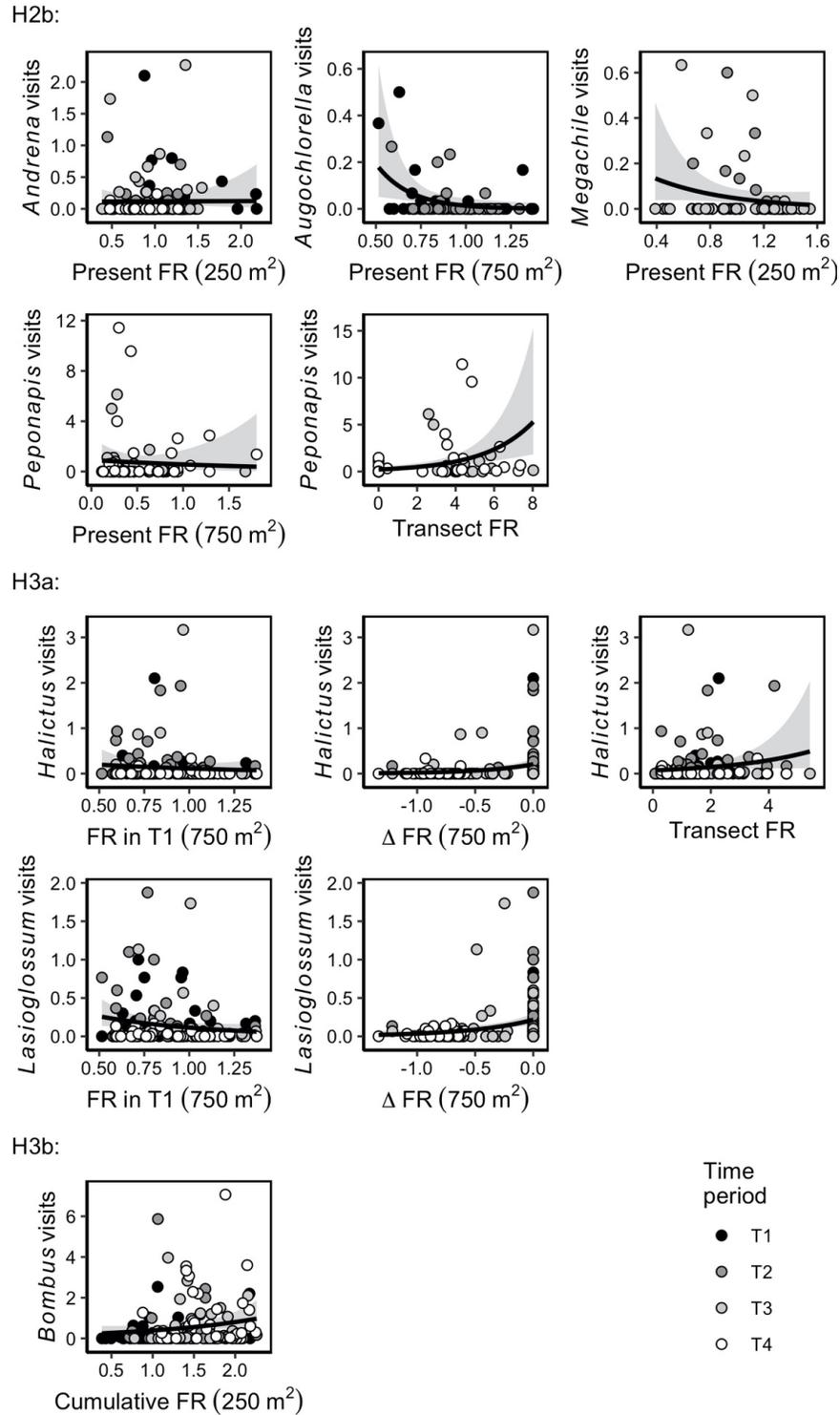
Fig. 4 Relationship between bee visits and floral resource ('FR') predictors from the best models (in Table 1) measured across four time periods (T1–T4) in four spatial scales (transect, 250 m, 500 m, 750 m) over one season, represented by the corresponding hypotheses: H2b, H3a, or H3b. Lines represent the negative

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binomial relationship between an FR predictor and bee visits, with a 95% confidence interval. FR were calculated with all unknown areas in a given radius assigned the median volume of FR measured across all known resource-providing land types during a given time period.

