Past floral resources as a predictor of present bee visits in agroecosystems

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ABSTRACT

Relying on wild bees for pollination services has become necessary as the global demand for crops dependent on animal pollination increases. If wild bee populations are to establish and persist in agricultural landscapes, there must be sufficient floral resources over time and space. This study examines the relationship between bee visits in agroecosystems and the spatiotemporal availability of floral resources over one season. I expected that landscapes with greater floral resources earlier in the season would subsequently experience more bee visits than landscapes with fewer early-season floral resources, and that the spatiotemporal scale of this effect would differ among taxa. I measured bee visitation rate and floral resource density over three spatial scales and during four time-periods spanning one season, in 27 agricultural sites across Ontario and Québec, Canada. The present abundance of floral resources at a local scale positively influenced bee visits across all sampling periods. However, differences in the temporal scale of bees' response to floral resources were observed at landscape scales. Past and present floral resources were positively or negatively associated with bee visits depending on the time of season and which taxon was examined. The number of visits by Andrenidae, honey bees, and bumble bees increased with floral resource abundance in previous time-periods, while other taxa exhibited a negative association with past floral resources, suggesting possible dilution of bee populations at a landscape scale. Understanding the scales at which bee taxa are influenced by floral resources can allow development of land management strategies that could enhance crop pollination and conserve species threatened by agricultural intensification.

RÉSUMÉ

Avec l'augmentation de la demande mondiale de produits agricoles dépendants de la pollinisation animale, il devient nécessaire d'avoir recours aux abeilles sauvages pour effectuer le service de pollinisation. Pour s'établir et persister dans un paysage agricole, les abeilles sauvages ont besoin de suffisamment de ressources florales dans le temps et dans l'espace. Cette étude examine les relations entre les visites d'abeilles et la disponibilité spatio-temporelle des ressources florales dans un agroécosystème, pendant une saison. Il était attendu qu'un paysage avec des ressources florales plus importantes et plus avancées dans la saison présenterait par conséquent plus de visites d'abeilles qu'un paysage avec moins de ressources florales précoces, et aussi que l'échelle spatio-temporelle de cet effet diffèrerait parmi les taxons. Le taux de visites d'abeilles ainsi que la densité de ressources florales sur trois échelles spatiales ont été mesurés pendant quatres périodes couvrant une saison, dans 27 sites agricoles à travers l'Ontario et le Québec, au Canada. L'abondance des ressources florales existantes à une échelle locale influence positivement les visites d'abeilles au sein de toutes les périodes d'échantillonnage. Toutefois, des différences chronologiques ont été observées entre les réponses des abeilles et les ressources florales à l'échelle du paysage. Les ressources florales présentes et antérieures sont positivement ou négativement associées avec les visites d'abeilles en fonction de la période dans la saison, et selon le taxon examiné. Le nombre de visites d'andrènes, d'abeilles mellifères et de bourdons augmentent avec l'abondance en ressource florale dans les périodes de temps précédentes, tandis que d'autres taxons montrent une association négative avec les ressources florales antérieures ; ce qui suggère une dilution possible des populations d'abeilles à l'échelle du paysage. Comprendre les degrés d'influence des ressources florales sur les taxons permettrait de développer des stratégies de gestion de l'environnement qui pourraient améliorer la pollinisation des cultures et conserver des espèces menacées par l'intensification de l'agriculture.

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CHAPTER 1: INTRODUCTION

1.1 Biodiversity and Ecosystem Services in Agricultural Landscapes

Conventional agricultural practices often lead to species-depauperate ecosystems, comprised of homogenous landscapes able to support few species (Bengtsson et al. 2005). This lack of biodiversity can hinder essential ecosystem processes, like nutrient or water cycling (Altieri 1999; Tscharntke et al. 2005a). Increasing homogeneity in agricultural land can also lead to decreased diversity or abundance of mobile organisms, at both local and landscape scales (Kennedy et al. 2013; Lichtenberg et al. 2017; Tscharntke et al. 2005a). In heterogeneous landscapes, mobile organisms persist due to their ability to locate and travel between patchily distributed resources, either spatially or temporally (Tsharntke et al. 2012). Patchy resources in agricultural landscapes can lead to species spill-over between natural habitats and crop fields, which can be beneficial for non-agricultural species that are able to use resources in crop fields and travel between habitats (Tsharntke et al. 2012).

The spill-over of mobile organisms from non-crop to crop land may also affect agricultural production. Negative effects include herbivory, pathogen transfer, or parasitism of crops or livestock directly, or of other mobile organisms that benefit agricultural production (reviewed in Blitzer et al. 2012). Nevertheless, many ecosystem services are also provided by mobile organisms, including natural predators providing biocontrol of pest species (reviewed in Tsharntke et al. 2005b), seed-dispersal, and pollination (reviewed in Blitzer et al. 2012 and Kremen et al. 2007). The pollination services provided by mobile organisms such as bees are essential for 35% of all crop production worldwide (Klein et al. 2007). The demand for crops that rely on animal pollination is increasing faster than human population size, and consequently, the current “supply” of managed honey bees is not able to meet this demand (Aizen and Harder 2009). Fortunately, the foraging activity of wild bees can provide sufficient pollination services for crops (Winfree et al. 2007; Winfree et al. 2008), and in many cases, wild bees are better pollinators than managed honey bees (Garibaldi et al. 2013). Bees rely on the pollen and nectar from flowers, or floral resources, as the primary source of food for the entirety of their lives (Michener 2007). However, the abundance and accessibility of food resources has been identified as the primary factor limiting wild bee populations globally (Roulston and Goodell 2011). The 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 floral resources that wild bee populations would rely on (Brosi et al. 2008; Kennedy et al. 2013; Kremen et al. 2002; Murray et al. 2009). Therefore, if wild bee populations are to become established and persist in agricultural landscapes, there must be sufficient provision of floral resources over both time and space.

1.2 Spatial Availability of Floral Resources

The spatial availability of floral resources to a bee in an agroecosystem depends on the ability of that bee to locate and travel to them. Optimal foraging theory suggests, in its simplest form, that an animal foraging within a landscape should maximize the rate of resource collection, while minimizing energy expenditure, or the distance needed to reach resources (Pyke et al. 1977). Female bees are central-place foragers, limiting their foraging to a certain distance around their nest, then returning to their nest to provision pollen and nectar for their larvae (Bronstein 1994; Schoener 1979). The maximum flight range of different bee species can be roughly predicted by body size: foraging range increases with increasing width of the thorax between the points of wing attachment, or the intertegular span (Greenleaf et al. 2007). Some large-bodied, social bees, such as bumble bees (*Bombus* spp.) and honey bees (*Apis mellifera*), have maximum foraging ranges as large as 10 km (Beekman and Ratnieks 2000; Steffan-Dewenter and Kuhn 2003), and landscape-level floral resources can strongly influence their abundances (Kennedy et al. 2013) or foraging behaviours within landscapes (Steffan-Dewenter and Kuhn 2003). Bumble bees will sometimes fly further than their estimated maximum foraging ranges to access floral resources from patches with high species richness, particularly in landscapes with relatively homogeneous floral resources (Jha and Kremen 2013). However, bumble bees are not representative of the majority of bee species, most of which are solitary, smaller-bodied, and often specialized on a few host plants (Linsley 1958). These traits translate to smaller foraging ranges, and greater influence of local-scale floral resources (Bommarco et al. 2010; Gathmann and Tscharntke 2002; Steffan-Dewenter et al. 2002).

The availability of floral resources in an agroecosystem also depends on the arrangement of those resources across a landscape. The influence of spatial arrangement of land covers on foraging bees has been well studied at both local and landscape scales (reviewed in Kennedy et al. 2013); the general consensus for many of these studies is that high homogeneity will negatively influence wild bee diversity or abundance (Brosi et al. 2008; Carvalheiro et al. 2011; Holzschuh et al. 2007; Holzschuh et al. 2012; Jha and Kremen 2013; Kremen et al. 2002; Kremen et al. 2004; Pontin et al. 2006). Heterogeneity can be introduced into agricultural landscapes by increasing the spatial complexity of either the configuration or the composition of a landscape (Fahrig et al. 2011). Increased heterogeneity in agroecosystems can enhance crop pollination by wild bees, and can be achieved by increasing crop diversity within fields (Kennedy et al. 2013), creating hedgerows at field margins (Morandin and Kremen 2013), increasing the proportion of natural or semi-natural habitat in the landscape (Garibaldi et al.

2011; Holzschuh et al. 2012; Kremen et al. 2004; Mandelik et al. 2012), or preserving forest remnants (Chacoff and Aizen 2006; De Marco Jr and Coelho 2004). Providing uncultivated areas near crop fields in particular appears to be essential for enhancing the crop pollination services of wild bees (Kremen et al. 2004; Ricketts et al. 2008).

Recent research has shown that highly homogenous mass-flowering crops can also have a positive effect on wild bee abundance, at least locally and in the short term. Todd et al. (2016) found that wild bee abundance was higher in a mass-flowering sunflower crop compared to a more diverse meadow habitat. Diekötter et al. (2014) observed that species richness of cavity-nesting bees increased with access to mass-flowering oilseed rape fields, although bee abundance was only influenced by the proportion of semi-natural land. Similarly, Holzschuh et al. (2013) found the cavity-nesting bee *Osmia bicornis* benefitted from nesting near oilseed rape fields; brood cell production increased with the amount of oilseed rape pollen in larval provisions. Several studies have looked at the influence of mass-flowering crops on bumble bees in particular. Both Westphal et al. (2003) and Rundlöf et al. (2014) found that the inclusion of mass-flowering clover fields in landscapes has a positive effect on bumble bee density. Increased visitation by bumble bees to hedgerow plants has been observed when hedgerows are adjacent to mass-flowering bean fields, indicating the possibility of mass-flowering crops facilitating pollination of nearby native plant species (Hanley et al. 2011). Although mass-flowering crops appear to benefit wild bee populations, this may not translate to growth of populations; rather, observed densities may represent pollinators being attracted to highly concentrated patches, resulting in a dilution of pollinators elsewhere in the landscape (Holzschuh et al. 2016; Tscharntke et al. 2012). Recently, Holzschuh et al. (2016) looked at agricultural landscapes across Europe, and found that bee densities in mass-flowering crop fields and bumble bee densities in semi-natural habitat were negatively associated with mass-flowering crop cover within the landscape, providing evidence for a dilution of bees at the landscape scale. Kovács-Hostyánszki et al. (2013) found a similar dilution effect of mass-flowering oilseed rape fields on bumble bee density at a landscape scale, but when they looked at pollination of shrubs in adjacent habitats only, there was a positive effect of oilseed rape fields. These results highlight the importance of examining multiple spatial scales when assessing the availability of floral resources and their influence on wild bees.

1.3 Temporal Availability of Floral Resources

The temporal availability of floral resources can also influence wild bee abundance in agroecosystems. Agricultural landscapes with mass-flowering crops may experience resource "pulses", or periods of time when floral resources are abundant (Holzschuh et al. 2016; Mandelik et al. 2012). Mass-flowering crops can potentially provide a significant amount of the floral resources necessary for wild bees, particularly for bees that produce a single brood per season and have foraging periods that overlap entirely with periods of mass-flowering. However, for species that produce multiple broods in a season and forage over longer time periods, a mass-flowering crop may only provide short-term resources; for *Bombus terrestris*, early-flowering oilseed rape increased colony growth, but only early in the season, which did not translate to higher sexual reproduction later in the season (Westphal et al. 2009). Bee populations in agricultural landscapes can reach a "resource bottle-neck" when the abundance of floral resources is inconsistent over the entire life cycle of a population; these fluctuations in resource availability can diminish the benefits of plentiful resources at earlier times within a season

(Pelletier and McNeil 2003; Rundlöf et al. 2014). When mass-flowering crops are present over the entire life cycle, wild bee populations should be less resource-limited, resulting in increased growth and reproduction. Indeed, Rundlöf et al. (2014) found that when both early- and late-season mass-flowering crops were present in close proximity to bumblebee colonies, higher densities of both queens and males were found later in the season, suggesting a possible positive effect of floral abundance on sexual reproduction. However, Crone and Williams (2016) also measured colony growth rates and queen production of *Bombus vosnesenskii* over an entire colony cycle in response to floral resource availability in the landscape, and found that both increased with greater floral resources, but colony growth rate was a stronger predictor of queen production than was the average amount of floral resources within the landscape.

Complementarity in the flowering of species or habitats over time should benefit wild bee populations; this should in turn increase the observed densities or visitation rates of bees on flowers (Mandelik et al. 2012; Mallinger et al. 2016). Functional complementarity has been described as the coexistence of two or more species through niche-partitioning; in terms of ecosystem functioning, complementarity can enhance functional effect sizes beyond the additive effects of individual species (Blüthgen and Klein 2011). In agricultural landscapes, complementarity in flowering time should yield relatively continuous and stable provisioning of floral resources over time. Crops flowering sequentially should be able to support pollinator communities through the growing season, thereby enhancing pollination of later-flowering crops. Waser and Real (1979) first described this situation (termed “sequential mutualism”) in a theoretical community of sympatric plant species with shared pollinator species. They suggested that with separation between plant species’ flowering times, competition between plants for pollinators could be avoided, and if plant species flowered sequentially over a season, then earlier-flowering plant species would provide continuous resources for the resident pollinator populations over time, maintaining population sizes which are then available for plant species flowering subsequently (Waser and Real 1979).

Mandelik et al. (2012) examined complementary resource use by bees in an agricultural landscape by measuring abundance and richness of bee communities in natural wooded habitat, crop fields, and old-field habitat over a season. They found that both early and late in the season, when floral resources from crops were lacking, bees were able to take advantage of resources provided in old-field habitats (Mandelik et al. 2012). Kovács-Hostyánszki et al. (2013) also examined complementary resource use by bee communities over time, in conjunction with the spatial scale of floral resource abundance. As described previously, they examined the effects of mass-flowering oilseed rape fields on bee visitation rates, and found that during flowering there was a negative effect of oilseed rape on bee density at a landscape scale, and a positive effect on pollination rates at a local scale (Kovács-Hostyánszki et al. 2013). However, following the period of mass-flowering, bee density was higher in forest edges later in the season (Kovács-Hostyánszki et al. 2013). This finding highlights the importance of examining both the spatial and temporal scale of resource effects on wild bee populations, as the direction of effect can change across spatial scales within a time-period, or across time-periods within a spatial scale.

Most studies looking at the influence of floral resource on wild bees in agroecosystems have not directly examined this interplay between spatial and temporal scale of resources, and generally focus on one or a few taxa. Studies that have examined bee community responses to floral resources often assume all species are responding similarly, or will group certain bees together based on a few shared attributes; perhaps the most common method is to segregate the entire bee community into solitary bees, bumble bees, and honey bees. Other functional traits such as life-cycle length, degree of pollen specialization, foraging ranges and sociality may influence the sensitivity of certain taxa to temporal fluctuations in floral resource abundance (Ogilvie and Forrest 2017). Understanding the responses of specific bee taxa to the floral resources in agricultural landscapes is important for development of land management strategies that can both enhance pollination services and conserve bee diversity.

1.4 Research Objectives

The objective of this study was to examine the relationship between visitation rates of bees and floral resources in agricultural landscapes, and to determine how the spatial and temporal availability of resources influences this relationship. When agricultural landscapes provide sufficient floral resources over time, bee populations should be able to grow and persist over a season; therefore, I expected that (1) landscapes with a higher abundance of floral resources earlier in the season would experience increased bee visits in subsequent time periods. As species of bees differ in their emergence times and life-cycle lengths, foraging should occur at different times and for differing lengths of time over a season; based on this, I expected that (2) the number of observed visits would be influenced by past floral resources at shorter or longer time-scales depending on which taxon of bee is examined. Bee species can also differ greatly in their foraging ranges and ability to locate resources; therefore, I expected that (3) the spatial scale of floral resources that best predicts the number of bee visits would differ among bee taxa.

CHAPTER 2: METHODS

2.1 Study Sites

The study was conducted in 27 farm sites growing fruit or vegetable crops in Eastern Ontario and the Outaouais region of Québec, Canada (Fig. 1). Farm sites were initially chosen because they planned to grow squash crops; however, due to drought conditions experienced throughout the region, some sites were not able to grow squash. To maximize independence among farm sites (i.e., to minimize the chance that an individual bee could move between sites), the chosen farms were 4–211 km apart (see Appendix 1 for sampling locations). The largest estimates for foraging distance of non-*Apis* bees occurring in eastern Canada extend to 2.8 km (Zurbuchen et al. 2010), while *Apis mellifera* foraging ranges have been estimated at distances up to 10 km (Beekman and Ratnieks 2000). Across all farm sites, 102 locations were sampled for bees and floral resource abundance, ranging from one to six locations per site depending on the number of distinct land-use types and accessibility. Within farm sites, sampling locations occurred in fields or patches of land (henceforth "parcels") that comprised a distinct land-use or habitat type, with resource-providing flowers in bloom. Locations were limited to those that were accessible and where permission from land owners was given. The distance between sampling locations within the same site was as great as possible given these constraints, with a minimum distance of 3.8 m, and a maximum distance of 1040 m. Sampling locations within parcels were selected based on the estimated location of the parcel's centre, or, if the parcel was over 25 m wide, were located 10 m or more from the edge. In three parcels wider than 25 m, sampling locations less than 10 m from the edge were used due to an absence of flowers in bloom in the parcel centre. Farm sites were visited in approximately the same order, in four rotations during the season; the four sampling periods were late-spring (20 May – 10 June 2016), early-summer

(10 June – 4 July 2016), mid-summer (5 July – 1 August 2016), and late-summer (1 August – 1 September 2016).

2.2 Bee Observations

Bee observation methods were adapted from commonly used pollinator surveying designs (Alarcón et al. 2008, Gibson et al. 2011, Memmott 1999). At each sampling location, one transect of 30 m × 4 m was set up to survey bee activity (102 transects in total). When crop rows were shorter than 30 m or when only one row (< 4 m wide) was available, transects had reduced dimensions; this resulted in eight 30 m × 2 m transects, one 25 m × 4 m transect, and four 24 m × 4m transects. Bee observations occurred over 30-minute intervals by slowly walking the length of the transect (transects smaller than 30 m × 4 m had observation periods shortened proportionally, i.e. one minute per 4 m^2 of transect). Immediately before the observation period, shaded and unshaded temperature as well as maximum 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. 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 the average was used. Observations were not conducted at temperatures below 11.9°C, or when average wind speeds exceeded 1.9 m/s or maximum wind speeds exceeded 4 m/s.

During the observation period, all occurrences of bees visiting open flowers were recorded by the same two observers, standing 4 m across from one another, on either side of the transect. 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 genus or species identification was not possible by one observer, the observation time was paused and both observers attempted to catch the bee and either take a photograph from inside a glass vial, or collect as a voucher (79 specimens total). Vouchers were then identified to species or genus, and will be deposited in Dr. Jessica Forrest's lab 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 Apoidea. Analyses of bee visitation rate per transect were conducted on observations from all bees (8422 visits), and separately with the most commonly observed bee taxa: honey bees (*Apis mellifera* L., 2455 visits), bumble bees (*Bombus* Latreille, 2212 visits), squash bees (*Peponapis pruinosa* (Say), 1519 visits), and bees from the families Halictidae (1255 visits), Andrenidae (528 visits), and Megachilidae (171 visits). Spatial autocorrelation among sites in the number of visits by each taxon was assessed using Moran's I (Paradis et al. 2004).

2.3 Floral Resources

Floral density was recorded at each sampling location, using three quadrats of 1.5 m × 1.5 m. Quadrats were placed in randomly generated locations along the transects used for observations of bee visits, immediately following the observation period. If no open flowers were present in a quadrat location, the absence was recorded and a new location was randomly selected. In each quadrat, the number of open non-graminoid flowers or inflorescences was counted for each species encountered within a quadrat. Species with many small-flowered inflorescences had five individuals selected haphazardly on which the number of flowers on a randomly chosen inflorescence was counted. In members of the Asteraceae family, the inflorescences or capitula were treated as single flowers (see Appendix 2 for descriptions of floral units used for counts of each species). 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.