Appendix

**Table A1** Land-types used to quantify landscape structure and floral resources around sampling locations. The range in proportion of each land type across all sampling periods is represented as the percent of total area within a 750-m radius around each sampling location. Areas with water, exposed or barren land, and urban or developed land were not digitized, and exact proportions were not calculated for these land types. The unknown crop, hedgerow, and potentially resource-providing crop land types were not assessed for floral resources, and a range is presented for values assigned in models run, from the minimum to the median floral resource volume from all resource-providing land types in a given spatial scale and sampling period.

Land type	Description	Area in 750-m radius (%)	Median floral resources by sampling period (cm^3/m^2)
Areas not digitized	Barren, developed, exposed, water, urban land	N/A	0.00
Cereal crop	Barley, millet, oats, rye, spelt, triticale, wheat	0.002 –15	0.00
Corn	Anecdotal evidence of floral resources provided (but see Roulston et al. 2000)	0.3–38	0.00
Soybean	Anecdotal evidence of floral resources provided (but see Erickson et al. 1978, Ahrent and Caviness 1994)	1.5–55	0.00
Herbs, field vegetables	Non-flowering or harvested before flowering	0.02–5.4	0.00
Semi-natural	Grass land, shrub land	0.4–35	0.20 (late-spring) 2.82 (early-summer) 1.00 (mid-summer) 1.53 (late-summer)
Forage	*Medicago sativa*, hay, pasture, *Trifolium* spp.	1.7–60	3.67 (late-spring) 3.49 (early-summer) 4.23 (mid-summer) 1.49 (late-summer)
Forest		4.6–87	0.14 (late-spring) 0.55 (early-summer)
Apple	*Malus pumila*	0.05–4.2	41.6 (late-spring)
Asparagus	*Asparagus officinalis*	0.01–0.5	0.84 (early-summer)
Bean	*Phaseolus vulgaris*	0.006–0.5	0.08 (mid-summer)
Cucumber	*Cucumis sativus*	0.003–0.02	0.28 (late-summer)
Melon	*Cucumis melo*	0.01–0.8	0.24 (mid-summer)

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Land type	Description	Area in 750-m radius (%)	Median floral resources by sampling period (cm^3/m^2)
Potato	*Solanum tuberosum*	0.26–0.29	0.75 (early-summer) 0.88 (mid-summer)
Raspberry	*Rubus idaeus, R. strigosus, R. occidentalis*	0.002–0.9	2.31 (early-summer)
Squash	*Cucurbita* spp.	0.01–7.1	0.37 (early-summer) 0.66 (mid-summer) 1.09 (late-summer)
Strawberry	*Fragaria × ananassa*	0.5–3.5	12.6 (late-spring) 13.0 (early-summer)
Sunflower	*Helianthus annuus*	0.005–0.05	31.2 (early-summer) 33.8 (mid-summer) 36.3 (late-summer)
Watermelon	*Citrullus lanatus*	0.01–0.2	0.14 (mid-summer)
Unknown crop		0.08–21	0–1.30 (late-spring) 0–1.57 (early-summer) 0–0.84 (mid-summer) 0–0.54 (late-summer)
Hedgerow	Areas bordering agricultural fields with shrubs or trees	0.05–6.8	0–1.30 (late-spring) 0–1.57 (early-summer) 0–0.84 (mid-summer) 0–0.54 (late-summer)
Potentially resource-providing crop	*Brassica rapa, B. napus, B. juncea, Capsicum annuum, Fagopyrum esculentum, Lycopersicon esculentum, Physalis* spp., *Pisum sativum, Prunus avium, Pyrus communis, Rubus fruticosus*	0.002–1.1	0–1.30 (late-spring) 0–1.57 (early-summer) 0–0.84 (mid-summer) 0–0.54 (late-summer)