To estimate the amount of floral resources, or pollen and nectar, provided by a flowering species, floral dimensions were measured on all species encountered in quadrats. On five haphazardly selected individuals of each species, the length and width of the receptacle (or capitulum in Asteraceae species), as well as the height from the receptacle to the end of the longest sexual organ (stamen or pistil) were measured; in species with sexual organs completely hidden within a corolla, the height was measured from the receptacle to the end of the corolla. Measurements were done with calipers and rounded to the nearest 1 mm. Any species not measured (or for which the number of flowers per inflorescence was not counted) in the field had floral unit measurements obtained from literature and from digital images of herbarium specimens (see Appendix 2 for measurements and literature sources for each species). Measurements of length, width and height were then used to calculate both the area (area of an ellipse = π × 0.5 × length × 0.5 × width) and the volume (elliptic cylinder volume = π × 0.5 × length × 0.5 × width × height) of flowers.

To determine which floral measurement was the best proxy for the amount of floral resources per flower, literature searches for daily nectar sugar mass (µg/day) and pollen volume (in µl/flower) were conducted for all flowering species encountered; these measurements are commonly used to assess the floral resources available to pollinators (Baude et al. 2016; Hicks et al. 2016). Additionally, literature sources for flowering species that provided counts of pollen grains per flower were used in conjunction with literature values of pollen grain volume to calculate an estimate of pollen volume per flower. Out of 93 flowering species or cultivars encountered in quadrat surveys, nectar production values were obtained for 46 species and pollen volumes for 33 species (see Appendices 3 and 4 for full species lists). Pearson correlations were then run between nectar sugar mass or pollen volume and the length, width, height, area, and volume measurements of each species (all variables log-transformed to approximate normal distributions), to determine which floral dimension(s) could best estimate the amount of floral resources.

Depending on floral morphology, rewards of certain flowering species may only be accessible to certain functional groups of bees (Fenster et al. 2004). Floral resources available to a given bee taxon should therefore be weighted based on whether rewards are accessible to those bees, specifically. Although I did not record whether individual bees accessed rewards during each observed interaction with a flower, resource availability to a given bee taxon can be reasonably estimated based on the observed number of interactions between that taxon and the plant species in question. Thus, each flowering species was assigned a weight proportional to the number of visits received by a given taxon of bees. This weight was multiplied by the estimated floral resources of each flowering species to calculate bee taxon-specific floral resource abundances, which were used as predictors in “weighted” analyses. These were run in addition to analyses with unweighted floral resource abundance (“unweighted” analyses).

2.4 Landscape Structure

The composition of the landscape within a 750-m, 500-m, and 250-m radius of each sampling location was quantified to determine how landscape structure influences the presence of foraging bees. This scale (250–750 m) 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 between the two spatial extremes. Sampling locations with overlapping radii were considered to be within the same site, and thus were not treated as independent for statistical analysis. Within a 750-m radius around a sampling location, each parcel was identified and boundaries were manually digitized at a resolution of 1:1000 in QGIS version 2.18.7, using waypoints taken on-site with a Trimble® Juno SD handheld GPS unit (Trimble Navigation Limited, Westminster, CO, USA), Google Earth satellite imagery taken between 26 September 2013 and 5 September 2016, and Bing Aerial satellite imagery taken between December 2009 and May 2014 (Fig. 2).

Each parcel in the landscape was then categorized by type of land-use (hereafter, "land type"), primarily through on-site inspections, and, when this was not possible, through raster imagery from Agriculture and Agri-Food Canada's (AAFC) 2016 Annual Crop Inventory. Land types were divided into three groups: non-resource land, resource land, and unknown area (see Table 1 for full list of land types and descriptions). Non-resource land was comprised of land area that did not provide floral resources, which included crops with flowers that are exclusively wind-pollinated, and crops with only anecdotal or no evidence indicating that bees obtain resources from flowers. Non-resource land was comprised of seven land-types (Table 1). Urban and developed land was included in non-resource land, because although urban gardens or lawns may provide floral resources for bees, the amount is inconsistent over time and space, and species richness of bees that are supported is usually low (Cane 2005, Matteson et al. 2008). Resource-providing land was either crop land or unmanaged land areas that provide floral resources for bees during a period of time over the season (Table 1). All sampling locations were within resource-providing land, and at least one parcel of each resource-providing land type was sampled during each of the sampling periods (late-spring, early-, mid-, and late-summer). Unknown land was comprised of areas where I 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 floral resources were not measured during the field season (0.7%; Table 1).

The total area of each land type was calculated within radii of 250, 500, and 750 m around each sampling location using QGIS version 2.18.7, with Projected Coordinate System WGS 84/UTM zone 18N (EPSG:32618). The abundance of floral resources in the landscape surrounding each sampling location was calculated by determining the mean floral resource value per flower of each species (see *Floral Resources*, above), and multiplying this value by the count of each flower in a quadrat. The mean abundance of floral resources 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 sampling 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 floral resources during a given sampling period.

All analyses were initially run with unknown land area assigned the median floral resource value calculated from all land types within a specific radius during a given sampling period (hereafter “median” models). For models with floral resources weighted by the proportion of bee visits, the median weighted value from all land types for a specific bee taxon was used. As a test of the sensitivity of my conclusions to these estimated resource values, all weighted models were also run with floral resource terms that included unknown areas assigned the minimum floral resource value calculated, which was always zero (hereafter “minimum” models), as well as with unknown areas assigned the maximum floral resource value calculated from all land types over the entire season (hereafter “maximum” models). For maximum models with floral resources weighted by the proportion of bee visits, the maximum weighted value from all land types for a specific bee taxon was used.

2.5 Statistical Analyses

To examine how the temporal and spatial scale of floral resources affects the presence of bees within a season, models were run separately for all bees and for each taxon of bees (honey bees, bumble bees, squash bees, Halictidae, Andrenidae, Megachilidae) during each sampling period (late-spring, early-, mid-, and late-summer). As described in the previous section, four iterations of analyses were run: either “weighted” models, with floral resource values weighted by the proportion of visits received by a particular bee taxon, or “unweighted” models, with floral resource values calculated from measured floral dimensions, which were consistent across all bee taxa examined; both weighted and unweighted analyses included “median” models, wherein unknown land area is assigned the median calculated floral resource value from all land types during a given sampling period, and weighted models were additionally run with “minimum” models, wherein unknown land is assigned a floral resource value of zero, and “maximum” models, wherein unknown land is assigned the maximum calculated floral resource value from all land types.

For each set of analyses, generalized linear mixed models were run with a zero-inflated negative binomial distribution and log link function, using the glmmADMB package (Fournier et al. 2012), with the total number of visits observed (by all bees or each bee taxon) within a transect as the response variable. Models included the following five potential fixed effects, all $\log_{10}$ transformed to approximate normality: floral resource abundance during the present sampling period, within the transect used for sampling (local scale); floral resource abundance during the present sampling period, within a given radius around a sampling location (250-m, 500-m, or 750-m; radius selection described below); for models of bee visits in early-summer, mid-summer, and late-summer, the floral resource abundance from the previous sampling period, within the same radius distance around a sampling location; for models of bee visits in mid-summer and late-summer, the floral resource abundance from two sampling periods previous, within the same radius distance around a sampling location; and for models of bee visits in late-summer, the floral resource abundance from three sampling periods previous, within the same radius distance around a sampling location. When two or more floral resource terms from different sampling periods were included in models, only consecutive terms were included (i.e., a model would only include floral resources from late-spring and mid-summer sampling periods if it also included floral resources from early-summer). Farm site identity was included as a random effect in all models, and a log offset of the length of observation period (in minutes) was included in all models to account for different sizes of transects. Models were checked for multicollinearity, and were excluded from analyses when VIF values were ≥ 4. See Appendix 5 for an example of all candidate models run.

To determine the spatial scale which best described the number of visits observed from each bee taxon, all models were initially run with floral resource terms at each spatial scale (250-

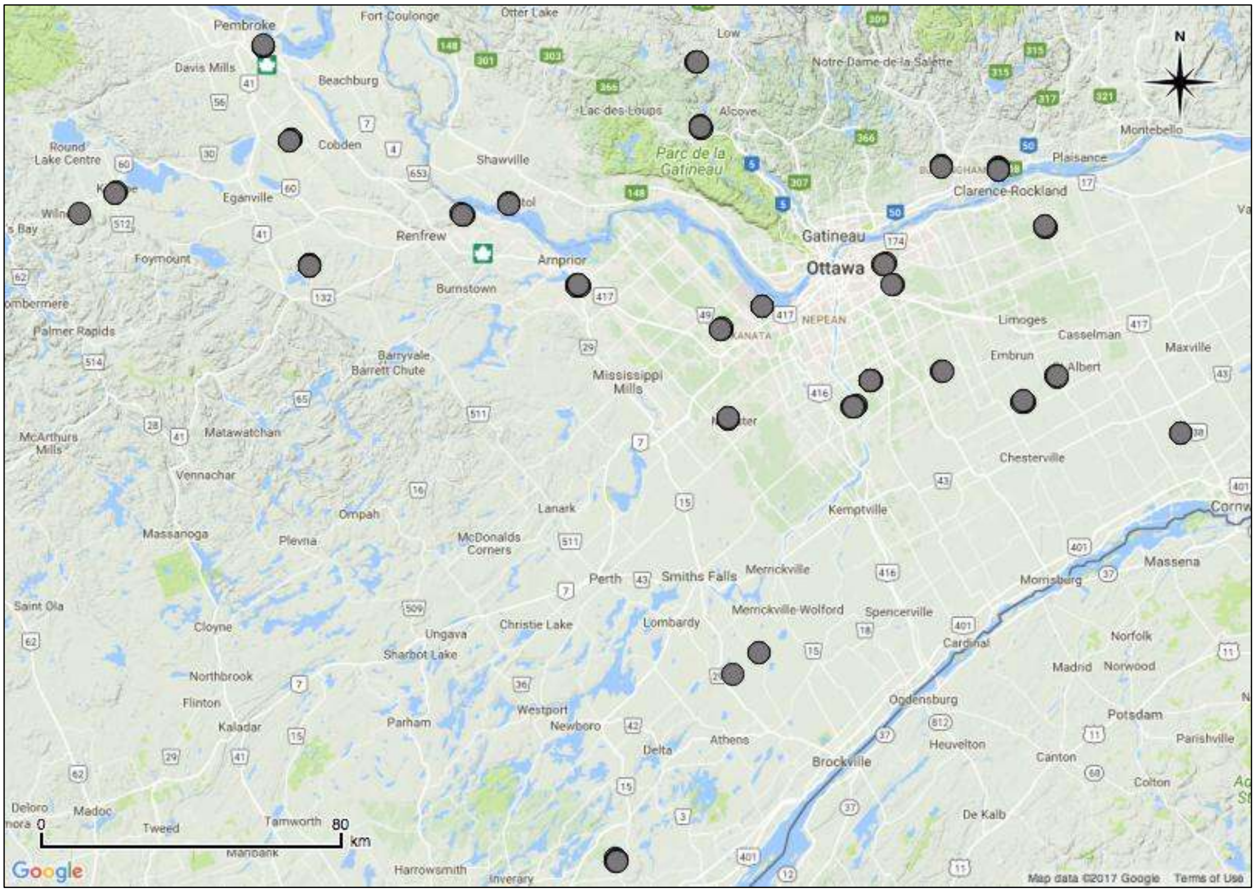
m, 500-m, or 750-m). A model selection process was used to compare all possible models for bee visits during each sampling period for a given bee taxon using the model.sel command from the MuMIn package in R (Bartoń 2016). All models with ΔAICc values < 2 were assigned scores, with the highest score given to the models with ΔAICc of 0 for each sampling period. The spatial scale with the highest score, summed across sampling periods, was then determined for each bee taxon, across median, minimum, and maximum models for weighted analyses, and for the unweighted models, to determine the appropriate spatial scale for each taxon. The highest-scoring spatial scale for a given bee taxon was then used to re-run models with the same fixed effects, to determine the temporal scale of floral resources that best predicted bee visits. The best model for each bee taxon was chosen based on AICc values computed using the MuMIn package in R (Bartoń 2016). All statistical analyses were performed in R version 3.2.2 (R Core Team, 2015).

Table 1. Land-types within “non-resource” land, resource-providing land, and unknown land 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.

Table 1.

	Land type	Description	% of total area in 750 m
Non-resource land	Water		Not digitized
	Exposed/barren land		Not digitized
	Cereal crops	Barley, millet, oats, rye, spelt, triticale, wheat	0.002 –15%
	Corn		0.3–38%
	Soybean		1.5–55%
	Herbs/field vegetables	Non-flowering, or harvested before flowering	0.02–5.4%
	Urban/developed land		Not digitized
Resource-providing land	Semi-natural land	Shrub land, grassland	0.4–35%
	Pasture/forage	Hay, alfalfa (*Medicago sativa*), clover (*Trifolium* spp.)	1.7–60%
	Forest		4.6–87%
	Apple	*Malus pumila*	0.05–4.2%
	Asparagus	*Asparagus officinalis*	0.01–0.5%
	Bean	Green beans, snap beans, pole beans, kidney beans, haricots (*Phaseolus vulgaris*)	0.006–0.5%
	Cucumber	*Cucumis sativus*	0.003–0.02%
	Melon	Honeydew, sweet melon, cantaloupe (*Cucumis melo*)	0.01–0.8%
	Potato	*Solanum tuberosum*	0.26–0.29%
	Raspberry	*Rubus idaeus*, *R. strigosus*, *R. occidentalis*	0.002–0.9%
	Squash	*Cucurbita* spp.	0.01–7.1%
	Strawberry	*Fragaria* × *ananassa*	0.5–3.5%
	Sunflower	*Helianthus annuus*	0.005–0.05%
	Watermelon	*Citrullus lanatus*	0.01–0.2%
Unknown land	Undetermined crop land		0.08–21%
	Hedgerow	Areas bordering agricultural fields with shrubs or trees	0.05–6.8%
	Potential resource-providing crops	Blackberry (*Rubus fruticosus*), ground cherry (*Physalis* spp.), buckwheat (*Fagopyrum esculentum*), canola (*Brassica rapa*, *B. napus*, *B. juncea*), peas (*Pisum sativum*), pears (*Pyrus communis*), peppers (*Capsicum annuum*), cherries (*Prunus avium*), tomatoes (*Lycopersicon esculentum*)	0.002–1.1%

Figure 1. Map of farm sites (n = 27) in Eastern Ontario and the Outaouais region of Québec, Canada. Sampling locations are represented with filled grey circles, ranging north–south 45.7937 to 44.4167 and east–west −74.8702 to −77.5061 (see Appendix 1 for coordinates of all sampling locations). Base map image is taken from Google Maps Physical in QGIS v. 2.18.7.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Notre-Dame-de-la-Salette
Davis Mills
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Alcove
Montebello
Round Lake Centre
Cobden
Shawville
Parc de la Gatineau
Plaisance
Eganville
Clarence-Rockland
Renfrew
Gatineau
Foymount
Arnprior
Ottawa
Burnstown
NEPEAN
KANATA
Limoges
Casselman
Palmer Rapids
Embrun
Maxville
Barryvale
Barrett Chute
Mississippi Mills
Matawatchan
McArthurs Mills
Chesterville
Vennachar
Kemptville
Lanark
Ompah
Massanoga
Plevna
McDonalds Corners
Massena
Perth
Smiths Falls
Merrickville
Morrisburg
Saint Ola
Merrickville-Wolford
Spencerville
Cloyne
Christie Lake
Lombardy
Ungava
Cardinal
Norfolk
Sharbot Lake
Madrid
Norwood
Northbrook
Flinton
Westport
Ogdensburg
Potsdam
Kaladar
Parham
Newboro
Heuvelton
Delta
Athens
Parishville
Brockville
Canton
Colton
Deloro
Madoc
Tweed
Tamworth
De Kalb
Marlbank
Harrowsmith
Inverary
Google
Map data ©2017 Google
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Figure 1.

Figure 2. Schematic of site with sampling locations represented as filled black triangles, and radii of 250 m, 500 m, and 750 m represented as concentric overlapping circles around each sampling location. Polygons, or non-circular black lines, represent parcels delineating different land types, and white or empty spaces indicate areas that were not digitized (water, exposed/barren land, or urban/developed land). Image was created in QGIS v. 2.18.7.

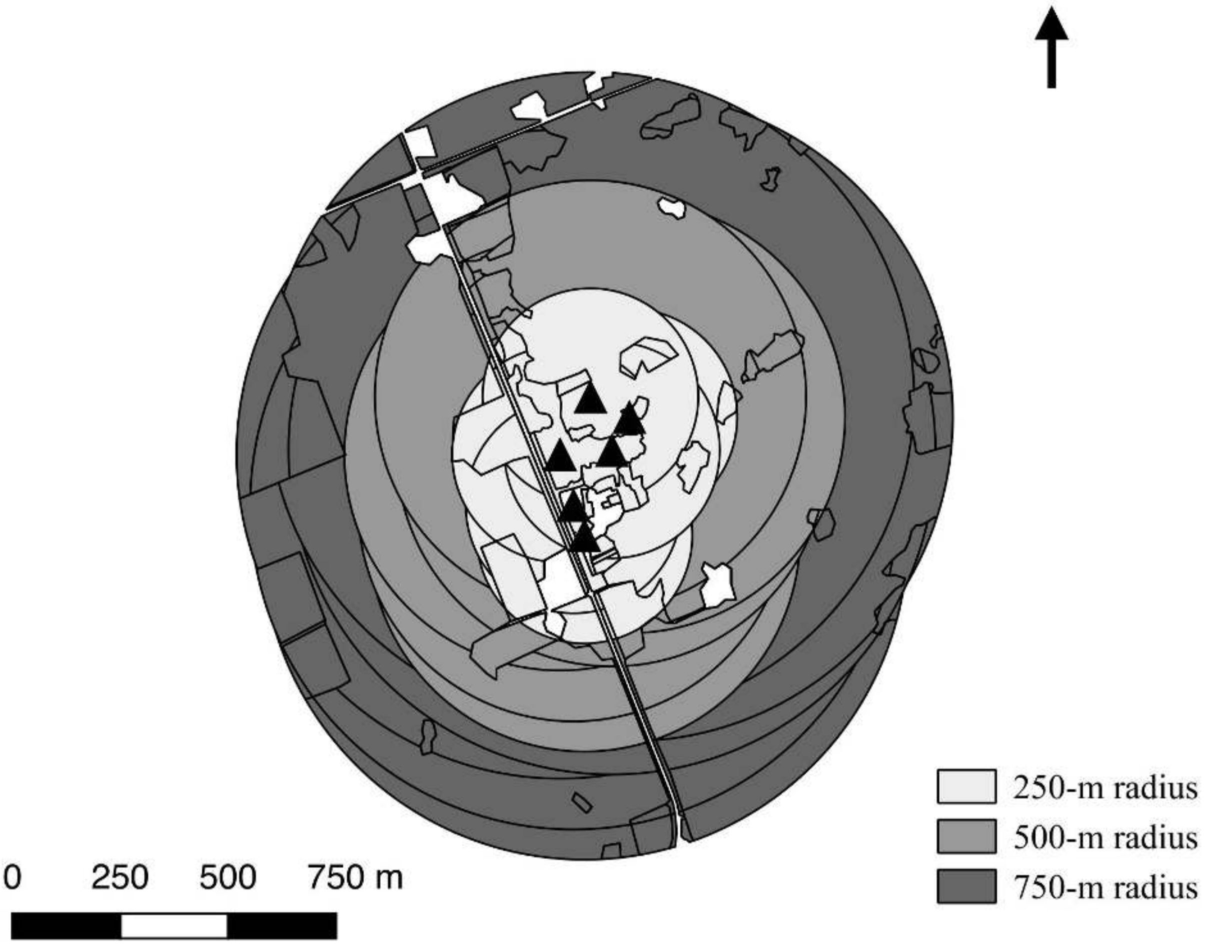


Figure 2.

CHAPTER 3: RESULTS

3.1 Measurement of Floral Resources

Daily nectar sugar mass (µg/day) was best predicted by floral volume ($R^2 = 0.39$, $p = 3.6\times10^{-6}$, n = 46, Fig. 3a); all other measurements (flower length, width, height, and surface area) were also significantly correlated with nectar, but to a lesser degree, with height being the second best predictor ($R^2 = 0.33$, $p = 2.7\times10^{-5}$, n = 46). Pollen volume (µl/flower) was also best predicted by floral volume ($R^2 = 0.40$, $p = 6.0\times10^{-5}$, n = 33, Fig. 3b); again, all other measurements were also significantly correlated with pollen, and height was the second best predictor ($R^2 = 0.34$, $p = 0.0003$, n = 33). Thus, floral volume was used to represent floral resources in all subsequent analyses.

3.2 Floral Resources Weighted by Bee Visits

Flowering species (and, consequently, land types) varied greatly in the extent to which they were visited by different bee taxa (see Table 2 for weighted values and unweighted floral resource volumes of land types). Weighted values for land types ranged from 0, when members of a bee taxon were not observed visiting any flowering species in a given land type, to 99.7, wherein 99.7% of visits observed by a bee taxon were to only one flowering species. The latter was the weighted value for squash bees visiting *Cucurbita* spp.; hence, the “squash” land type was given the weighted value of 99.7 in squash bee analyses (Table 2).

3.3 Spatial Scale

The spatial scale at which floral resources best predicted bee visits differed among bee taxa, as well as between models wherein unknown areas were assigned median, minimum, or maximum floral resource values, and between models with weighted or unweighted floral resources (see Appendix 6 for summary of all models run). Across all models, the spatial scale with the highest score for all bee visits, honey bee visits, and Andrenidae visits was a 750-m radius around sampling locations, while a 500-m radius was the spatial scale with the highest score for models of Megachilidae visits, and a 250-m radius had the highest score for models of bumble bee, squash bee, and Halictidae visits. There was no spatial autocorrelation among sites in the number of bee visits by any taxon during any sampling-period ($p > 0.12$ for all taxa, Moran's I |observed – expected| values ranged from 0.003-0.43).

3.4 Present and Past Floral Resources as Predictors of Bee Visits

3.4.1 Present, local-scale floral resources

For each bee taxon other than squash bees, transects with a greater amount of weighted floral resources at the time of sampling experienced more bee visits, during at least one sampling period (Table 3, Figure 4). However, unweighted floral resources were found to be positively or negatively associated with bee visits, depending on the taxon or sampling period that was examined (Table 4).

In late-spring, transects with more weighted floral resources experienced more bee visits from Andrenidae (β_{median} = 1.0, p_{median} = 0.04, Fig. 4e; see Appendix 8 for all minimum and maximum models of weighted floral resources). Megachilidae visits were also positively correlated with weighted floral resources, though only in the median and minimum models (β_{median} = 0.72, p_{median} = 0.002, Fig. 4f, Appendix 8), and Megachilidae were observed in only four sampling locations in late-spring. Weighted floral resources at the transect level did not predict late-spring bee visits by any other taxa (Table 3). Transects in late-spring with higher values of unweighted floral resources experienced a higher number of visits by all bees (β_{median} = 0.47, p_{median} = 0.001) and by Megachilidae specifically (β_{median} = 1.0, p_{median} = 0.005), but not by other individual bee taxa (Table 4). Squash bee visits in late-spring were not analyzed, as squash bees were not observed in any sampling locations.

In early-summer, the number of visits by honey bees (β_{median} = 1.1, $p_{median} < 0.001$, Fig. 4b, Appendix 8) and Megachilidae (β_{median} = 0.73, p_{median} = 0.006, Fig. 4f, Appendix 8) was higher in transects with more weighted floral resources. The total number of bee visits was also best predicted by weighted floral resources within transects, although this relationship was not significant in the maximum model (β_{median} = 0.38, p_{median} = 0.03, Fig. 4a, Appendix 8). Halictidae visits in early-summer were also positively associated with weighted floral resources, though this relationship was not significant (Fig. 4d, Table 3). Weighted floral resources in transects during early-summer did not predict bee visits for any other taxa (Table 3). Unweighted floral resources within transects were positively correlated with the total number of bee visits in early-summer (β_{median} = 0.51, p_{median} = 0.047), but were not significantly correlated with the number of bee visits observed from individual taxa (Table 4). Squash bee visits in early-summer were not analyzed individually, as squash bees were present in only one sampling location.

Weighted floral resource abundance within transects during mid-summer was significantly positively associated with the number of visits observed for all bees ($\beta_{median} = 0.52$, $p_{median} = 0.003$, Fig. 4a, Appendix 8), bumble bees ($\beta_{median} = 0.56$, $p_{median} < 0.001$, Fig. 4c, Appendix 8), Halictidae ($\beta_{median} = 0.96$, $p_{median} < 0.001$, Fig. 4d, Appendix 8), Andrenidae ($\beta_{median} = 1.0$, $p_{median} < 0.001$, Fig. 4e, Appendix 8), and Megachilidae ($\beta_{median} = 0.87$, $p_{median} = 0.008$, Fig. 4f, Appendix 8). Honey bee visits were also positively correlated with weighted floral resources at a local scale, though only in median and minimum models ($\beta_{median} = 0.78$, $p_{median} = 0.01$, Fig. 4b, Appendix 8). Squash bee visits in mid-summer were not predicted from weighted floral resources within a transect (Table 3). Unweighted local floral resources were significantly correlated with Halictidae visits in mid-summer ($\beta_{median} = 0.96$, $p_{median} = 0.01$), but not with visits by any other taxa (Table 4).

During late-summer, weighted floral resources in a transect did not predict visitation rate of any taxa observed, other than Andrenidae (Table 3), wherein the number of visits was higher in transects with more floral resources ($\beta_{median} = 0.77$, $p_{median} = 0.04$, Figure 4e, Appendix 8). However, Andrenidae visits were only observed in four sampling locations during late-summer. For unweighted values of floral resources, there was a significant negative association with squash bee visits in late-summer ($\beta_{median} = -3.8$, $p_{median} < 0.001$), and a positive association with Megachilidae visits ($\beta_{median} = 3.3$, $p_{median} = 0.02$).

3.4.2 Present, landscape-scale floral resources

The average amount of floral resources in a landscape changed depending on which spatial and temporal scale was examined. Within a 250-m radius, the average amount of floral resources was highest in late-spring, and steadily decreased with each consecutive sampling period. At both 500-m and 750-m spatial scales, the average amount of floral resources increased from late-spring to early-summer, then decreased in subsequent sampling periods. At each spatial scale, floral resources in late-summer were the lowest on average of all sampling periods. Conversely, late-summer experienced the highest average number of bee visits per sampling location over the entire season, with each previous sampling period decreasing in the average number of bee visits observed.

In late-spring, the total number of bee visits increased with the weighted floral resources within a 750-m radius during the same time period ($\beta_{median} = 0.92$, $p_{median} = 0.02$, Fig. 5a), although this relationship was not significant in the maximum model (Appendix 8). Both bumble bee (Fig. 5c) and Halictidae (Fig. 5e) visits appeared to be positively associated with the amount of weighted and unweighted floral resources within 250 m during late-spring, though not significantly (Table 3 & 4). The number of Megachilidae visits observed in late-spring decreased with increasing floral resources within a 500-m radius (weighted $\beta_{median} = -5.3$, $p_{median} < 0.001$, Fig. 5f, Appendix 8; unweighted $\beta_{median} = -10.5$, $p_{median} < 0.001$); however, Megachilidae were observed in only four sampling locations during late-spring. Honey bee visits were positively associated with the amount of unweighted floral resources at 750 m, though non-significantly ($\beta_{median} = 1.07$, $p_{median} = 0.75$). Models of bee visits in late-spring for all other taxa examined did not include the present amount of weighted (Table 3) or unweighted floral resources (Table 4) at a landscape scale.

In early-summer, the total number of bee visits was negatively but non-significantly associated with the present amount of weighted floral resources within a 750-m radius ($\beta_{median} = -2.07$, $p_{median} = 0.06$, Fig. 5a, Appendix 8). This relationship was significant for unweighted floral resource values ($\beta_{median} = -2.3$, $p_{median} = 0.04$). On the other hand, bumble bee visits in early-summer had a positive but non-significant relationship with unweighted floral resources within 250 m ($\beta_{median} = 0.41$, $p_{median} = 0.5$). Landscape-level floral resources in early-summer were not correlated with bee visits from any other taxa during the same sampling period (Table 3 & 4).

In mid-summer, weighted floral resources at the landscape scale were not correlated with visits from bee taxa examined during the same sampling period (Table 3), other than squash bees, which showed a non-significant negative correlation with resources in a 250-m radius ($\beta_{median} = -1.4$, $p_{median} = 0.06$, Fig. 5d, Appendix 8). However, the amount of unweighted floral resources within 250 m was positively associated with both squash bee visits in mid-summer ($\beta_{median} = 5.0$, $p_{median} < 0.001$) and bumble bee visits ($\beta_{median} = 2.6$, $p_{median} = 0.01$). Unweighted floral resources in mid-summer was also the best predictor of total bee visits during the same sampling period, though this relationship was not significant ($\beta_{median} = -0.06$, $p_{median} = 0.93$).

Honey bee visits in late-summer were negatively correlated with weighted floral resources at a landscape scale during the same sampling period, though only in median and minimum models ($\beta_{median} = -26.5$, $p_{median} = 0.02$, Fig. 5b, Appendix 8, Table 3). Bumble bee visits were, however, positively correlated with unweighted floral resources in a 250-m radius during late-summer ($\beta_{median} = 2.0$, $p_{median} = 0.02$), while Megachilidae visits were negatively associated with unweighted floral resources in a 500-m radius, though not significantly ($\beta_{median} = -9.9$, $p_{median} = 0.06$). Late-summer bee visits for all other taxa were not predicted by the present abundance of floral resources in the landscape (Table 3 & 4).

3.4.3 Past, landscape-scale floral resources

Andrenidae visits in early-summer were best predicted by the abundance of late-spring floral resources in a 750-m radius (weighted: $\beta_{median} = 2.1$; $p_{median} = 0.001$; Fig. 6d; Appendix 8, unweighted: $\beta_{median} = 2.1$; $p_{median} < 0.001$). Conversely, Megachilidae visits in early-summer were negatively associated late-spring floral resources within 500 m (weighted: $\beta_{median} = -2.9$; $p_{median} = 0.009$; Fig. 6e; Appendix 8, unweighted: $\beta_{median} = -3.6$; $p_{median} = 0.06$). Bumble bee visits in early-summer were also negatively associated with floral resources during late-spring, though not significantly ($\beta_{median} = -0.03$, $p_{median} = 0.9$, Fig. 6b, Appendix 8). Late-spring floral resources did not predict early-summer bee visits in any other taxa (Table 3 & 4).

In mid-summer, the total number of bee visits was negatively yet non-significantly associated with the abundance of weighted floral resources in late-spring ($\beta_{median} = -0.32$, $p_{median} = 0.5$, Fig. 6a). Unweighted floral resources during late-spring were negatively correlated with mid-summer bumble bee visits ($\beta_{median} = -2.7$, $p_{median} = 0.008$), and honey bee visits, though not significantly ($\beta_{median} = -1.4$, $p_{median} = 0.11$). Late-spring floral resources did not predict mid-summer bee visits for any other taxa in weighted or unweighted models (Table 3 & 4).

The total number of bee visits in late-summer was negatively associated with late-spring floral resources in a 750-m radius, which was a significant relationship in all models except the weighted maximum model (weighted: $\beta_{median} = -0.68$; $p_{median} = 0.03$; Fig. 6a; Appendix 8, unweighted: $\beta_{median} = -0.89$, $p_{median} = 0.04$). Megachilidae visits in late-summer also decreased with increasing late-spring weighted floral resources ($\beta_{median} = -1.7$, $p_{median} = 0.01$, Fig. 6e, Appendix 8); however, Megachilidae were observed in only three sampling locations during late-summer. Halictidae visits in late-summer were also negatively associated with late-spring floral resource abundance; however, this relationship was only significant for unweighted values (weighted: $\beta_{median} = -1.9$; $p_{median} = 0.08$; Fig. 6c; Appendix 8, unweighted: $\beta_{median} = -2.7$; $p_{median} = 0.02$). Late-summer honey bee visits, unlike the other taxa examined, increased with unweighted floral resources within a 750-m radius during late-spring ($\beta_{median} = 6.0$, $p_{median} = 0.04$); for all other taxa examined in late-summer, bee visits were not predicted by late-spring floral resource availability, either weighted or unweighted (Table 3 & 4).

Early-summer floral resources only predicted mid-summer bee visits in unweighted models (Table 3 & 4). Unweighted early-summer floral resources were negatively correlated with the number of visits by bumble bees and squash bees during mid-summer (Table 4), but only significantly so with squash bee visits ($\beta_{median} = -3.7$, $p_{median} = 0.02$). Early-summer weighted floral resources were positively associated with late-summer honey bee visits, although the direction of this relationship was inconsistent across models ($\beta_{median} = 8.0$, $p_{median} = 0.08$, Fig. 7a, Appendix 8). Late-summer bumble bee visits were also positively correlated with weighted floral resources from early-summer, though only in median and minimum models ($\beta_{median} = 2.1$, $p_{median} = 0.02$, Fig. 7b, Appendix 8). Early-summer floral resources did not predict bee visits in subsequent sampling periods for any other taxa examined (Table 3 & 4).

Weighted mid-summer floral resources were positively correlated with late-summer honey bee visits ($\beta_{median} = 17.5$, $p_{median} = 0.04$, Fig. 7c) and negatively but non-significantly with squash bee visits ($\beta_{median} = -0.42$, $p_{median} = 0.4$, Fig. 7d); however, neither relationship was consistent across minimum and maximum models (Appendix 8). Conversely, unweighted mid-summer floral resources were negatively, though non-significantly associated with honey bee visits in late-summer ($\beta_{median} = -0.5$, $p_{median} = 0.6$) Mid-summer floral resources did not predict late-summer visits by any other bee taxa.

Table 2. Weighted values and unweighted volumes of all resource-providing land types for each bee taxon over all sampling periods. Values in table represent the median weighted floral volume per 1 m^2 of a land type divided by the median measured (or unweighted) floral volume (cm^3) per 1 m^2 of a land type. Weighted floral volumes were calculated with the percent of visits observed to each flowering species by each bee taxon, multiplied by the measured floral volume of each species. Weighted floral volumes were used to calculate the average floral volume per 1 m^2 of transect, then the median value of floral resources across all transects of the same land type during a given sampling period (see Appendix 9 for sample calculation of weighted floral resources). Sample sizes represent the total number of sampling locations where floral resources were measured during a given sampling-period. Any resource-providing land types that had a median floral resource value of zero (0 cm^3/m^2) during a given sampling period are not shown (see Table 1 for list of all resource-providing land types).

Table 2.

Sampling Period	Land Type (sample size)	Unweighted volume (cm^3/m^2)	All bees	Honey bees	Bumble bees	Squash bees	Halictidae	Andrenidae	Megachilidae
Late-spring	Apple (2)	41.6	5.94	16.3	2.98	0	1.27	2.46	0
	Forage (13)	3.7	4.43	6.78	2.46	0	5.55	7.93	4.80
	Forest (16)	0.1	0.022	0	0.011	0	0.049	0	0
	Semi-natural (6)	0.2	1.06	0.12	0.0083	0	5.57	0.20	5.77
	Strawberry (2)	12.6	3.30	7.34	0.77	0	4.46	3.32	1.46
Early-summer	Asparagus (1)	0.8	3.16	1.71	5.64	0	4.52	4.74	5.11
	Squash (2)	1.4	26.9	10.3	21.9	99.7	1.27	0	0
	Forage (13)	3.5	2.18	1.68	2.93	0	2.77	2.95	5.49
	Potato (1)	0.8	0.10	0.013	0.014	0	0.62	0	0
	Raspberry (3)	2.3	5.39	13.7	2.54	0	2.22	2.50	0.67
	Semi-natural (10)	2.8	3.74	1.49	8.08	0	4.38	6.64	6.25
	Strawberry (1)	13.0	1.89	3.67	0	0	5.18	0.19	0
	Sunflower (1)	31.2	0.81	0	1.53	0	0.16	0.38	9.8×10^{-5}
Mid-summer	Bean (1)	0.1	0	0	0	0	0	0	0
	Squash (16)	1.9	21.7	10.3	21.9	99.7	1.27	0	0
	Forage (10)	4.2	3.19	1.95	6.81	0	3.98	3.62	3.92
	Melon (1)	0.2	0.34	1.02	0.09	0	0.16	0	0
	Potato (1)	0.9	0.13	0	0	0	0.88	0	0
	Semi-natural (8)	1.0	2.96	4.86	4.06	0	2.11	2.29	6.40
	Watermelon (1)	0.1	0.60	1.91	0	0	0.32	0	0

Sampling Period	Land Type (sample size)	Unweighted volume (cm^3/m^2)	All bees	Honey bees	Bumble bees	Squash bees	Halictidae	Andrenidae	Megachilidae
Late-summer	Cucumber (1)	0.3	0.12	1.18	0	0.33	0.24	0	0
	Squash (20)	3.7	20.6	8.97	19.0	86.4	1.27	0	0
	Forage (12)	1.5	2.24	1.43	3.88	0	1.37	1.56	1.64
	Semi-natural (6)	1.5	2.81	1.48	2.43	0	2.56	1.51	4.87
	Sunflower (1)	36.3	0.81	0	1.53	0	0.16	0.38	0

Table 3. Model estimates and AICc values obtained from best models for bee visits in late-spring, early-summer, mid-summer, and late-summer sampling periods for all bee taxa. Generalized linear mixed models were run, with a zero-inflated negative binomial distribution and log link function. Floral resource (FR) terms in models represent the median floral volume per 1 m^2 of a land type, weighted by the proportion of visits to each flowering species by a given taxon. Spatial scale indicates the radius distance (250, 500, or 750 m) of floral resources surrounding a sampling location, with local spatial scale including only floral resources per 1 m^2 of the transect used for observation. Unknown areas within a given radius of a sampling location were assigned the median floral resource volume of all land types during a given sampling period, and used in calculations for FR values. Significant FR coefficients are indicated with * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$. Significant FR coefficients that are in bold indicate that both weighted models with unknown areas assigned either minimum or maximum floral resource values also produced significant FR coefficients of the same directional relationship. Shaded grey areas in table represent which past FR were not included in models of bee visits from a given sampling period.

Table 3.