Table A2 Measurements and literature sources of floral dimensions for all non-graminoid flowering species. Floral units describe the scale at which species were counted in quadrats (flower, inflorescence, or capitulum in Asteraceae species). '*l*' is length in mm of corolla opening (or receptacle length for capitula), '*w*' is width in mm of corolla opening (or receptacle width for capitula), '*h*' is height in mm, measured from the receptacle to the longest sexual organ (stamen or pistil), and '*V*' is floral volume in mm^3, calculated using the formula for volume of an elliptic cylinder ($V = \pi \times \frac{l}{2} \times \frac{w}{2} \times h$). Inflorescence volume was calculated by multiplying floral volume by the average number of flowers per inflorescence and was left blank when individual flowers were counted rather than inflorescences. Measurements were made on five individuals per species, or values were obtained from literature sources.

Species	Floral unit	*l*	*w*	*h*	*V*	Inflorescence *V* (mm^3)	Sources
Acer spicatum	inflorescence	2.0	2.0	3.0	9.42	1649	(Sullivan 1983)
Achillea millefolium	inflorescence	6.0	6.0	3.4	96.1	1442	Measured; https://
Actaea pachypoda	inflorescence	2.0	2.0	5.0	15.7	298	(Pellmyr 1985); htt
Agrimonia gryposepala	flower	5.0	5.0	5.0	98.2		http://plants.jstor
Anthemis arvensis	capitulum	6.2	6.2	6.4	226		Measured

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Species	Floral unit	l	w	h	V	Inflorescence V (mm^3)	Sources
Asclepias syriaca	inflorescence	2.0	2.0	2.0	6.28	126	Measured
Asparagus officinalis	flower	1.2	1.2	4.8	6.13		Measured
Barbarea vulgaris	inflorescence	1.0	1.0	2.0	1.57	12.6	Measured; http://
Capsella bursa-pastoris	inflorescence	2.0	2.0	2.0	6.28	37.7	(Nave et al. 2016);
Cardamine bulbosa	flower	1.8	1.8	1.0	2.98		Measured
Cardamine diphylla	flower	2.0	2.8	7.0	29.5		Measured
Centaurea sp.	capitulum	8.0	8.0	22.0	1143		Measured
Cerastium fontanum	flower	1.0	1.0	3.6	2.83		Measured
Chelidonium sp.	flower	5.0	5.0	8.0	157		(Kang et al. 1991)
Cichorium intybus	capitulum	4.6	4.6	9.4	161		Measured
Citrullus lanatus	flower	5.0	5.0	5.2	102		Measured
Coptis trifolia	flower	7.6	7.6	4.2	197		Measured
Cornus canadensis	flower	7.8	7.8	4.0	193		Measured
Cornus sericea	inflorescence	1.0	1.0	5.4	4.24	106	Measured; http://
Cucumis melo	flower	7.5	7.5	4.5	199		http://www.efloras
Cucumis sativus	flower	2.0	2.0	6.2	19.5		Measured
Cucurbita pepo (female zucchini)	flower	10.2	10.2	16.6	1353		Measured
Cucurbita pepo (male zucchini)	flower	8.4	8.4	16.0	934		Measured
Cucurbita pepo (zucchini)	flower	9.3	9.3	16.3	1107		Measured
Cucurbita sp. (female squash)	flower	13.8	13.8	19.8	3091		Measured
Cucurbita sp. (male squash*)*	flower	10.4	8.4	15.8	1127		Measured
Cucurbita sp. (squash*)*	flower	12.1	11.1	17.8	1878		Measured
Cucurbita spp.	flower	10.7	10.2	17.1	1461		Measured
Cucurbita spp. (female)	flower	12.0	12.0	18.2	2058		Measured
Cucurbita spp. (male*)*	flower	9.4	8.4	15.9	986		Measured
Daucus carota	inflorescence	2.0	2.0	1.0	3.14	358	Measured; (Sivinsk
Echium vulgare	flower	2.4	3.8	9.2	65.5		Measured
Erigeron canadensis	inflorescence	1.0	1.0	3.0	2.36	1275	Measured
Erigeron philadelphicus	capitulum	7.6	7.6	3.4	157		Measured
Erigeron sp.	capitulum	3.55	3.55	12.6	52.5		Measured
Erysimum cheiranthoides	inflorescence	1.0	1.0	3.0	2.36	18.8	(Idris and Grafius
Erythronium americanum	flower	3.0	3.0	11.0	77.8		Measured
Euthamia graminifolia	inflorescence	1.0	1.0	1.0	0.79	20.4	(Harder 1985); http
Fagopyrum esculentum	inflorescence	2.0	2.0	2.0	6.28	980	(Cawoy et al. 2006
Fragaria × ananassa	flower	7.8	7.8	6.2	304		Measured
Fragaria virginiana	flower	3.0	3.0	2.4	26.4		Measured
Galinsoga quadriradiata	capitulum	2.0	2.0	2.0	0.01		(Warwick and Swe
Galium mollugo	inflorescence	1.0	1.0	1.0	0.79	14.1	https://weedecolog
Galium palustre	inflorescence	1.0	1.0	1.0	0.79	5.50	https://weedecolog
Geum aleppicum	flower	6.0	6.0	8.0	226		http://symbiota.m
Glechoma hederacea	flower	1.0	1.0	9.8	7.70		Measured
Helianthus annuus	capitulum	35.4	35.4	20.7	27435		Measured
Hieracium caespitosum	capitulum	7.4	7.4	3.4	153		Measured
Hieracium pilosella	capitulum	10.4	10.4	6.4	538		Measured
Lactuca sp.	capitulum	2.0	2.0	3.0	9.42		http://www.nature
Leucanthemum vulgare	capitulum	10.5	10.5	3.5	311		Measured
Linaria vulgaris	flower	2.4	1.0	20.6	39.1		Measured
Lotus corniculatus	flower	4.73	4.73	12.0	211		http://ucjeps.berke
Maianthemum canadense	inflorescence	1.0	1.0	1.0	0.79	14.9	http://plants.jstor.
Malus pumila	flower	9.2	9.4	9.8	674		Measured