Sampling period	Bee taxon	Spatial scale	Log_{10} Local FR	Log_{10} Present FR	Log_{10} Past FR			AICc
					Late-spring	Early-summer	Mid-summer	
Late-spring	All bees	750		0.92*				340.5
	Honey bees	All models failed to converge						
	Bumble bees	250		1.23				151
	Halictidae	250		0.50				239
	Andrenidae	Local	**1.00***					113.3
	Megachilidae	500	0.72**	**−5.30*****				47.4
Early-summer	All bees	750	0.38*	−2.07				343.9
	Honey bees	Local	**1.06*****					177.5
	Bumble bees	250			−0.026			213.2
	Halictidae	Local	0.05					256.6
	Andrenidae	750	−0.03		**2.07****			138.3
	Megachilidae	500	**0.73****		**−2.94****			82.3
Mid-summer	All bees	750	**0.52****		−0.32			384.7
	Honey bees	Local	0.78*					214.9
	Bumble bees	Local	**0.56*****					239.5
	Squash bees	250		−1.39				166.1
	Halictidae	Local	**0.96*****					204.8
	Andrenidae	Local	**1.04*****					118.7
	Megachilidae	Local	**0.87****					77.7
Late-summer	All bees	750			−0.73*			411.4
	Honey bees	750		−26.5*		8.04	17.5*	200.4
	Bumble bees	250				2.08*		306.4
	Squash bees	250					−0.42	228
	Halictidae	250			−1.91			130
	Andrenidae	Local	**0.77***					125.6
	Megachilidae	500			1.68*			43.5

Table 4. Model estimates and AICc values obtained from best models for bee visits in late-spring, early-summer, mid-summer, and late-summer sampling periods for all bee taxa. Generalized linear mixed models were run, with a zero-inflated negative binomial distribution and log link function. Floral resource (FR) terms in models represent the median floral volume per 1 m^2 of a land type (not weighted by bee visitation). Spatial scale indicates the radius distance (250, 500, or 750 m) of floral resources surrounding a sampling location, with local spatial scale including only floral resources per 1 m^2 in the transect used for observation. Unknown areas within a given radius of a sampling location were assigned the median floral resource volume of all land types during a given sampling period, and used in calculations for FR values. Significant FR coefficients are indicated with * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$. Significant FR coefficients that are bold indicate that median models with weighted FR also produced significant FR coefficients of the same directional relationship. Shaded grey areas in table represent which past FR were not included in models of bee visits from a given sampling period.

Table 4.

Sampling period	Bee taxon	Spatial scale	Log$_{10}$ Local FR	Log$_{10}$ Present FR	Log$_{10}$ Past FR			AICc
					Late-spring	Early-summer	Mid-summer	
Late-spring	All bees	Local	0.47**					336.2
	Honey bees	750		1.07				381.9
	Bumble bees	250	−0.17	2.17				154
	Halictidae	250		0.59				240.4
	Andrenidae	750		2.49				119.5
	Megachilidae	500	**1.03****	−10.5***				48.9
Early-summer	All bees	750	**0.51***	−2.3*				343.8
	Honey bees	Local	−0.09					185
	Bumble bees	250		0.41				212.9
	Halictidae	Local	−0.02					256.7
	Andrenidae	750			**2.12*****			135.4
	Megachilidae	500	0.68		−3.62			87
Mid-summer	All bees	750		−0.06				389.1
	Honey bees	750			−1.41			215.7
	Bumble bees	250	1.02	2.58**	−2.66**	−1.46		245.2
	Squash bees	250		4.99***		−3.67*		160.7
	Halictidae	Local	**0.96***					209.4
	Andrenidae	Local	0.41					133.1
	Megachilidae	Local	0.36					83
Late-summer	All bees	750			**−0.89***			412
	Honey bees	750			5.98*	−1.21	−0.51	220.5
	Bumble bees	250		2.02*				306.6
	Squash bees	Local	−3.82***					220.2
	Halictidae	250			−2.68*			128
	Andrenidae	All models failed to converge						
	Megachilidae	500	3.26*	−9.94				43.3

Figure 3. Correlation between floral volume (mm^3) and *(a)* daily nectar sugar mass (μg/day) in 46 flowering species (see Appendix 3 for species list); and *(b)* pollen volume (μl/flower) in 33 flowering species (see Appendix 4 for species list). Floral volume was calculated using measurements of length and width of receptacle, and height from the receptacle to the end of the longest sexual organ (stamen or pistil). Nectar and pollen measurements were obtained from literature sources. Black lines represent linear model estimates of nectar mass or pollen volume by floral volume, with shaded grey area representing 95% confidence intervals. Note logarithmic axes.

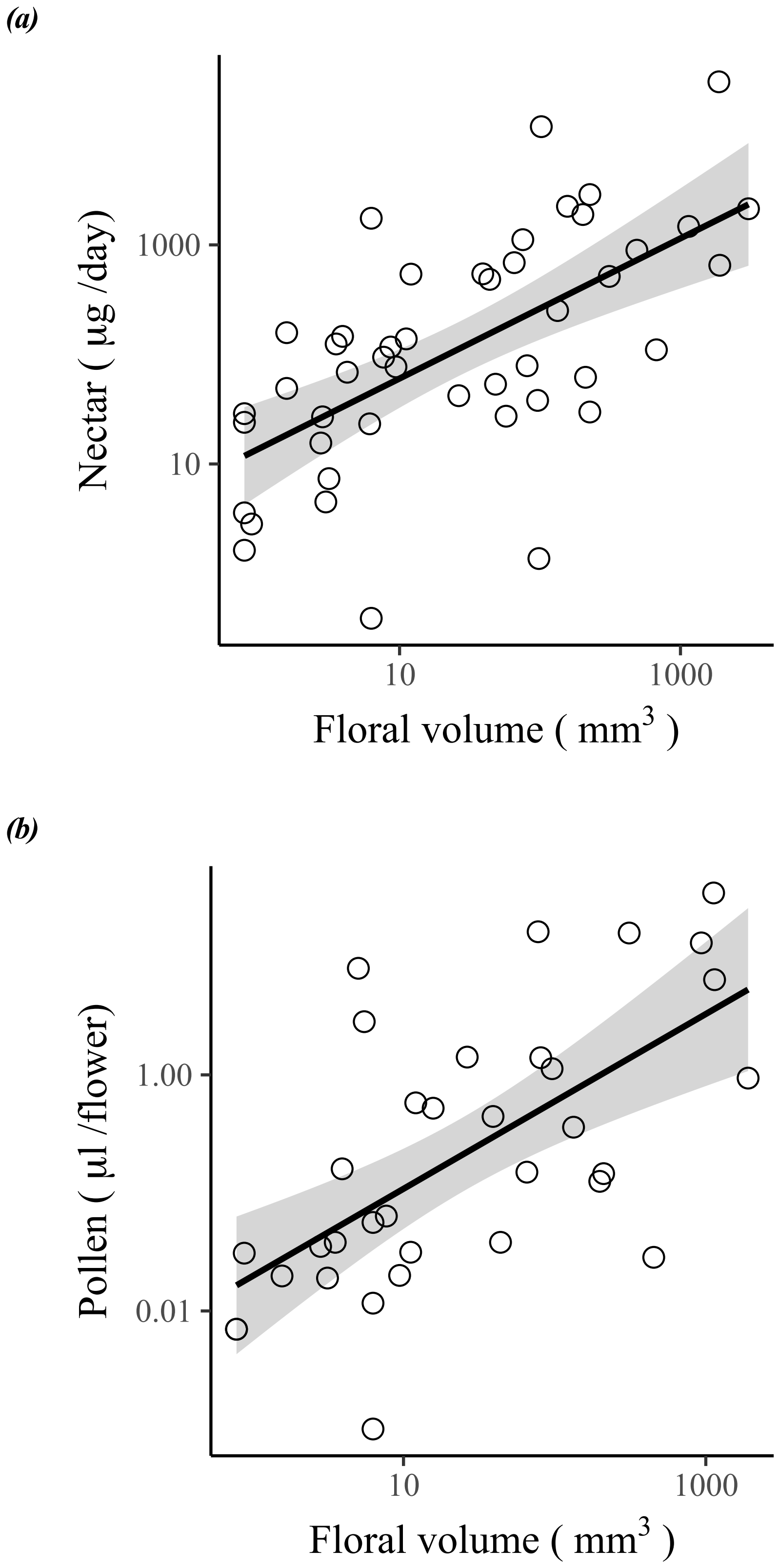

(a)
Nectar (µg /day)
1000
10
10
1000
Floral volume (mm^3)
(b)
Pollen (µl /flower)
1.00
0.01
10
1000
Floral volume (mm^3)

Figure 3.

Figure 4. Relationship between the abundance of weighted floral resources (FR) at a local scale (within a transect) and the number of bee visits observed during the same sampling period, where 1 = late-spring (20 May – 10 June), 2 = early-summer (10 June – 4 July), 3 = mid-summer (5 July – 1 August), and 4 = late-summer (1 August – 1 September). Bee taxa and sampling-periods shown are those in which the best models (with weighted floral resources and unknown areas assigned median values; Table 3) included the local floral resource term: ***(a)*** all bee visits in early- and mid-summer; ***(b)*** honey bee visits in early- and mid-summer; ***(c)*** bumble bee visits in mid-summer; ***(d)*** Halictidae visits in early- and mid-summer; ***(e)*** Andrenidae visits in all sampling periods; and ***(f)*** Megachilidae visits in late-spring, early-summer, and mid-summer. Floral resources are represented as the average floral volume (cm^3) of all flowering species per 1 m^2 of a transect, which was $\log_{10}$ transformed and is presented on a $\log_{10}$-scale axis. Circles represent raw data, and black lines represent the negative binomial fit of predicted values extracted from full models; solid lines repesent a significant relationship across median, minimum, and maximum models, and dashed lines represent a non-significant relationship, in at least one of the three models. In ***(b)*** and ***(d)*** plots, data points with weighted floral resource values of zero and zero bee visits are not shown, but are included as predicted values for fitted lines and were included in all analyses.

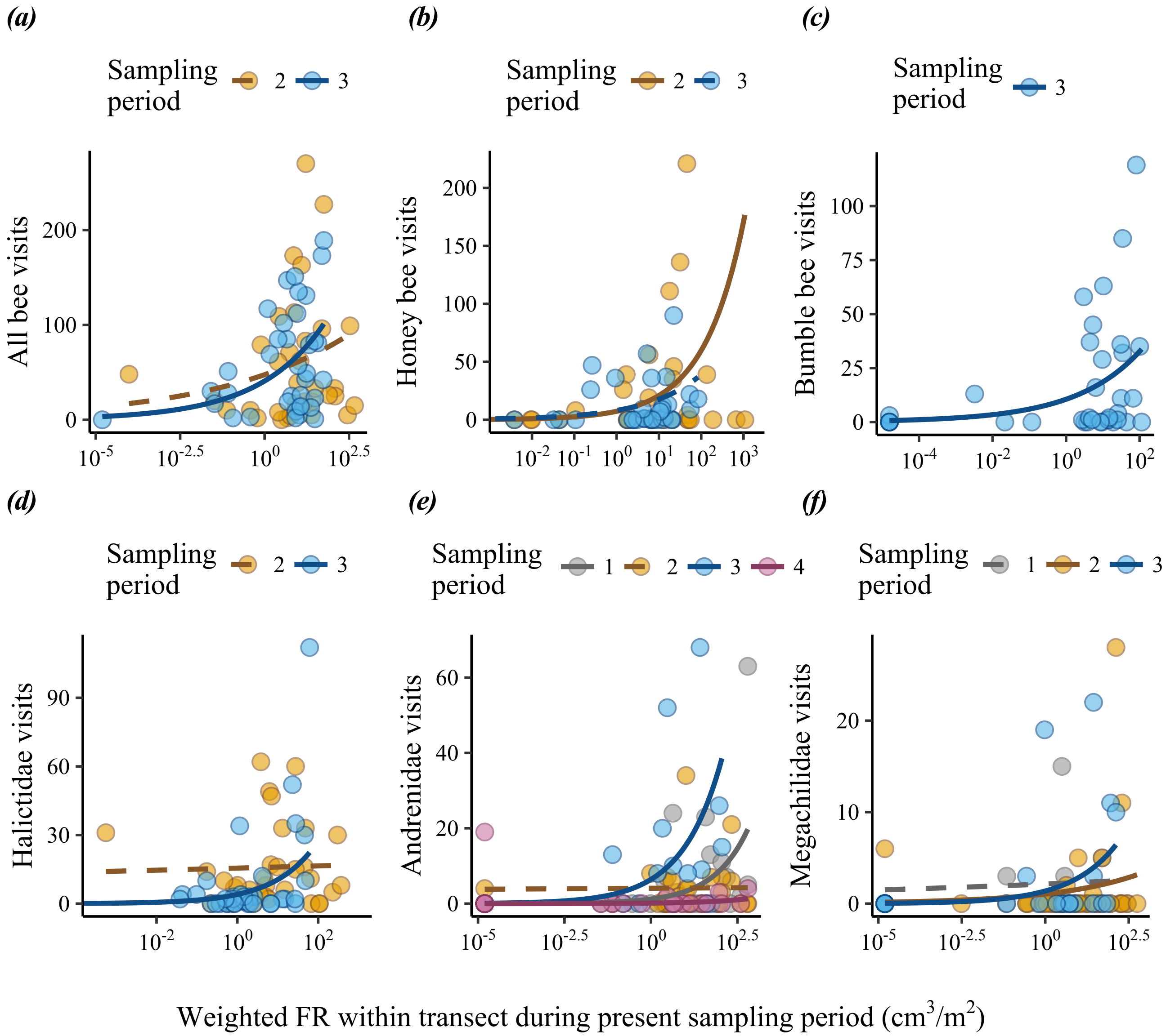
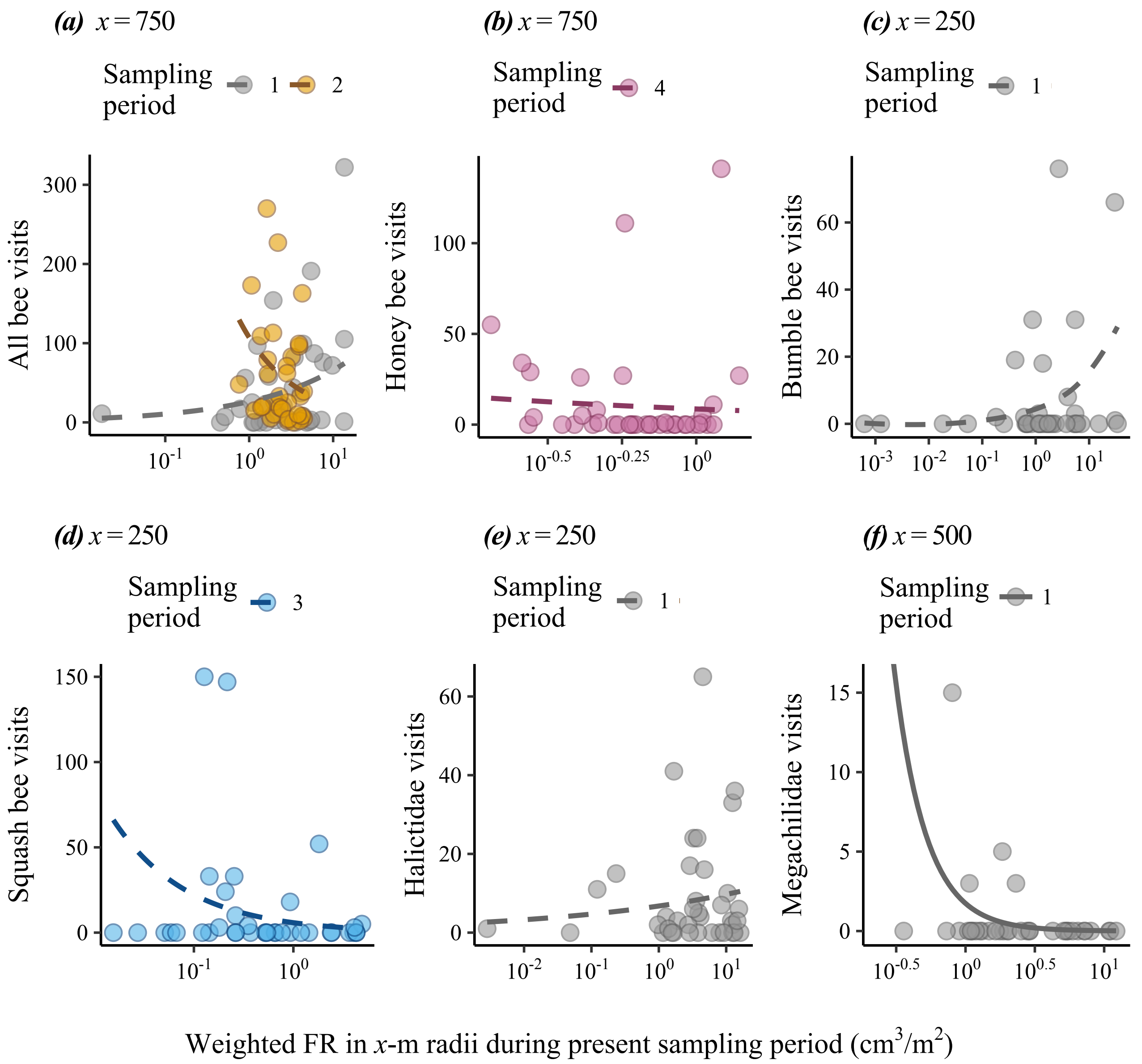

(a)
Sampling period
2
3
All bee visits
0
100
200
10^{-5}
$10^{-2.5}$
10^{0}
$10^{2.5}$
(b)
Sampling period
2
3
Honey bee visits
0
50
100
150
200
10^{-2}
10^{-1}
10^{0}
10^{1}
10^{2}
10^{3}
(c)
Sampling period
3
Bumble bee visits
0
25
50
75
100
10^{-4}
10^{-2}
10^{0}
10^{2}
(d)
Sampling period
2
3
Halictidae visits
0
30
60
90
10^{-2}
10^{0}
10^{2}
(e)
Sampling period
1
2
3
4
Andrenidae visits
0
20
40
60
10^{-5}
$10^{-2.5}$
10^{0}
$10^{2.5}$
(f)
Sampling period
1
2
3
Megachilidae visits
0
10
20
10^{-5}
$10^{-2.5}$
10^{0}
$10^{2.5}$
Weighted FR within transect during present sampling period (cm^3/m^2)

Figure 4.

Figure 5. Relationship between the abundance of weighted floral resources (FR) at a landscape scale (within a 250-m, 500-m, or 750-m radius around sampling locations) and the number of bee visits observed during the same sampling period, where 1 = late-spring (20 May – 10 June), 2 = early-summer (10 June – 4 July), 3 = mid-summer (5 July – 1 August), and 4 = late-summer (1 August – 1 September). Bee taxa and sampling-periods shown are those in which the best models (with weighted floral resources and unknown areas assigned median values; Table 3) included the amount of present floral resource at the landscape scale: ***(a)*** all bee visits in late-spring and early-summer at 750 m; ***(b)*** honey bee visits in late-summer at 750 m; ***(c)*** bumble bee visits in late-spring at 250 m; ***(d)*** squash bee visits in mid-summer at 250 m; ***(e)*** Halictidae visits in late-spring at 250 m; and ***(f)*** Megachilidae visits in late-spring at 500 m. Floral resources are represented as the average floral volume (cm^3) per 1 m^2 within a certain radius distance from a sampling location, calculated from the median floral volumes per 1 m^2 of each land type, which was $\log_{10}$ transformed and is presented on a $\log_{10}$-scale axis. Circles represent raw data, and black lines represent the negative binomial fit of predicted values extracted from full models; solid lines repesent a significant relationship across median, minimum, and maximum models, and dashed lines represent a non-significant relationship in at least one of the three models.



(a) x = 750
Sampling period
1
2
All bee visits
300
200
100
0
10^-1
10^0
10^1
(b) x = 750
Sampling period
4
Honey bee visits
100
50
0
10^-0.5
10^-0.25
10^0
(c) x = 250
Sampling period
1
Bumble bee visits
60
40
20
0
10^-3
10^-2
10^-1
10^0
10^1
(d) x = 250
Sampling period
3
Squash bee visits
150
100
50
0
10^-1
10^0
(e) x = 250
Sampling period
1
Halictidae visits
60
40
20
0
10^-2
10^-1
10^0
10^1
(f) x = 500
Sampling period
1
Megachilidae visits
15
10
5
0
10^-0.5
10^0
10^0.5
10^1
Weighted FR in x-m radii during present sampling period (cm^3/m^2)

Figure 5.

Figure 6. Relationship between the abundance of weighted floral resources (FR) at a landscape scale (within a 250-m, 500-m, or 750-m radius around sampling locations) during the late-spring sampling period (20 May – 10 June) and the number of bee visits observed in subsequent sampling periods, where 2 = early-summer (10 June – 4 July), 3 = mid-summer (5 July – 1 August), and 4 = late-summer (1 August – 1 September). Bee taxa and sampling-periods shown are those in which the best models (with weighted floral resources and unknown areas assigned median values; Table 3) included the previous amount of floral resources from late-spring, at the landscape-scale: ***(a)*** all bee visits in mid- and late-summer at 750 m; ***(b)*** bumble bee visits in early-summer at 250 m; ***(c)*** Halictidae visits in late-summer at 250 m; ***(d)*** Andrenidae visits in early-summer at 750 m; and ***(e)*** Megachilidae visits in early- and late-summer at 500 m. Floral resources are represented as the average floral volume (cm^3) per 1 m^2 within a certain radius distance from a sampling location, calculated from the median floral volumes per 1 m^2 of each land type, which was $\log_{10}$ transformed and is presented on a $\log_{10}$-scale axis. Circles represent raw data, and lines represent the negative binomial fit of predicted values extracted from full models; solid lines repesent a significant relationship across median, minimum, and maximum models, and dashed lines represent a non-significant relationship in at least one of the three models.

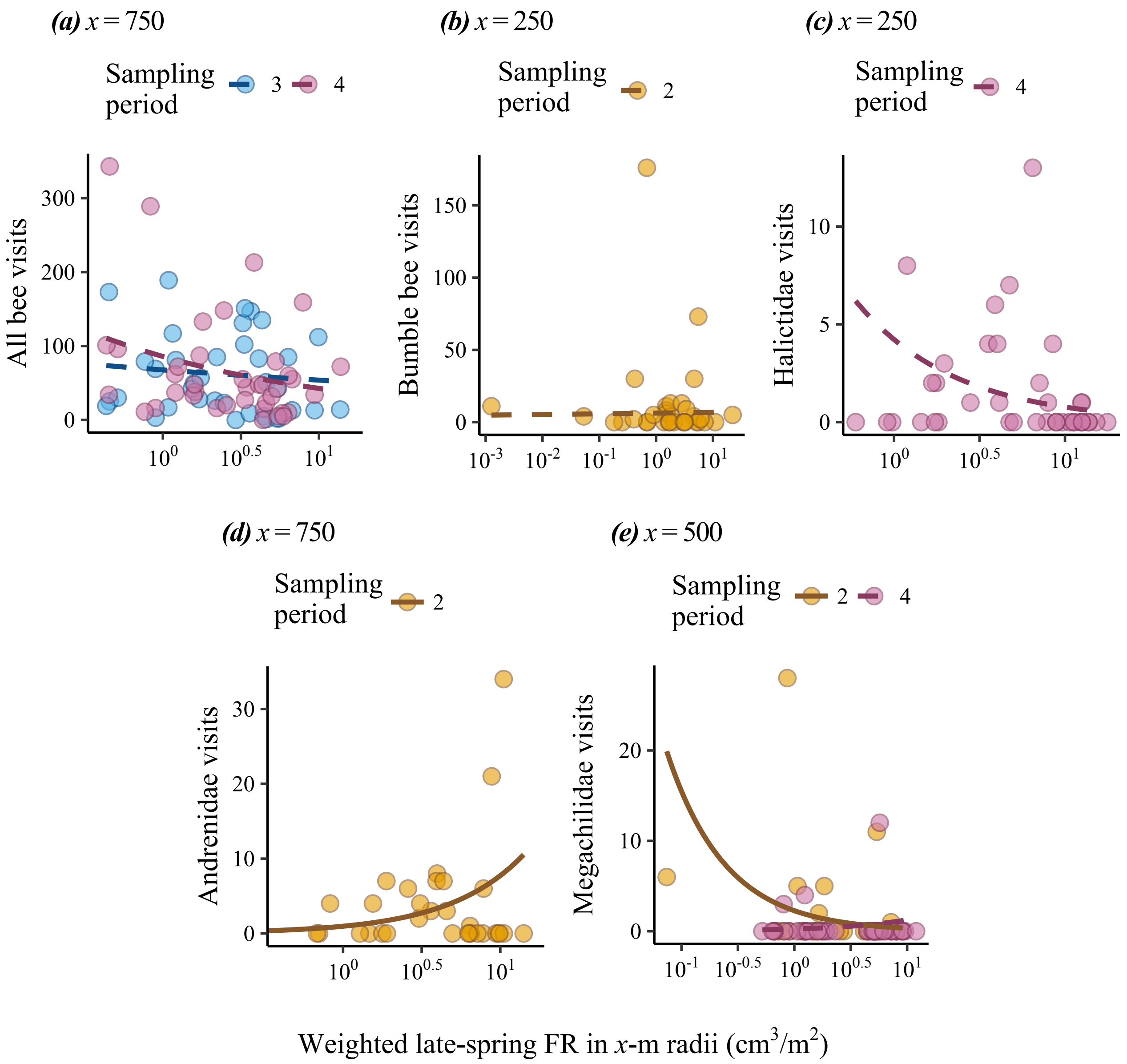
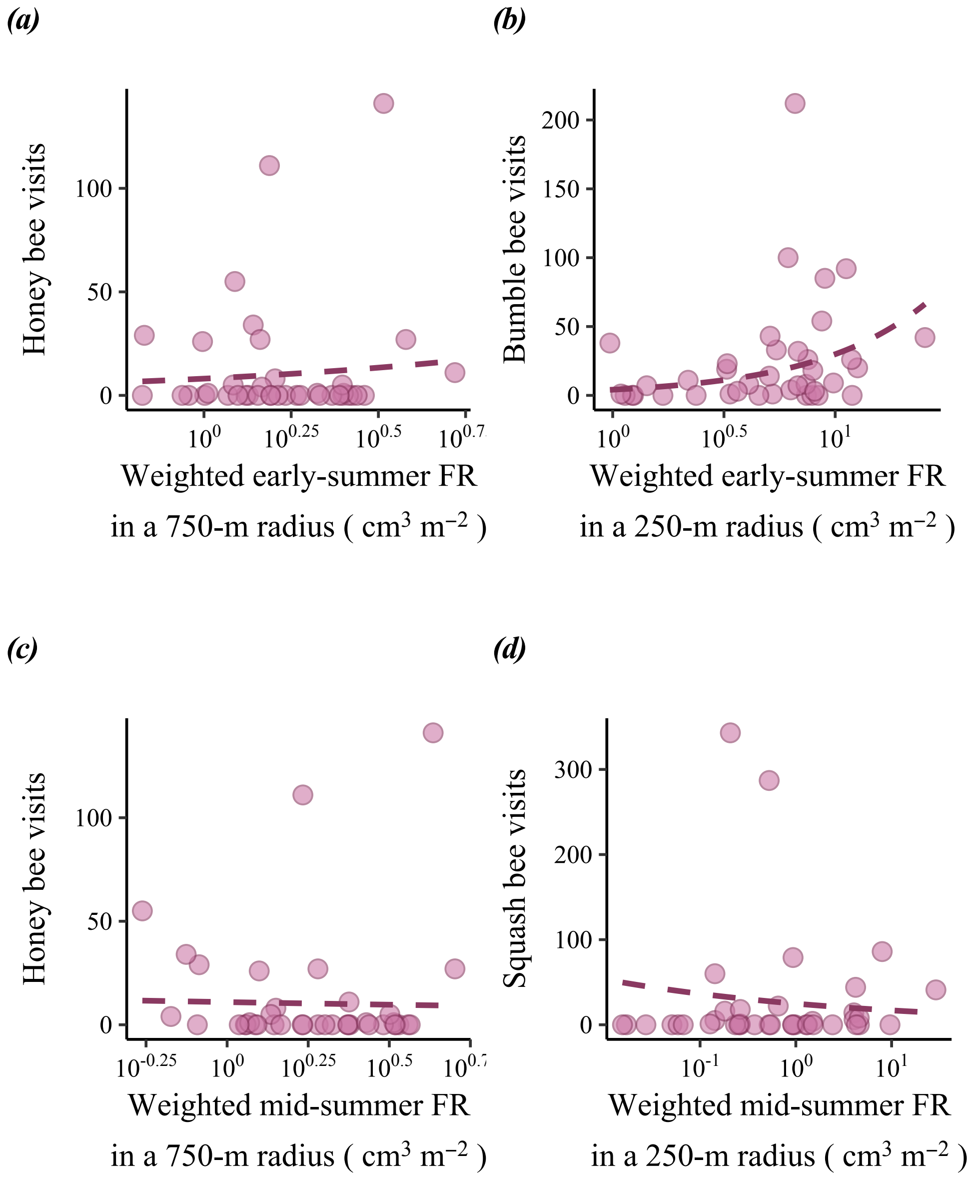

(a) x = 750
Sampling period
3
4
All bee visits
0
100
200
300
10^{0}
$10^{0.5}$
10^{1}
(b) x = 250
Sampling period
2
Bumble bee visits
0
50
100
150
10^{-3}
10^{-2}
10^{-1}
10^{0}
10^{1}
(c) x = 250
Sampling period
4
Halictidae visits
0
5
10
10^{0}
$10^{0.5}$
10^{1}
(d) x = 750
Sampling period
2
Andrenidae visits
0
10
20
30
10^{0}
$10^{0.5}$
10^{1}
(e) x = 500
Sampling period
2
4
Megachilidae visits
0
10
20
10^{-1}
$10^{-0.5}$
10^{0}
$10^{0.5}$
10^{1}
Weighted late-spring FR in x-m radii (cm³/m²)

Figure 6.

Figure 7. Relationship between the abundance of weighted floral resources (FR) at a landscape scale (within a 250-m, 500-m, or 750-m radius around sampling locations) during early-summer (10 June – 4 July) or mid-summer (5 July – 1 August) sampling periods, and the number of bee visits observed in the late-summer sampling period (= 4; 1 August – 1 September). Bee taxa shown are those in which the best models (with weighted floral resources and unknown areas assigned median values; Table 3) included the previous amount of floral resources from either early- or mid-summer sampling periods, at the landscape-scale: ***(a)*** honey bee visits and early-summer FR within 750 m; ***(b)*** bumble bee visits and early-summer FR within 250 m; ***(c)*** honey bee visits and mid-summer FR within 250 m; and ***(d)*** Squash bee visits and mid-summer FR within 250 m. Floral resources are represented as the average floral volume (cm^3) per 1 m^2 within a certain radius distance from a sampling location, calculated from the median floral volumes per 1 m^2 of each land type, which was $\log_{10}$ transformed and is presented on a $\log_{10}$-scale axis. Circles represent raw data, and lines represent the negative binomial fit of predicted values extracted from full models; solid lines repesent a significant relationship across median, minimum, and maximum models, and dashed lines represent a non-significant relationship in at least one of the three models.



(a)
Honey bee visits
0
50
100
10^{0}
$10^{0.25}$
$10^{0.5}$
$10^{0.7}$
Weighted early-summer FR
in a 750-m radius (cm^3 m^{-2})
(b)
Bumble bee visits
0
50
100
150
200
10^{0}
$10^{0.5}$
10^{1}
Weighted early-summer FR
in a 250-m radius (cm^3 m^{-2})
(c)
Honey bee visits
0
50
100
$10^{-0.25}$
10^{0}
$10^{0.25}$
$10^{0.5}$
$10^{0.7}$
Weighted mid-summer FR
in a 750-m radius (cm^3 m^{-2})
(d)
Squash bee visits
0
100
200
300
10^{-1}
10^{0}
10^{1}
Weighted mid-summer FR
in a 250-m radius (cm^3 m^{-2})

Figure 7.

CHAPTER 4: DISCUSSION

4.1 Summary

As outlined in the research objectives, I expected that (1) landscapes with a higher abundance of floral resources earlier in the season would experience increased bee visits in subsequent time periods. This was not found to be case for most taxa examined; rather, the only consistent relationship between floral resources and bee visits observed across all sampling periods was the positive influence of present abundance of floral resources at a local scale. Only Andrenidae visits in early-summer were significantly higher in landscapes where there were more floral resources during late-spring. Other taxa that showed weakly positive relationships with increasing amount of past floral were honey bees and bumble bees, with the number of visits observed during late-summer slightly higher in landscapes with more floral resources during either early- or mid-summer. However, neither of these relationships was significant across all models. Megachilidae was the only other taxa examined wherein the observed number of visits was significantly correlated with floral resource abundance in a past sampling period; however, the opposite trend was observed, with fewer visits in early-summer when the surrounding landscape had more floral resources during late-spring. This seemingly negative influence of past floral resources will be discussed further in the following sections.

My second expectation was that (2) the number of observed bee visits would be influenced by past floral resources at shorter or longer time scales depending on the taxon of bee considered. As most bee taxa responded most strongly to resources in the present sampling period, this expectation was more difficult to assess. However, both bumble bee and honey bee visits were (weakly) influenced by past floral resources at a longer time scale (two months previous) than were visits by Andrenidae and Megachilidae (one month previous).

My third expectation was that (3) the spatial scale of floral resources that best predicts the number of bee visits would differ among bee taxa. This expectation was supported by the data. However, the spatial scales observed did not always correspond to the expected foraging ranges of individual taxa. The implications of this finding, along with potential influences of landscape configuration and other taxon-specific functional traits, are discussed below.

4.2 Floral Resources at a Landscape Scale

The best estimate of both pollen and nectar production was floral volume. Previous studies have examined similar relationships between floral size and resource production, with inconsistent results across studies. Nectar volume has been found to be associated with corolla length among *Nicotiana* species (Kaczorowski et al. 2005), while examination of a broader range of species showed that length (referred to as “height” in this study) and shape of nectar tubes were the traits most associated with nectar sugar content (Carvalheiro et al. 2014). Similarly, the amount of sugar per flower has been found to be positively associated with flower dry weight; but this correlation is strongest in species with tubular corollas (Herrera 1985). A study by Hicks et al. (2016) found that nectar sugar per flower could not be adequately predicted using models of corolla diameter or corolla length across a variety of European weed species, but the pollen volume per flower could be reasonably predicted using models of anther size and stamen number per flower. Floral volume is most likely a better proxy for flower size or mass than just measurement of height, length, or width of flowers independently, which may allow better prediction of a plant’s allocation to floral resource production. The pollen volume measures used in correlations with floral volume may not, however, adequately represent the resource richness of flowers; bees harvest pollen for protein, and protein content was not considered in this study. The protein mass found in pollen grains has been found to be highly correlated with the distance between stigma and ovule, which varies between flowering species; bees generally do not display preferences specifically for species with high protein content pollen, but may compensate for low protein in certain species by collecting a higher volume of pollen (Roulston et al. 2000). Therefore, the amount of resources per flower may not be directly represented by pollen volume, rather by the protein content per volume found in a flower.

Nectar concentration and nectar volume can differ between male and female plants of dioecious species, male and female flowers of monoecious species, or male and female phases of dichogamous hermaphrodite species (Freeman et al. 1981; Pacini et al. 2003). The majority of species surveyed do have hermaphrodite flowers; however, 15 of the 86 species surveyed are monoecious, and five species surveyed can have populations with unisexual individuals; one dioecious species, *Asparagus officinalus* (1180 flowers at 1 sampling location), and four gynodioecious species: *Fragaria virginiana* (147 individuals across 5 sampling locations) *Glechoma hederacea* (270 flowers at 1 sampling location); *Plantago lanceolata* (312 inflorescences across 2 sampling locations); and *Silene vulgaris* (592 flowers across 8 sampling locations). The "asparagus" land type made up 0.01–0.5% of all land surveyed (Table 2); all other species were found inconsistently across sampling locations of a particular land type. For *F. virginiana*, *G. hederacea*, and *S. vulgaris*, nectar measurements used in correlations with floral volume were obtained from literature sources; unfortunately, neither source indicated whether nectar was collected from pistillate or hermaphrodite flowers (Baude et al. 2016; Heinrich 1976). Sex-ratios in populations of dioecious plants can also be quite varied: *F. virginiana* populations can be 30–40% female (Ashman 2006); *G. hederacea* populations range from 0% to 100% female (Widén and Widén 2000); *P. lanceolata* populations range from 0% to 30% (Krohne et al. 1980); and 0% to 75% for *S. vulgaris* (McCauley and Brock 1998). Although sex was not determined in flowers encountered during quadrat surveys in this study, any differences in resource production between sexes would probably not signifcantly alter estimates of floral resources at a landscape scale.

Six species encountered in surveys did not produce nectar: *Actaea pachypoda* (2 inflorescences at 1 sampling location) *Chelidonium* sp. (4 flowers at 1 sampling location); *Cornus canadensis* (4 flowers at 1 sampling location); *Maianthemum canadense* (36 inflorescences across 3 sampling locations); *Plantago lanceolata* (312 inflorescences across 2 sampling locations); and *Trillium erectum* (2 flowers at 1 sampling location). Other than *P. lanceolata*, non-nectar producing flowers made up a small proportion of the total floral abundance surveyed. When the six non-nectar producing species were included in correlations between nectar and floral measurements (with nectar values of 0 µg/day), floral volume was still significantly correlated with nectar sugar mass ($r = 0.29$, $p = 0.03$, $n = 52$), but to a lesser extent than when these species were excluded ($r = 0.62$, $p = 3.6\times10^{-6}$, $n = 46$). Height measurements were more correlated with nectar than floral volume when including species that did not produce nectar ($r = 0.46$, $p = 0.0007$). However, floral volume is probably still the best estimate of floral resources, as non-nectar producing flowers are not representative of the majority of species encountered (6 out of 86 species examined).

Two species were encountered that provided potentially no reward accessible to bees, and were initially excluded from floral resource estimates: *Arisaema triphyllum* is pollinated by fungus gnats, is rarely visited by bees (Barriault et al. 2010), and was only encountered in one sampling location. The other species was soybean (*Glycine max*), which was present in the landscape surrounding almost every sampling location. Over 2 million acres of soybeans are grown in the province of Ontario annually (OMAFRA 2014), and soybeans covered up to 55% of the land area within a 750-m radius around sampling locations. However, many varieties are cleistogamous, or self-fertilize before flowers open; insect pollination of Ontario-grown varieties is not expected to increase yields (OMAFRA 2015). There is, however, some anecdotal evidence for cross-pollination by honey bees resulting in increased yields (Ahrent and Caviness 1994; Erickson et al. 1978), and 29 species of wild bees (including 8 of the species observed in this study) have been found visiting soybean crops in Delaware, Wisconsin and Missouri, USA (Rust et al. 1980). In 2016, soybeans in Ontario were at non-reproductive stages on June 14 (OMAFRA 2016 a), and by July 27, most soybeans were in early pod stage (OMAFRA 2016 b); therefore, flowering most likely coincided with only early-summer and mid-summer sampling periods (between June 10 and August 1).

Given the extent of soybean cover in most landscapes, I re-ran weighted floral resource models for all bee taxa, treating soybean area as resource-providing land in early- and mid-summer sampling periods. Land area with soybean crops was assigned the median floral resource value calculated from all land-types for a given sampling period. Six of 20 models that were re-run resulted in "best" models that had equal or lower AICc values, and differed from models wherein soybean was assigned a floral resource value of zero (Appendix 10, compare to Table 3). However, all models that differed showed evidence of either non-significant or negative associations between bee visits and floral resources including soybean (Appendix 10). The only instance of a positive association with bee visits was for bumble bee visits in early summer, which were non-significantly correlated with present floral resources when soybean was treated as resource-providing (Appendix 10), compared to the negative and non-significant correlation with late-spring floral resources when soybeans were treated as non-resource-providing (Table 3). As neither relationship was significantly associated with bumble bee visits, it is difficult to determine whether soybeans acted as an important resource for bumble bees.