Species	Floral unit	l	w	h	V	Inflorescence V (mm^3)	Sources
Malva neglecta	flower	1.9	1.9	4.25	12.0		(Nave et al. 2016)
Medicago lupulina	inflorescence	1.0	1.0	1.0	0.79	11.8	Measured; http://v
Medicago sativa	inflorescence	1.0	1.0	5.0	3.93	68.7	Measured; (Winkle
Mitella diphylla	flower	1.0	1.0	3.0	2.36		Measured
Oenothera biennis	flower	1.0	1.0	6.4	5.03		Measured
Oxalis stricta	flower	1.0	1.0	3.5	2.75		Measured
Phaseolus vulgaris	flower	2.8	2.8	7.6	48.2		Measured
Physalis heterophylla	flower	2.8	2.8	9.0	58.1		Measured
Plantago lanceolata	inflorescence	1.0	1.0	2.0	6.28	452	(Cavers et al. 1980
Potentilla argentea	flower	2.4	2.4	1.2	6.13		Measured
Prunella vulgaris	flower	1.2	1.6	7.0	11.2		Measured
Ranunculus acris	flower	5.8	5.8	2.8	80.9		Measured
Ranunculus recurvatus	flower	1.6	1.6	2.6	6.28		Measured
Rubus allegheniensis	flower	11.6	11.6	4.6	489		Measured
Rubus sp. (raspberry)	flower	6.4	6.4	6.0	202		Measured
Rudbeckia hirta	capitulum	15.0	15.0	3.6	636		http://www.efloras
Silene vulgaris	flower	3.2	3.2	15.6	133		Measured
Sisyrinchium montanum	flower	1.0	1.0	4.5	3.53		Measured
Solanum tuberosum	flower	2.8	2.8	9.0	57.3		Measured
Solidago canadensis	inflorescence	1.0	1.0	1.0	0.79	26.7	Measured; (Harden
Solidago sp.	inflorescence	1.0	1.0	1.0	0.79	26.7	Measured; (Harden
Sonchus arvensis	capitulum	10.5	10.5	22	1905		(Lemna and Messe
Symphotrichum lanceolatum	capitulum	4.0	4.0	6.0	75.4		(Chmielewski and
Taraxacum agg.	capitulum	19.6	19.6	8.4	3050		Measured
Trifolium aureum	inflorescence	1.0	1.0	7.0	5.50	179	http://www.efloras
Trifolium pratense	inflorescence	1.0	1.0	11.0	8.64	432	(Winkler et al. 200
Trifolium repens	inflorescence	1.0	1.0	2.0	1.57	55.0	(Nave et al. 2016);
Trillium erectum	flower	8.0	8.0	9.0	452		http://www.efloras
Trillium grandiflorum	flower	5.4	5.6	11.0	292		Measured
Verbena hastata	inflorescence	1.0	1.0	2.0	1.57	8.80	Measured
Veronica serpyllifolia	flower	1.0	1.0	1.13	0.88		Measured
Veronica sp.	flower	1.04	1.04	1.04	0.88		Measured
Vicia cracca	inflorescence	3.0	3.0	6.2	43.8	1972	Measured; http://l
Viola pubescens	flower	1.0	1.0	4.5	3.53		Measured