4.3 Bees' Floral Preferences

Collectively, the bees observed in this study interacted with 78 flower species, of which only 65 were encountered in floral surveys; bee visits to these additional species made up only 0.9% of all visits. Over the entire season, the total number of observed visits was highest in crops. Across all sampling locations, the most frequently visited species was apple (*Malus pumila*) in late-spring; raspberry (*Rubus* sp.) in early-summer; and squash (*Cucurbita* spp.) in both mid- and late-summer (Appendix 11). As farm sites were initially chosen because they planned to grow squash crops, there was a bias towards squash fields as sampling locations, and squash flowers were frequently encountered in surveys and bee visit observations. After squash visits, the second most visited species were white clover (*Trifolium repens*) in mid-summer and alfalfa (*Medicago sativa*) in late-summer (Appendix 11). Compared to the measurements of floral abundance in each sampling period, apple was also the most abundant species in late-spring across all sampling locations, despite being present at only two locations; white clover was also the most abundant species in mid-summer, and alfalfa was most abundant in late-summer. However, the most abundant species in early-summer was tufted vetch (*Vicia cracca*), while raspberry was the sixth most abundant species; and in mid- and late-summer, squash was only the sixth and the fourth most abundant species, respectively (Appendix 11). When comparing the five most abundant species across all sampling locations with the five most visited species (Appendix 11), the most abundant species generally seem to be the most visited, although there are some discrepancies, suggesting bee preferences for certain species, especially when considering individual bee taxa.

The bee taxon that visited the largest range of flowering species was the Halictidae family, which interacted with 63 different species, but had the fourth lowest number of visits observed of all taxa examined. In late-spring, the most common flowering species visited by Halictidae were wild strawberries (*Fragaria virginiana*) and cultivated strawberries (*Fragaria* × *ananassa*); in early-summer, the most visited species was ox-eye daisy (*Leucanthemum vulgare*); in mid-summer, corn chamomile (*Anthemis arvensis*) was most visited; and visits to goldenrod (*Solidago* spp.) were most common in late-summer. Of these, only cultivated strawberries and goldenrod were among the five most abundant species at the time (Appendix 11). Despite the wide range of species visited by members of Halictidae, it is evident that there is preferential foraging on certain species based on observed visits. Halictidae found in this region are short-tongued, and therefore tend to visit only flowers with shallow nectar tubes (McGinley 1986) Some halictids are oligolectic (Thorp 1979; Michener 2007), but the majority of subfamily Halictinae are polylectic (Michener 2007); all halictid bees identified to genus or species in this study were members of Halictinae. The two most common halictid species identified (*Halictus confusus* and *Halictus ligatus*) are both polylectic, or collect pollen from many species; both have been previously recorded visiting flowers from the genera *Fragaria*, *Leucanthemum* (syn. *Chrysanthemum*), *Anthemis*, and *Solidago* (Mitchell 1960).

Bumble bees visited the second largest range of flowering species, with 43 species interactions, and had the second highest number of visits observed of any taxa. In late-spring, bumble bees visited blackberries (*Rubus allegheniensis*) most often; white clover was the most visited in early- and mid-summer; and squash was most visited in late-summer, followed by alfalfa. Virtually all bumble bee species are generalist foragers, probably due to their ability to learn complex floral handling skills for many floral morphologies (Laverty 1994), and because they have season-long life cycles, they need to forage on a range of floral resources (Michener 2007). The most visited species by bumble bees were among the three most abundant species during each sampling period (Appendix 11). The observed pattern of foraging on the most abundant species corroborates that bumble bees foraging for nectar may be following an ideal free distribution (Dreisig 1995). However, bumble bees tend to collect pollen from a smaller subset of flowering species than those from which they collect nectar (Goulson and Darvill 2004; Rasheed and Harder 1997) and may select certain species based on how efficiently they are able to collect pollen (Rasheed and Harder 1997). Certain species may also restrict foraging to fewer species depending on the life cycle length of the colony, or based on tongue-length (Goulson and Darvill 2004).

Honey bees interacted with only 34 plant species despite having the highest number of visits observed of any taxon. The most visits were observed to apple in late-spring; raspberry in early-summer; squash and white clover in mid-summer; and bird's-foot trefoil (*Lotus corniculatus*) in late-summer. Other than raspberry, the most visited species corresponded to species with high abundances. Because of the long life cycles of honey bee colonies, individuals need to be generalists and make use of most floral resources that are available at a given time (Westerkamp 1991). However, other studies have found that honey bees do not always forage based on which species is most abundant (Keller et al. 2005) and display preferences for certain types of pollen (Cook et al. 2003; Pernal and Currie 2002; Schmidt et al. 1995). Managed honey bee colonies were prevalent across farm sites in this study, which may have translated to higher abundances observed in fruit crops and forage fields.

Andrenidae were observed visiting 29 species; the highest number of visits was to mountain maple (*Acer spicatum*) in late-spring; white clover was the most visited species in early- and mid-summer; and goldenrods (*Solidago* spp.) were the most visited in late-summer. Most Andrenidae visits during late-spring occurred during one observation period at a sampling location in a stand of mountain maple (*Acer spicatum*). *Acer* pollen and nectar appears to be a vital resource for a number of *Andrena* species; Sullivan (1983) found that *Andrena* was the most abundant visitor to *A. spicatum*, and other studies have reported a number of *Andrena* species collecting *Acer* nectar and pollen (Batra 1985; Batra 1990; Chambers 1986). Nearctic species of *Andrena* include both polylectic and oligolectic species, which collect pollen from only a few plant species (Larkin et al. 2008). It is difficult to determine the proportion of oligolectic species that were observed, though there is clear evidence for preferential foraging based on observations of the family as a whole.

Megachilidae only interacted with 20 flowering species, but also had the lowest observed number of visits of any taxa. Most visits in late-spring were to wild strawberry; in early-summer to white clover; viper's bugloss (*Echium vulgare*) in mid-summer; and bird's-foot trefoil in late-summer. Other than *E. vulgare*, the most visited species were also some of the most abundant species (Appendix 11). Interestingly, a number Megachilidae species are specialists on *Echium* pollen (Sedivy et al. 2013). Even though *E. vulgare* is an introduced species in North America, there may be oligolectic or polylectic members of Megachilidae that exhibit a predisposition for collection of pollen from certain plant families, based on floral morphologies and pollen digestibility (Haider et al. 2014). As with the Andrenidae and Halictidae families, it is difficult to estimate the proportion of oligolectic species that might have been observed without species identifications. Even so, some degree of preferential foraging is evident within the family.

Squash bees were the third most frequently observed visitors, yet interacted with only two crops: 99.7% of visits were to squash flowers, while 0.3% of visits were to cucumber flowers (*Cucumis sativus*), and these were only observed when cucumber transects were bordered by squash crops. Squash bees are oligolectic, and collect all pollen required to provision nests from *Cucurbita* spp.; however, they will collect nectar from various sources (Hurd et al. 1974). Unlike the other taxa examined, the proportion of oligolectic bees in this group is known to be 100%, and therefore unweighted floral resources almost certainly do not provide an adequate estimate of the resources actually utilized by squash bees.

The range of floral preferences observed among bee taxa likely reflects, in part, how accessible resources are for bees. Complex floral morphologies may prevent resource access by certain bees. Papilionate legume flowers, for example, are inaccessible to bee species that lack the strength to manipulate them (Córdoba and Cocucci 2011). Nectar-holder depth and width can also be negatively correlated with number of flower visitors across species, by limiting nectar consumption to bees with a long proboscis (Stang et al. 2006). Similarly, trumpet or bell-shaped flowers can exclude bees with body sizes larger than the width of the corolla opening (Willmer 2011). Complex anther or stamen morphology may also preclude pollen removal by bees. Poricidal anthers, which are present in crops such as tomato, potato, and blueberry, require buzz pollination, wherein bees must vibrate anthers through rapid wing movement (Buchmann and Hurley 1978). This ability is possessed only by certain bee species, including bumble bees and members of Halictidae (Buchmann and Hurley 1978). Pollen may also be “inaccessible” in terms of digestibility; pollen collected from non-host plants can negatively affect larval development

(Praz et al. 2008), and non-native weeds or crop pollen may not be utilized by wild bee species that specialize on pollen of unrelated native host plants. The number of visits recorded in this study may not precisely represent the proportion of each floral resource consumed by a given bee guild; nonetheless, it is evident that each bee taxon examined visited only a subset of all available species in a landscape, and not always in proportion to their relative abundance.

As a result of bee taxon-specific floral preferences, weighting plant species by their usage should provide a more accurate picture of the floral resources perceived by bees. In fact, comparing the fits of models with weighted and unweighted floral resources provides a means of testing the utility of resource weighting. Out of 25 models run, 17 weighted models had lower AICc values than then models run with unweighted floral resources (Table 3 & 4). Of the eight unweighted models that had lower AICc values, only four had differences greater than 2; this included all bee visits in late-spring, Andrenidae visits in early-summer, and both models of squash bee visits. Squash bee visits resulted in weighted models that perhaps underestimated the importance of certain floral resources, especially if squash bees are using other flowers as nectar sources other than squash flowers. Also, weighted models of squash bee visits had floral resource terms that were highly correlated, so no model was run that had more than one term (Appendix 7). This prevented examination of floral resources from multiple sampling-periods simultaneously on squash bee visits. For all other taxa, weighted floral resources did appear to be at least equal if not a better predictor of bee visits than unweighted floral resources.

4.4 Bees' Responses to Spatial Scale of Floral Resources

The spatial scale of floral resources influencing bee visits is most likely a combination of the proximity of floral resources to emergence sites and nest sites, the maximum foraging range, patch attractiveness, and social information available to make foraging decisions. In this study, floral resources within a 750-m radius around sampling locations was the best predictor in models of all bee visits. This was the largest scale examined, and it is possible that floral resources within an even larger radius may have been more correlated with all bee visits. Thirty percent of all visits observed were from honey bees, and floral resources were also most correlated with honey bee visits at a 750-m spatial scale. This spatial scale may not be indicative of honey bee foraging ranges, as other studies have found that only 10% of bees forage within 500 m of their hive, and 50% of bees forage more than 6 km away from the hive (Beekman and Ratnieks 2000). Honey bees can average 1.5 km travelled during foraging trips, and travel even further during months when resource abundance is low (Steffan-Dewenter and Kuhn 2003). The 750-m scale may indicate a concentration of attractive patches within a potentially larger foraging radius; honey bees are able to assess and compare the resource quality of patches, and tend to concentrate on the most resource-abundant patches within their foraging range (Visscher and Seeley 1982). The areas within 750 m of sampling locations may contain a higher diversity or abundance of resources, compared to much of the crop land surrounding the fruit and vegetable farm sites chosen in this study; most of the region where this study took place is comprised of field crops such as soybean, corn, and cereal crops (AAFC 2016). Honey bee hive proximity was not examined, but it is likely that hive locations were also biased towards areas growing fruit or vegetable crops, or locations chosen based on a need for pollination services.

The spatial scale of floral resources with the most influence on bumble bee visits was within a 250-m radius. As with honey bees, this scale probably does not represent the maximum foraging ranges of species. Osborne et al. (1999) tracked *Bombus terrestris* foraging distances in farm land, and found that distances ranged from 70 to 631 m from colonies, with a mean distance of 275 m, which is very similar to the spatial scale that was found most associated with bee visits in this study. The social nature of colonies allows sharing of resources and information on location of resource patches (Dornhaus and Chittka 2004), and a 250-m scale may indicate a concentrated area of attractive patches within their possible foraging range; bumble bees foraging in agroecosystems with more floral resources have significantly shorter foraging trips (Westphal et al. 2006), and show some degree of constancy to foraging patches over subsequent days (Osborne et al. 1999). Their ability to perceive resources at local and landscape scales allows them to be highly selective with where they are foraging, as Jha and Kremen (2013) found with bumble bees travelling further than would be expected to forage in patches with a higher diversity of resources.

Squash bee visits were also most strongly associated with floral resources at a 250-m spatial scale. Their estimated maximum foraging range is 1.6 km, based on body size (or intertegular span) of *P. pruinosa* (Greenleaf et al. 2007; Ullmann 2015). However, since squash bees are oligolectic and collect all pollen from *Cucurbita* spp. (Hurd et al. 1974), they may be subsisting on resources from squash fields only. It is, therefore, likely that other floral resources located outside of squash fields have little effect on observed patterns of visitation for this taxon. Squash fields in this study ranged from 48 m^2 to 9440 m^2, and all were contained within the 250-m radius around a squash field sampling location, in which all squash bees were observed. Squash bees are an aggregative ground-nesting species and most often nest in areas within or bordering squash fields (Hurd et al. 1974; Julier and Roulston 2009). All farms with squash crops had also grown squash in the previous year; squash field connectivity between years has been found to affect squash bee densities in the current year, as squash bees are able to track resources over a multiple-year time scale (Ullmann 2015). Therefore, the landscape configuration, or the distance and connectivity between emergence sites and squash crops in present years, may be the most important spatial factor limiting squash bee populations.

Halictidae visits had the strongest association with floral resources at a 250-m spatial scale, while the maximum foraging distances of Halictidae species are reported to be between 200 m and 1250 m (Zurbuchen et al. 2010). The wide range of foraging distances probably represents the range in body sizes across Halictidae species; body length ranges from 4 mm to 20 mm in the species that are present in this region (Mitchell 1960). Members of the Halictidae family also exhibit a range in sociality, from solitary species to eusocial species, and depending on degree of sociality, nesting can be in colonies, in communal or aggregative nests, or solitary nests (Michener 2007). Some Halictidae species also display philopatry, returning to emergence sites to construct new nests; this trait is beneficial in agricultural schemes wherein crops with high-quality resources are close to nest sites and close to their former location (Cane 1997). However, Halictidae visits only showed a significant relationship with floral resource abundance at a local scale; the actual spatial scale of response may therefore be much smaller than a 250-m radius around sampling locations.

Andrenidae visits were most correlated with floral resources at a 750-m spatial scale based on the summed score across all models run; however, the spatial scale with the greatest response was inconsistent between models (Appendix 6). In models of weighted floral resources and median estimates for unknown areas, the highest-scoring spatial scale was actually a 500-m radius, while for weighted models with minimum estimates the best spatial scale was 250 m, and in unweighted median models, both 250-m and 500-m radii scored higher than 750 m (Appendix 6). Reported foraging distances of Andrenidae species range from 130 m to 1250 m (Zurbuchen et al. 2010), while body length ranges from approximately 4 to 15 mm for the species present in this region (Mitchell 1960). The inconsistencies across models might be explained by differences in foraging ranges among species, and hence in the spatial scales to which they are responding most strongly. As Andrenidae species display a range of floral preferences as well, there may be more incentive for oligolectic bees to travel further to reach host plants, rather than focusing foraging on whichever resources are abundant and close-by. However, maximum foraging ranges generally do not appear to differ between polylectic and oligolectic bees (Gathmann and Tscharntke 2002).

Megachilidae visits were best predicted by floral resources within a 500-m radius around sampling locations. Two genera (*Osmia* and *Megachile*) made up the majority of Megachilidae visits observed in this study; the foraging ranges for smaller-bodied *Osmia* species have been reported between 150 m and 1 km, while the generally larger-bodied *Megachile* species have reported foraging distances of 100 m to 1 km (Zurbuchen et al. 2010). Again, the diversity across members of the Megachilidae family might result in different spatial scales influencing individual species, potentially at either larger or smaller spatial scales than were measured. Most of the visits observed from Megachilidae were concentrated at a few sites within a sampling period, and the absence of Megachilidae in certain sites may indicate a lack in suitable nest sites, rather than floral resources. Most *Megachile* and *Osmia* species nest above-ground (Cane et al. 2007; Krombein et al. 1979), often in woody substrates that tend to be less common in arable land than in natural areas (Forrest et al. 2015). The majority of sampling locations were within crop and forage fields, which are usually cleared of woody debris due to harvesting practices, and thus may have been lacking in suitable nesting sites.

Overall, the spatial scale of floral resources that influenced bee visits was quite variable among the taxa examined. Even selecting one spatial scale as the most influential for an entire family, as in Halictidae, Andrenidae, or Megachilidae, may not accurately reflect individual bee responses to floral resources, based on differences in body sizes, sociality, or pollen preferences. Nest site locations and landscape configuration, although not examined in this study, may also influence the locations in space where individual species are able to forage. Despite the variability in spatial scales observed, the abundance of local-scale floral resources consistently appeared to be the best predictor of bee visits from all taxa (Table 3 & 4).

4.5 Bees' Responses to Temporal Scale of Floral Resources

Throughout all sampling periods, the present amount of floral resources seemed to influence bee visits as much as or more than past floral resources. In late-spring, the present amount of both weighted and unweighted floral resources was positively associated with bee visits for all taxa examined, except for Megachilidae and bumble bees. After emerging, bees present in late-spring may be dispersing specifically to locations with higher resources. If locations with high resources in the current year also experienced a high abundance of late-spring resources in the previous year, this could positively affect reproduction of the previous generation, and consequently influence emergence sites of the present generation (Kim et al. 2006). Similarly, mass-flowering crops in the previous year can positively affect wild bee visits on the same crop in the current year (Riedinger et al. 2015). Although not examined, past floral resources at the scale of a year, rather than within a season, likely affect the number of bee visits in late-spring, perhaps more than present floral resources. Future work should look into how floral resource abundance in the previous season might influence bee abundance in the present.

I observed an apparent negative influence of present landscape-scale floral resources on Megachilidae visits in late-spring, and negative (though non-significant) associations were also evident in subsequent sampling periods for other taxa (see Table 3; all bee visits in early-summer, squash bee visits in mid-summer, and honey bee visits in late-summer). A negative association between landscape-scale floral resources and bee visits could be explained by the presence of other patches of floral resources within a landscape drawing bees away from sampling locations. In landscapes with patches of mass-flowering crops, there may be an overall dilution of pollinators, resulting in a negative effect of mass-flowering crops at a landscape scale, as both Holzschuh et al. (2016) and Kovács-Hostyánszki et al. (2013) have found. However, similar to what was found in the Kovács-Hostyánszki et al. (2013) study, present floral resources at the local scale simultaneously had a positive influence on visits by both Megachilidae in late-spring and all bee visits in early-summer.

Present floral resources at a local scale were positively associated with bee visits by most taxa examined during at least one sampling period. In late-spring, present floral resources at a local scale only significantly predicted the number of Andrenidae visits. Most Andrenidae observed in this study have vernal life-cycles and are oligolectic, and thus have foraging seasons synchronized with flowering of their pollen host plants (LaBerge 1986; Larkin et al. 2008). In both early- and mid-summer, the most prevalent relationship between bee visits and weighted floral resources was the present resource abundance at a local scale. This relationship suggests that most of the taxa examined respond to floral resources at shorter time-scales than what was examined (~1 month), or have foraging periods that are too short to observe an influence of previous months' floral resources.

However, the strong relationship between bee visits in mid-summer in particular and the present amount of resources could also be related to the abundance of late-emerging species, the populations of which may be most strongly limited by the floral resources experienced by past generations in previous years. For example, *Megachile rotundata*, an introduced species used for pollination of alfalfa crops, naturally emerge in June and July in North American populations (Kemp and Bosch 2001). Squash bees also represent a late-emerging species; in southern Ontario emergence is synchronized with the flowering of the pollen host plant, *Cucurbita pepo* (Willis and Kevan 1995). Only two sampling locations during mid-summer had open squash flowers in the previous sampling period, and most squash fields first began flowering in the mid-summer sampling period. If the squash bees observed in mid-summer represent those that have just emerged, then population sizes are most likely determined based on last year's resources, or other limits to population size experienced by overwintering brood, rather than current floral resources.

Past floral resources were positively correlated with subsequent (early-summer) Andrenidae visits, and weakly positively correlated with both honey bee and bumble bee visits in late-summer. Locations with abundant late-spring floral resources experienced more Andrenidae visits in early summer, suggesting that a significant number of Andrenidae species have foraging periods that overlapped the late-spring and early-summer sampling periods, and had been foraging on late-spring resources within a 750-m radius. Due to the vernal nature of many *Andrena* life-cycles (LaBerge 1986; Larkin et al. 2008), the early-summer sampling probably took place after most mating had occurred, and overlapped more with nest-construction activities by female bees. As most species of *Andrena* only produce one generation per year (Michener 2007), population sizes would not be growing over the course of a single season in response to late-spring floral resources; rather, these resources would simply allow the existing populations to persist within landscapes, resulting in a higher number of observed visits.

Conversely, the two other taxa wherein bee visits responded positively to floral resources, honey bees and bumble bees, have multiple generations per season, and could potentially respond to increasing floral resource availability with an increase in colony sizes (Crone and Williams 2016; Westphal et al. 2009). However, there was an inconsistent influence of past floral resources across all model iterations for both taxa: models with median and minimum estimates showed a positive association with past floral, while maximum and unweighted models showed non-significant or negative associations with floral resources (Table 3 & 4, Appendix 8). Running models with median, minimum, and maximum estimates should reduce the chance of making a type I error, as all models have to agree and yield significant results for a conclusion to be made. Across many taxa and sampling periods, maximum models often differed from median and minimum models (Table 3 & Appendix 8), and probably greatly overestimated the potential contribution of unknown areas to landscape-level floral resource abundance. As seen in Table 2, the land type with the largest unweighted volume per metre was apple orchards, with 41.6 cm^3/m^2, was much larger than the lowest resource-providing land types, at 0.1 cm^3/m^2. Assuming that all unknown areas within a landscape were providing a similar amount of resources as an apple orchard is almost certainly inaccurate, but also ensures that conclusions are robust when all models produce similar outcomes. Therefore, honey bees and bumble bees may be only weakly responding to past floral resources, and population sizes may be more limited by floral resources during other time periods, or limited by factors that were not measured.

Contrary to my initial expectations, there appeared to be some negative influences of past floral resources on bee visitation rates in subsequent time periods, particularly the amount of past floral resources in the late-spring sampling period (Fig. 6). The negative correlation between late-spring floral resources and visits by Megachilidae and bumble bees suggests a possible competition for pollinators from other resource-providing land parcels within the landscape during late-spring, which might cause a carry-over effect into early-summer when the decrease in bee visits was observed. Late-spring floral resources weighted by all bee visits were also highly correlated with mid-summer floral resources at a 750-m radius ($r = 0.87$; Appendix 7). So, a negative influence of present landscape-level floral abundance on mid-summer bee visits (discussed above) could carry over into late-summer and yield a negative relationship between bee visits and late-spring floral resources. The observation of fewer late-summer squash bee visits with increasing abundance of mid-summer resources is most likely due to the perfect correlation observed between mid-summer and late-summer floral resources within a 250-m radius ($r = 1.00$, Appendix 7). This perfect correlation was observed because of the weighted nature of squash bee visits, which were almost all to squash flowers (Table 2). Other than squash bee visits, the consistent negative influence of late-spring floral resource abundance suggests that other variables not measured in this study could also be correlated with the abundance of late-spring resources. For example, if the amount of floral resources in late-spring is correlated to certain landscape attributes or management practices, such as nest-site availability, or application of pesticides, floral resources may not be the cause of the negative bee-visit–floral-resource association.

4.6 General Conclusions and Implications

This study examined the simultaneous influence of spatial and temporal resource availability on bee visits in agroecosystems. The majority of the taxa examined responded most strongly to the amount of floral resources at a local scale in the present time period; however, past floral resources do appear to influence foraging of certain taxa. In particular, the number of Andrenidae visits observed in early-summer increased with increasing floral resources in the previous time-period, and past floral resources were also positively associated with bumble bee and honey bee visits in late-summer. There were also clear negative associations between bee visitation rates and landscape-level floral resources in both past and present time periods, indicating possible competition between patches or dilution of bee species at a landscape scale, and the potential for these negative effects to carry over into subsequent time-periods.

Future research should focus on the influence of resource fluctuations over shorter time-intervals, as well as resource abundance over multiple seasons, on the dynamics of wild bee populations. This study highlights the importance of examining multiple spatio-temporal scales when examining how floral resource availability affects not only the wild bee community, but individual bee taxa within agricultural landscapes. Understanding the individual responses of bee taxa to spatial and temporal changes in resources will allow for establishment of landscape management strategies that will both promote crop pollination and conserve wild bee species.

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APPENDICES

Appendix 1.

Latitude and longitude of all sampling locations (n = 102) in decimal degrees, recorded using a Trimble® Juno SB handheld GPS unit.

Sampling location	X	Y
1	−74.87016692	45.14499217
2	−74.87043608	45.14347949
3	−75.17040392	45.240218
4	−75.44307582	45.24731129
5	−75.44044993	45.24768895
6	−75.24284558	45.19594498
7	−75.24690246	45.1976179
8	−75.61362575	45.23302188
9	−75.61153558	45.23377825
10	−75.61133483	45.2339585
11	−75.61283925	45.23344792
12	−75.61262908	45.23340542
13	−75.96980783	45.317887
14	−75.96855517	45.32057425
15	−75.97248458	45.31790558
16	−75.97249192	45.31787825
17	−76.58967817	45.51091275
18	−76.59077192	45.51213942
19	−76.58650883	45.5107855
20	−76.58796225	45.51159858
21	−75.24750625	45.19592067
22	−75.44256383	45.59386892
23	−75.44506758	45.59213433
24	−75.44500892	45.59188792
25	−75.44504867	45.59178683
26	−75.1939482	45.49076631
27	−75.19480717	45.49230583
28	−75.19432528	45.49007317
29	−77.0661895	45.79243117
30	−77.06533825	45.79289975

Sampling location	X	Y
31	−75.94061325	44.73646317
32	−75.57811903	45.42920512
33	−75.58243875	45.42667683
34	−75.58012375	45.42837225
35	−77.41826979	45.54881982
36	−77.41989317	45.545928
37	−77.41989317	45.54602725
38	−76.02862417	45.76676883
39	−76.02928783	45.76631958
40	−76.02812117	45.76632483
41	−76.02861275	45.7656655
42	−75.16706208	45.238612
43	−75.16561358	45.24017667
44	−75.65861422	45.18898448
45	−75.64602133	45.19189475
46	−75.65160558	45.18952883
47	−75.65518017	45.18974125
48	−76.953473	45.42656975
49	−76.95462558	45.426993
50	−77.50610808	45.5133475
51	−76.31639258	45.39265575
52	−76.31369308	45.39236042
53	−76.3140695	45.39161308
54	−76.30979725	45.39174058
55	−75.55867675	45.39404483
56	−75.55990467	45.39319725
57	−75.8709035	45.35701083
58	−75.87279725	45.3587415
59	−75.872604	45.358064
60	−75.87275058	45.35873083

Sampling location	X	Y
61	−76.0179685	45.65934808
62	−76.020675	45.655557
63	−76.01753183	45.65603717
64	−76.02010133	45.65870375
65	−76.01976683	45.65809525
66	−76.22161867	44.42357267
67	−76.220106	44.4213515
68	−76.22130025	44.41773383
69	−75.87865608	44.77276258
70	−75.8785025	44.7734175
71	−75.95339083	45.17010008
72	−75.95142808	45.16725383
73	−75.952388	45.16800758
74	−75.953254	45.16947433
75	−76.99731575	45.638287
76	−75.30548478	45.58963091
77	−75.30705324	45.58858046
78	−75.30735507	45.58797606
79	−75.30655283	45.5864045
80	−75.30660525	45.5860195
81	−75.30687925	45.58648108
82	−76.47887142	45.529495
83	−76.4785255	45.52996933
84	−76.47697167	45.52969283
85	−75.61277405	45.23347059
86	−75.25070868	45.19637322
87	−75.24617342	45.19796795
88	−75.19636421	45.49162437
89	−77.06666564	45.79160153
90	−77.06378368	45.79374076
91	−74.87164371	45.14426626
92	−76.95480324	45.42410542
93	−76.95398878	45.42587721
94	−76.95512654	45.424733
95	−76.95552788	45.42579267
96	−76.31243663	45.39338825
97	−76.31200916	45.39298449
98	−76.9992138	45.63743254
99	−77.00133477	45.63567963
100	−77.00101131	45.63544592
101	−76.22076308	44.42140375
102	−76.22079048	44.41671249

Appendix 2.

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), and H is height in mm, measured from the receptacle to the longest sexual organ (stamen or pistil). Flower volume was calculated using the formula of an elliptic cylinder (volume = π × 0.5 × L × 0.5 × W × H), and inflorescence volume was calculated by multiplying flower volume by the average number of flowers per inflorescence. Measurements were made on five individuals per species, or values were obtained from literature sources.

Species	**Floral unit**	**L**	**W**	**H**	**Flower volume (mm^3)**	**Inflorescence volume (mm^3)**	**Flower measurement source**	**Inflorescence measurement source**
Acer spicatum	inflorescence	2.0	2.0	3.0	9.42	1649	Sullivan 1983	Sullivan 1983
Achillea millefolium	inflorescence	6.0	6.0	3.4	96.1	1442	measured; https://nature.ca/aaflora	http://www.efloras.org
Actaea pachypoda	inflorescence	2.0	2.0	5.0	15.7	298	Pellmyr 1985; http://plants.jstor.org	http://www.illinoiswildflowers.info
Agrimonia gryposepala	flower	5.0	5.0	5.0	98.2	n/a	http://plants.jstor.org	n/a
Anthemis arvensis	capitulum	6.2	6.2	6.4	226	n/a	measured	n/a
Asclepias syriaca	inflorescence	2.0	2.0	2.0	6.28	126	measured	measured
Asparagus officinalis	flower	1.2	1.2	4.8	6.13	n/a	measured	n/a
Barbarea vulgaris	inflorescence	1.0	1.0	2.0	1.57	12.6	measured	http://www.discoverlife.org

Species	**Floral unit**	**L**	**W**	**H**	**Flower volume (mm^3)**	**Inflorescence volume (mm^3)**	**Flower measurement source**	**Inflorescence measurement source**
Capsella bursa-pastoris	inflorescence	2.0	2.0	2.0	6.28	37.7	Nave et al. 2016; http://www.efloras.org	http://www.discoverlife.org
Cardamine bulbosa	flower	1.8	1.8	1.0	2.98	n/a	measured	n/a
Cardamine diphylla	flower	2.0	2.8	7.0	29.5	n/a	measured	n/a
Centaurea sp.	capitulum	8.0	8.0	22.0	1143	n/a	measured	n/a
Cerastium fontanum	flower	1.0	1.0	3.6	2.83	n/a	measured	n/a
Chelidonium sp.	flower	5.0	5.0	8.0	157	n/a	Kang et al. 1991; http://plants.jstor.org	n/a
Cichorium intybus	capitulum	4.6	4.6	9.4	161	n/a	measured	n/a
Citrullus lanatus	flower	5.0	5.0	5.2	102	n/a	measured	n/a
Coptis trifolia	flower	7.6	7.6	4.2	197	n/a	measured	n/a
Cornus canadensis	flower	7.8	7.8	4.0	193	n/a	measured	n/a
Cornus sericea	inflorescence	1.0	1.0	5.4	4.24	106	measured	http://www.discoverlife.org
Cucumis melo	flower	7.5	7.5	4.5	199	n/a	http://www.efloras.org	n/a
Cucumis sativus	flower	2.0	2.0	6.2	19.5	n/a	measured	n/a
Cucurbita pepo (female/zucchini)	flower	10.2	10.2	16.6	1353	n/a	measured	n/a
Cucurbita pepo (male/zucchini)	flower	8.4	8.4	16.0	934	n/a	measured	n/a
Cucurbita pepo (zucchini)	flower	9.3	9.3	16.3	1107	n/a	measured	n/a
Cucurbita sp. (female/squash)	flower	13.8	13.8	19.8	3091	n/a	measured	n/a
Cucurbita sp. (male/squash*)*	flower	10.4	8.4	15.8	1127	n/a	measured	n/a
Cucurbita sp. (squash*)*	flower	12.1	11.1	17.8	1878	n/a	measured	n/a
Cucurbita spp.	flower	10.7	10.2	17.1	1461	n/a	measured	n/a
Cucurbita spp. (female)	flower	12.0	12.0	18.2	2058	n/a	measured	n/a
Cucurbita spp. (male*)*	flower	9.4	8.4	15.9	986	n/a	measured	n/a

Species	**Floral unit**	**L**	**W**	**H**	**Flower volume (mm^3)**	**Inflorescence volume (mm^3)**	**Flower measurement source**	**Inflorescence measurement source**
Daucus carota	inflorescence	2.0	2.0	1.0	3.14	358.14	measured; Sivinski et al. 2011	Sivinski et al. 2011
Echium vulgare	flower	2.4	3.8	9.2	65.5	n/a	measured	n/a
Erigeron canadensis	inflorescence	1.0	1.0	3.0	2.36	1275	measured	measured
Erigeron philadelphicus	capitulum	7.6	7.6	3.4	157	n/a	measured	n/a
Erigeron sp.	capitulum	3.55	3.55	12.6	52.5	n/a	measured	n/a
Erysimum cheiranthoides	inflorescence	1.0	1.0	3.0	2.36	18.8	Idris and Grafius 1995	http://www.discoverlife.org
Erythronium americanum	flower	3.0	3.0	11.0	77.8	n/a	measured	n/a
Euthamia graminifolia	inflorescence	1.0	1.0	1.0	0.785	20.4	Harder 1985	http://plants.jstor.org
Fagopyrum esculentum	inflorescence	2.0	2.0	2.0	6.28	980	Cawoy et al. 2006; Cawoy et al. 2009	Cawoy et al. 2006
Fragaria × ananassa	flower	7.8	7.8	6.2	304	n/a	measured	n/a
Fragaria virginiana	flower	3.0	3.0	2.4	26.4	n/a	measured	n/a
Galinsoga quadriradiata	capitulum	2.0	2.0	2.0	0.013	n/a	Warwick and Sweet 1983	n/a
Galium mollugo	inflorescence	1.0	1.0	1.0	0.785	14.1	https://weedecology.css.cornell.edu	http://www.discoverlife.org
Galium palustre	inflorescence	1.0	1.0	1.0	0.785	5.50	https://weedecology.css.cornell.edu	http://www.luontoportti.com
Geum aleppicum	flower	6.0	6.0	8.0	226	n/a	http://symbiota.math.wisc.edu	n/a
Glechoma hederacea	flower	1.0	1.0	9.8	7.70	n/a	measured	n/a
Helianthus annuus	capitulum	35.4	35.4	20.7	27435	n/a	measured	n/a
Hieracium caespitosum	capitulum	7.4	7.4	3.4	153	n/a	measured	n/a
Hieracium pilosella	capitulum	10.4	10.4	6.4	538	n/a	measured	n/a
Lactuca sp.	capitulum	2.0	2.0	3.0	9.42	n/a	http://www.naturemanitob	n/a

Species	**Floral unit**	**L**	**W**	**H**	**Flower volume (mm^3)**	**Inflorescence volume (mm^3)**	**Flower measurement source**	**Inflorescence measurement source**
							a.ca	
Leucanthemum vulgare	capitulum	10.5	10.5	3.5	311	n/a	measured	n/a
Linaria vulgaris	flower	2.4	1.0	20.6	39.1	n/a	measured	n/a
Lotus corniculatus	flower	4.73	4.73	12.0	211	n/a	http://ucjeps.berkeley.edu/eflora	n/a
Maianthemum canadense	inflorescence	1.0	1.0	1.0	0.785	14.9	http://plants.jstor.org	http://plants.jstor.org
Malus pumila	flower	9.2	9.4	9.8	674	n/a	measured	n/a
Malva neglecta	flower	1.9	1.9	4.25	12.0	n/a	Nave et al. 2016	n/a
Medicago lupulina	inflorescence	1.0	1.0	1.0	0.785	11.8	measured	http://www.efloras.org
Medicago sativa	inflorescence	1.0	1.0	5.0	3.93	68.7	measured; Winkler et al. 2009	http://www.efloras.org
Mitella diphylla	flower	1.0	1.0	3.0	2.36	n/a	measured	n/a
Oenothera biennis	flower	1.0	1.0	6.4	5.03	n/a	measured	n/a
Oxalis stricta	flower	1.0	1.0	3.5	2.75	n/a	measured	n/a
Phaseolus vulgaris	flower	2.8	2.8	7.6	48.2	n/a	measured	n/a
Physalis heterophylla	flower	2.8	2.8	9.0	58.1	n/a	measured	n/a
Plantago lanceolata	inflorescence	1.0	1.0	2.0	6.28	452	Van Damme 1984; Cavers et al. 1980	Van Damme 1984
Potentilla argentea	flower	2.4	2.4	1.2	6.13	n/a	measured	n/a
Prunella vulgaris	flower	1.2	1.6	7.0	11.2	n/a	measured	n/a
Ranunculus acris	flower	5.8	5.8	2.8	80.9	n/a	measured	n/a
Ranunculus recurvatus	flower	1.6	1.6	2.6	6.28	n/a	measured	n/a
Rubus allegheniensis	flower	11.6	11.6	4.6	489	n/a	measured	n/a
Rubus sp. (raspberry*)*	flower	6.4	6.4	6.0	202	n/a	measured	n/a
Rudbeckia hirta	capitulum	15.0	15.0	3.6	636	n/a	http://www.efloras.org	n/a
Silene vulgaris	flower	3.2	3.2	15.6	133	n/a	measured	n/a
Sisyrinchium montanum	flower	1.0	1.0	4.5	3.53	n/a	measured	n/a

Species	**Floral unit**	**L**	**W**	**H**	**Flower volume (mm^3)**	**Inflorescence volume (mm^3)**	**Flower measurement source**	**Inflorescence measurement source**
Solanum tuberosum	flower	2.8	2.8	9.0	57.3	n/a	measured	n/a
Solidago canadensis	inflorescence	1.0	1.0	1.0	0.785	26.7	Harder 1985	measured
Solidago sp.	inflorescence	1.0	1.0	1.0	0.785	26.7	Harder 1985	measured
Sonchus arvensis	capitulum	10.5	10.5	22	1905	n/a	Lemna and Messersmith 1990	n/a
Symphotrichum lanceolatum	capitulum	4.0	4.0	6.0	75.4	n/a	Chmielewski and Semple 2001	n/a
Taraxacum agg.	capitulum	19.6	19.6	8.4	3050	n/a	measured	n/a
Trifolium aureum	inflorescence	1.0	1.0	7.0	5.50	179	http://www.efloras.org	http://www.efloras.org
Trifolium pratense	inflorescence	1.0	1.0	11.0	8.64	432	Winkler et al. 2009	http://www.efloras.org
Trifolium repens	inflorescence	1.0	1.0	2.0	1.57	55.0	Nave et al. 2016	http://www.efloras.org
Trillium erectum	flower	8.0	8.0	9.0	452	n/a	http://www.efloras.org	n/a
Trillium grandiflorum	flower	5.4	5.6	11.0	292	n/a	measured	n/a
Verbena hastata	inflorescence	1.0	1.0	2.0	1.57	8.80	measured	measured
Veronica serpyllifolia	flower	1.0	1.0	1.125	0.884	n/a	measured	n/a
Veronica sp.	flower	1.04	1.04	1.04	0.884	n/a	measured	n/a
Vicia cracca	inflorescence	3.0	3.0	6.2	43.8	1972	http://linnet.geog.ubc.ca/Atlas; measured	http://linnet.geog.ubc.ca/Atlas
Viola pubescens	flower	1.0	1.0	4.5	3.53	n/a	measured	n/a

Appendix 3.