Table A3 Literature values for nectar production in 46 flowering species. "Nectar unit" is the scale at which nectar was collected from species, with capitulum measurements for members of Asteraceae and individual flower measurements for all other species. "Source species" were used when nectar production values were only available for morphologically similar species within the same genus and is left blank when the species itself was used.

Species	Nectar (µg/day)	Nectar unit	Source species	Source
Acer spicatum	77.0	flower		(Heinrich 1976)
Achillea millefolium	38.1	capitulum		(Holl 1995, Hicks et al. 2016)
Agrimonia gryposepala	1.37	flower	*A. eupatoria*	(Baude et al. 2016)
Anthemis arvensis	2880	capitulum		(Schultz and Dlugosch 1999)
Asclepias syriaca	1750	flower		(Heinrich 1976)
Barbarea vulgaris	158	flower		(Holl 1995)
Capsella bursa-pastoris	0.39	flower		(Baude et al. 2016)

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Species	Nectar (µg/day)	Nectar unit	Source species	Source
Cardamine bulbosa	4.50	flower	*C.* spp.	(Baude et al. 2016)
Centaurea sp.	1474	capitulum	*C. nigra*	(Hicks et al. 2016)
Cerastium fontanum	26.9	flower		(Baude et al. 2016)
Citrullus lanatus	12000	flower		(Taha and Bayoumi 2009)
Cornus sericea	68.8	flower	*C. sanguinea*	(Baude et al. 2016)
Cucurbita sp. (female squash)	30810	flower	*C. pepo*	(Vidal et al. 2006)
Daucus carota	7.35	flower		(Baude et al. 2016)
Echium vulgare	688	flower		(Hicks et al. 2016)
Erigeron philadelphicus	2250	capitulum		(Holl 1995)
Euthamia graminifolia	24.0	capitulum		(Heinrich 1976)
Fragaria virginiana	42.0	flower		(Heinrich 1976)
Galium mollugo	3.58	flower		(Baude et al. 2016)
Geum aleppicum	29.8	flower	*G. urbanum*	(Baude et al. 2016)
Glechoma hederacea	94.4	flower		(Baude et al. 2016)
Leucanthemum vulgare	515	capitulum		(Hicks et al. 2016)
Linaria vulgaris	544	flower		(Baude et al. 2016)
Lotus corniculatus	61.8	flower		(Baude et al. 2016)
Malus pumila	110	flower		(Baude et al. 2016)
Malva neglecta	541	flower	*M. moschata*	(Hicks et al. 2016)
Medicago lupulina	1.63	flower		(Baude et al. 2016)
Medicago sativa	146	flower		(Baude et al. 2016)
Oxalis stricta	15.5	flower	*O. acetosella*	(Baude et al. 2016)
Phaseolus vulgaris	53.4	flower	Cultivated bean	(Baude et al. 2016)
Potentilla argentea	23.3	flower	*Potentilla* spp.	(Baude et al. 2016)
Prunella vulgaris	139	flower		(Baude et al. 2016)
Ranunculus acris	78.8	flower		(Baude et al. 2016)
Rubus allegheniensis	894	flower		(Holl 1995)
Rubus sp. (raspberry)	1893	flower	*R. fruticosus* agg.	(Baude et al. 2016)
Silene vulgaris	251	flower		(Baude et al. 2016)
Solanum tuberosum	27.3	flower		(Baude et al. 2016)
Solidago canadensis	28.8	capitulum		(Heinrich 1976)
Sonchus arvensis	651	capitulum		(Baude et al. 2016)
Symphotrichum lanceolatum	1116	capitulum		(Chmielewski and Semple 2001)
Taraxacum agg.	2137	capitulum		(Hicks et al. 2016)
Trifolium pratense	117	flower		(Baude et al. 2016)
Trifolium repens	49.0	flower		(Baude et al. 2016)
Veronica serpyllifolia	2.83	flower		(Baude et al. 2016)
Vicia cracca	484	flower		(Baude et al. 2016)
Viola pubescens	125	flower	*Viola* spp.	(Holl 1995, Baude et al. 2016)

Table A4 Literature values for pollen volume in 33 flowering species. Pollen volume was provided in literature sources directly or was calculated from literature values of pollen grain counts and pollen grain volumes. "Floral unit" is the scale at which pollen was collected from species, with capitulum measurements for members of Asteraceae and individual flower measurements for all other species. "Source species" were used when pollen production values were only available for morphologically similar species within the same genus and is left blank when the species itself was used.

Species	Pollen (µl/floral unit)	Source species	Literature source
Acer spicatum	0.02		(Biesboer 1975, Sullivan 1983)
Achillea millefolium	1.13		(Hicks et al. 2016)
Actaea pachypoda	0.52		(Pellmyr 1985); http://www.discoverlife.org
Capsella bursa-pastoris	0.001		(Hicks et al. 2016)
Centaurea sp.	6.40	*C. nigra*	(Hicks et al. 2016)
Cerastium fontanum	0.04		(Hicks et al. 2016)
Cucumis melo	0.13		(Perveen and Qaiser 2008, Kouonon et al. 2009)
Cucurbita pepo (zucchini)	13.1		(Nepi and Pacini 1993, Vidal et al. 2006)
Cucurbita sp. (squash)	34.8		(Vidal et al. 2006)
Daucus carota	0.02		(Hicks et al. 2016)
Echium vulgare	0.15		(Hicks et al. 2016)
Erythronium americanum	16.3		(Harder et al. 1985, Kosenko 1999)
Fagopyrum esculentum	0.06		(Cawoy et al. 2006)
Fragaria virginiana	1.42		(Hebda et al. 1988, Ashman and Hitchens 2000)
Galium mollugo	0.007	*G. verum, G. album*	(Hicks et al. 2016)
Galium palustre	0.007	*G. verum, G. album*	(Hicks et al. 2016)
Glechoma hederacea	0.06		(Hutchings and Price 1999, Moon et al. 2008)
Leucanthemum vulgare	15.9		(Hicks et al. 2016)
Linaria vulgaris	0.44		(Olsson 1974, Arnold 1982)
Lotus corniculatus	0.15		(Hicks et al. 2016)
Malva neglecta	0.58		(Cruden 1977); http://blogs.cornell.edu/pollengrains/
Medicago sativa	0.16		(Müller et al. 2006)
Oenothera biennis	8.00		(Cruden and Jensen 1979, Hall et al. 1988)
Plantago lanceolata	0.01		(Hicks et al. 2016)
Prunella vulgaris	0.03		(Hicks et al. 2016)
Ranunculus acris	1.40		(Hicks et al. 2016)
Silene vulgaris	0.36	*S. dioica, S. latifolia*	(Hicks et al. 2016)
Sonchus arvensis	0.94	*S. asper*	(Hicks et al. 2016)
Trifolium aureum	2.82		(Hicks et al. 2016)
Trifolium repens	0.02		(Hicks et al. 2016)
Trillium erectum	0.03		(Hicks et al. 2016)
Veronica sp.	0.03	*V. persica*	(Hicks et al. 2016)
Vicia cracca	0.04		(Hicks et al. 2016)