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	flower		Heinrich 1976
Achillea millefolium	38.05	capitulum		Hicks et al. 2016; Holl 1995
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
Cardamine bulbosa	4.5	flower	*C.* spp.	Baude et al. 2016
Centaurea sp.	1473.81	capitulum	*C. nigra*	Hicks et al. 2016
Cerastium fontanum	26.93	flower		Baude et al. 2016
Citrullus lanatus	12000	flower		Taha and Bayoumi 2009
Cornus sericea	68.79	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	688.27	flower		Hicks et al. 2016
Erigeron philadelphicus	2250	capitulum		Holl 1995
Euthamia graminifolia	24	capitulum		Heinrich 1976
Fragaria virginiana	42	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	94.37	flower		Baude et al. 2016
Leucanthemum vulgare	515.213	capitulum		Hicks et al. 2016
Linaria vulgaris	543.89	flower		Baude et al. 2016
Lotus corniculatus	61.82	flower		Baude et al. 2016
Malus pumila	110.21	flower		Baude et al. 2016

Species	**Nectar (µg/day)**	**Nectar unit**	**Source species**	**Source**
Malva neglecta	540.65	flower	*M. moschata*	Hicks et al. 2016
Medicago lupulina	1.63	flower		Baude et al. 2016
Medicago sativa	146.14	flower		Baude et al. 2016
Oxalis stricta	15.53	flower	*O. acetosella*	Baude et al. 2016
Phaseolus vulgaris	53.44	flower	Cultivated bean	Baude et al. 2016
Potentilla argentea	23.25	flower	*Potentilla* spp.	Baude et al. 2016
Prunella vulgaris	138.62	flower		Baude et al. 2016
Ranunculus acris	78.83	flower		Baude et al. 2016
Rubus allegheniensis	894	flower		Holl 1995
Rubus sp. (raspberry)	1892.83	flower	*R. fruticosus* agg.	Baude et al. 2016
Silene vulgaris	251.47	flower		Baude et al. 2016
Solanum tuberosum	27.29	flower		Baude et al. 2016
Solidago canadensis	28.8	capitulum		Heinrich 1976
Sonchus arvensis	651.3	capitulum		Baude et al. 2016
Symphotrichum lanceolatum	1116	capitulum		Chmielewski and Semple 2001
Taraxacum agg.	2137.2	capitulum		Hicks et al. 2016
Trifolium pratense	116.86	flower		Baude et al. 2016
Trifolium repens	48.97	flower		Baude et al. 2016
Veronica serpyllifolia	2.83	flower		Baude et al. 2016
Vicia cracca	484.4	flower		Baude et al. 2016
Viola pubescens	124.62	flower	*Viola* spp.	Baude et al. 2016; Holl 1995

Appendix 4.

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**	**Source**
Acer spicatum	0.02		Biesboer 1975; Sullivan 1983
Achillea millefolium	1.128		Hicks et al. 2016
Actaea pachypoda	0.522		Pellmyr 1985; http://www.discoverlife.org
Capsella bursa-pastoris	0.001		Hicks et al. 2016
Centaurea sp.	6.404	*C. nigra*	Hicks et al. 2016
Cerastium fontanum	0.035		Hicks et al. 2016
Cucumis melo	0.125		Kouonon et al. 2009; Perveen and Qaiser 2008
Cucurbita pepo (zucchini)	13.129		Nepi and Pacini 1993; Vidal et al. 2006
Cucurbita sp. (squash)	34.775		Vidal et al. 2006
Daucus carota	0.019		Hicks et al. 2016
Echium vulgare	0.1499		Hicks et al. 2016
Erythronium americanum	16.313		Harder et al. 1985; Kosenko 1999
Fagopyrum esculentum	0.0562		Cawoy et al. 2006
Fragaria virginiana	1.415		Ashman and Hitchens 2000; Hebda et al. 1988
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	0.0637		Hutchings and Price 1999; Moon et al. 2008
Leucanthemum vulgare	15.918		Hicks et al. 2016

Species	**Pollen (µl/floral unit)**	**Source species**	**Source**
Linaria vulgaris	0.444		Arnold 1982; Olsson 1974
Lotus corniculatus	0.146		Hicks et al. 2016
Malva neglecta	0.579		Cruden 1977; http://blogs.cornell.edu/pollengrains/
Medicago sativa	0.16		Müller et al. 2006
Oenothera biennis	7.998		Cruden and Jensen 1979; Hall et al. 1988
Plantago lanceolata	0.0116		Hicks et al. 2016
Prunella vulgaris	0.0314		Hicks et al. 2016
Ranunculus acris	1.398		Hicks et al. 2016
Silene vulgaris	0.3603	*S. dioica/latifolia*	Hicks et al. 2016
Sonchus arvensis	0.939	*S. asper*	Hicks et al. 2016
Trifolium aureum	2.823		Hicks et al. 2016
Trifolium repens	0.0198		Hicks et al. 2016
Trillium erectum	0.0285		Hicks et al. 2016
Veronica sp.	0.0309	*V. persica*	Hicks et al. 2016
Vicia cracca	0.0381		Hicks et al. 2016

Appendix 5.

All candidate models for late-summer bee visits at a given spatial scale, where "local FR" is the abundance of floral resources within the transect used for sampling, "1st FR" is the abundance of floral resources during the late-spring sampling period at a given spatial scale, "2nd FR" is the abundance of floral resources during the early-summer sampling, "3rd FR" is the abundance of floral resources during the mid-summer sampling, and "4th FR" is the abundance of floral resources during the late-summer sampling period. Models were run both with and without the local FR term. All models also included an offset of the length of the observation period (log-transformed), and the random effect of farm site identity.

Late-summer bee visits = local FR

Late-summer bee visits = 1st FR (+ local FR)

Late-summer bee visits = 2nd FR (+ local FR)

Late-summer bee visits = 3rd FR (+ local FR)

Late-summer bee visits = 4th FR (+ local FR)

Late-summer bee visits = 1st FR + 2nd FR (+ local FR)

Late-summer bee visits = 2nd FR + 3rd FR (+ local FR)

Late-summer bee visits = 3rd FR + 4th FR (+ local FR)

Late-summer bee visits = 1st FR + 2nd FR + 3rd FR (+ local FR)

Late-summer bee visits = 2nd FR + 3rd FR + 4th FR (+ local FR)

Late-summer bee visits = 1st FR + 2nd FR + 3rd FR + 4th FR (+ local FR)

Appendix 6.

The chosen spatial scales as determined by models of bee visits for either weighted (W) or unweighted (UW) analyses of floral resources at each spatial scale (250 m, 500 m, or 750 m), wherein unknown areas were assigned floral resources values from either minimum estimates ($_{\text{min}}$), maximum estimates ($_{\text{max}}$), or median estimates ($_{\text{median}}$) calculated from all land types. All candidate models were run and models with ΔAICc values less than 2 were assigned scores, with the highest scores given to the models with ΔAICc of 0 within each sampling period. The spatial scale with the highest score, summed across sampling periods and expressed as a percent of the maximum possible summed score for a given set of models, was then determined for all bee taxa, separately for median, minimum, and maximum models, and for both weighted and unweighted analyses (7 taxa × 4 analyses = 28 sets of ranked models). The chosen spatial scale for each taxon was the scale with the highest total score across weighted and unweighted analyses. The chosen scale is indicated in bold, and * indicates when the scale with the highest summed score for an individual analysis was not the chosen spatial scale.

Bee taxon	Spatial scale	Summed scores of models with ΔAICc <2 (as % of maximum possible score)				
		W_{median}	W_{min}	W_{max}	UW_{median}	Total
All bees	250	29.9	30.0	31.5	30.7	122.1
	500	28.0	30.7	20.5	30.2	109.4
	750	**37.4**	**34.0**	**42.5**	**31.6**	**145.4**
	Local	4.7	5.3	5.5	7.6	23.1
Honey bees	250	25.0	24.6	40.0*	26.4	116.0
	500	10.0	18.0	15.0	22.6	65.7
	750	**35.0**	**37.7**	**35.0**	**43.4**	**151.1**
	Local	30.0	19.7	10.0	7.5	67.2
Bumble bees	**250**	**29.0**	**31.0**	**43.6**	**38.7**	**142.3**
	500	29.0	23.8	16.4	32.0	101.2
	750	29.0	33.3*	34.5	26.0	122.9
	Local	12.9	11.9	5.5	3.3	33.6
Squash bees	**250**	**26.7**	**34.1**	**64.3**	**60.0**	**185.0**
	500	46.7*	36.4*	21.4	0.0	104.5
	750	26.7	29.5	14.3	40.0	110.5
	Local	0.0	0.0	0.0	0.0	0.0
Halictidae	**250**	**45.0**	**39.1**	**34.2**	**31.6**	**149.9**
	500	22.5	26.8	18.5	15.8	83.6
	750	13.8	17.3	29.9	36.8*	97.8
	Local	18.8	16.8	17.4	15.8	68.7
Andrenidae	250	9.1	34.4*	22.2	36.1*	101.8
	500	36.4*	9.4	0.0	27.9*	73.6
	750	**18.2**	**31.3**	**33.3**	**21.9**	**104.6**
	Local	36.4	25.0	44.4	14.2	120.0
Megachilidae	250	23.5	17.6	23.5*	51.3*	116.0
	500	**58.8**	**47.1**	**17.6**	**37.2**	**160.7**
	750	0.0	20.6	44.1*	9.0	73.7
	Local	17.6	14.7	14.7	2.6	49.6

Appendix 7.

Pearson’s correlation coefficients from pairwise correlations between the abundance of floral resources (FR), at each spatial scale (“L” or local/within the transect used for sampling, 250-m radius, 500-m radius, and 750-m radius), and at each sampling period (1 = late-spring, 2 = early-summer, 3 = mid-summer, and 4 = late-summer). Correlations were run separately for unweighted floral resources, and floral resources weighted by the proportion of visits received by each taxon examined (all bees, honey bees, bumble bees, squash bees, Halictidae, Andrenidae, and Megachilidae). Correlation coefficients ≥ 0.8 are indicated in bold. Local spatial scale correlations were not run between time-periods with other local values, as models only included local spatial scale FR in the present sampling period.

Sampling period		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
	Spatial scale	L	L	L	L	250	250	250	250	500	500	500	500	750	750	750
Unweighted FR																
1	250	0.43	0.45	0.12	0.15											
2	250	0.16	0.32	0.12	0.10	0.38										
3	250	0.16	0.20	0.26	0.08	0.44	**0.90**									
4	250	0.09	0.13	0.18	0.00	0.31	**0.92**	**0.95**								
1	500	0.44	0.39	0.08	0.06	**0.85**	0.14	0.25	0.10							
2	500	0.40	0.37	0.11	0.06	0.55	0.65	0.67	0.60	0.62						
3	500	0.35	0.28	0.24	0.03	0.65	0.57	0.75	0.64	0.71	**0.87**					
4	500	0.25	0.15	0.18	-0.02	0.45	0.64	0.77	0.73	0.49	**0.89**	**0.92**				
1	750	0.40	0.34	0.13	0.03	0.70	0.07	0.22	0.10	**0.91**	0.50	0.65	0.42			
2	750	0.42	0.40	0.23	0.06	0.46	0.46	0.55	0.50	0.62	**0.86**	**0.82**	**0.81**	0.65		

Sampling period		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
	Spatial scale	L	L	L	L	250	250	250	250	500	500	500	500	750	750	750
3	750	0.42	0.38	0.27	0.07	0.59	0.34	0.53	0.41	0.77	0.75	**0.88**	0.74	**0.86**	**0.90**	
4	750	0.33	0.26	0.27	0.08	0.40	0.46	0.61	0.56	0.52	**0.83**	0.**85**	**0.89**	0.53	**0.96**	**0.85**
Weighted FR for all bees																
1	250	0.32	0.57	0.25	0.12											
2	250	0.06	0.38	0.16	0.00	0.48										
3	250	0.10	0.32	0.33	0.04	0.61	**0.89**									
4	250	0.04	0.27	0.22	0.10	0.47	**0.93**	**0.92**								
1	500	0.47	0.57	0.13	0.09	0.76	0.07	0.29	0.12							
2	500	0.40	0.38	0.05	-0.04	0.42	0.59	0.62	0.50	0.48						
3	500	0.38	0.38	0.16	-0.01	0.64	0.47	0.70	0.51	0.75	**0.82**					
4	500	0.32	0.31	-0.09	0.01	0.39	0.52	0.64	0.58	0.50	**0.87**	**0.87**				
1	750	0.42	0.52	0.09	0.15	0.65	0.05	0.28	0.14	**0.93**	0.37	0.71	0.47			
2	750	0.36	0.37	0.07	0.09	0.34	0.45	0.53	0.43	0.46	**0.88**	0.78	**0.85**	0.43		
3	750	0.41	0.41	0.13	0.09	0.57	0.28	0.52	0.36	**0.80**	0.67	**0.91**	0.76	**0.87**	**0.75**	
4	750	0.31	0.33	-0.06	0.09	0.33	0.40	0.52	0.45	0.48	**0.81**	**0.80**	**0.91**	0.49	**0.96**	0.79
Weighted FR for honey bees																
1	250	0.24	0.48	0.20	0.19											
2	250	0.07	0.37	0.02	0.07	0.66										
3	250	0.03	0.24	0.16	-0.05	0.54	**0.84**									
4	250	0.01	0.23	0.09	-0.02	0.54	**0.86**	**0.95**								
1	500	0.39	0.50	0.06	0.12	0.70	0.15	0.10	0.09							
2	500	0.43	0.40	-0.08	0.09	0.46	0.55	0.42	0.37	0.60						
3	500	0.23	0.34	0.07	-0.04	0.49	0.48	0.72	0.60	0.49	0.69					
4	500	0.21	0.33	-0.08	0.00	0.40	0.47	0.67	0.62	0.46	0.73	**0.94**				
1	750	0.33	0.46	0.00	0.14	0.63	0.12	0.10	0.12	**0.95**	0.53	0.44	0.44			
2	750	0.35	0.41	-0.11	0.17	0.40	0.41	0.38	0.37	0.63	**0.88**	0.69	0.77	0.65		

Sampling period		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
	Spatial scale	L	L	L	L	250	250	250	250	500	500	500	500	750	750	750
3	750	0.27	0.37	0.00	0.07	0.43	0.33	0.55	0.46	0.59	0.70	**0.90**	**0.88**	0.61	**0.85**	
4	750	0.20	0.36	-0.11	0.09	0.33	0.35	0.54	0.48	0.47	0.68	**0.86**	**0.92**	0.48	**0.86**	**0.96**
Weighted FR for bumble bees																
1	250	0.33	0.36	0.15	0.21											
2	250	0.06	0.21	0.18	0.11	0.38										
3	250	0.11	0.30	0.14	0.16	0.64	**0.87**									
4	250	0.06	0.30	0.13	0.24	0.54	**0.90**	**0.93**								
1	500	0.50	0.38	0.07	0.18	**0.81**	0.03	0.34	0.23							
2	500	0.27	0.16	0.10	0.03	0.37	0.70	0.65	0.55	0.32						
3	500	0.47	0.31	0.06	0.15	0.72	0.47	0.72	0.58	**0.80**	0.71					
4	500	0.44	0.33	-0.04	0.20	0.57	0.50	0.69	0.62	0.67	0.75	**0.92**				
1	750	0.45	0.36	-0.03	0.18	0.72	-0.01	0.31	0.23	**0.94**	0.18	0.72	0.61			
2	750	0.32	0.29	0.01	0.13	0.30	0.55	0.53	0.43	0.31	**0.88**	0.64	0.72	0.21		
3	750	0.49	0.35	-0.03	0.19	0.64	0.23	0.52	0.41	**0.84**	0.46	**0.90**	**0.83**	**0.89**	0.49	
4	750	0.48	0.37	-0.10	0.24	0.53	0.36	0.55	0.48	0.70	0.63	**0.87**	**0.93**	0.71	0.74	**0.91**
Weighted FR for squash bees																
2	250		0.03	0.24	0.35											
3	250		0.02	0.23	0.35		**1.00**									
4	250		0.03	0.24	0.35		**1.00**	**1.00**								
2	500		-0.05	0.10	0.23		0.67	0.66	0.66							
3	500		-0.06	0.09	0.22		0.67	0.67	0.66		**1.00**					
4	500		-0.05	0.10	0.22		0.67	0.67	0.66		**1.00**	**1.00**				
2	750		0.03	0.10	0.23		0.65	0.64	0.63		**0.99**	**0.99**	**0.99**			
3	750		0.02	0.09	0.23		0.65	0.64	0.63		**0.99**	**0.99**	**0.99**		**1.00**	
4	750		0.03	0.10	0.23		0.65	0.65	0.64		**1.00**	**1.00**	**0.99**		**1.00**	**1.00**

Sampling period		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
	Spatial scale	L	L	L	L	250	250	250	250	500	500	500	500	750	750	750
Weighted FR for Halictidae																
1	250	0.28	0.48	0.11	0.09											
2	250	0.13	0.26	0.05	0.09	0.65										
3	250	0.16	0.23	0.36	0.04	0.72	**0.80**									
4	250	0.08	0.05	0.37	-0.02	0.52	**0.87**	**0.87**								
1	500	0.44	0.47	0.01	0.00	0.76	0.26	0.46	0.19							
2	500	0.42	0.31	-0.07	0.04	0.58	0.61	0.56	0.52	0.66						
3	500	0.34	0.30	0.31	-0.02	0.74	0.44	0.75	0.54	**0.84**	0.67					
4	500	0.23	0.09	0.28	-0.06	0.46	0.56	0.73	0.76	0.44	0.76	0.77				
1	750	0.37	0.42	0.04	0.01	0.60	0.12	0.35	0.10	**0.91**	0.47	0.74	0.28			
2	750	0.38	0.37	0.05	0.15	0.48	0.43	0.51	0.47	0.63	**0.83**	0.66	0.71	0.59		
3	750	0.36	0.36	0.19	0.02	0.61	0.20	0.51	0.28	**0.89**	0.54	**0.86**	0.50	**0.96**	0.68	
4	750	0.26	0.22	0.29	0.13	0.39	0.42	0.61	0.60	0.44	0.71	0.69	**0.88**	0.34	**0.88**	0.54
Weighted FR for Andrenidae																
1	250	0.24	0.27	0.07	0.14											
2	250	0.14	-0.02	0.21	0.19	0.61										
3	250	0.20	0.02	0.24	0.23	0.73	**0.89**									
4	250	0.19	-0.01	0.22	0.22	0.63	**0.98**	**0.95**								
1	500	0.45	0.31	-0.04	0.06	0.72	0.17	0.40	0.25							
2	500	0.34	0.03	0.14	0.09	0.48	0.76	0.74	0.79	0.41						
3	500	0.43	0.13	0.08	0.11	0.71	0.56	0.74	0.64	0.79	**0.80**					
4	500	0.38	0.06	0.12	0.09	0.57	0.72	0.77	0.78	0.55	**0.98**	**0.90**				
1	750	0.39	0.29	-0.09	0.00	0.63	0.05	0.29	0.13	**0.94**	0.24	0.67	0.38			
2	750	0.39	0.15	0.13	0.12	0.40	0.60	0.61	0.63	0.44	**0.86**	0.72	**0.85**	0.32		
3	750	0.47	0.19	0.00	0.06	0.60	0.26	0.49	0.35	**0.87**	0.50	**0.85**	0.64	**0.89**	0.59	
4	750	0.46	0.18	0.10	0.11	0.50	0.53	0.62	0.59	0.62	**0.82**	**0.84**	**0.87**	0.55	**0.95**	**0.80**

Sampling period		1	2	3	4	1	2	3	4	1	2	3	4	1	2	3
	Spatial scale	L	L	L	L	250	250	250	250	500	500	500	500	750	750	750
Weighted FR for Megachilidae																
1	250	0.18	0.15	0.13	0.05											
2	250	0.18	0.13	0.19	0.06	**0.87**										
3	250	0.20	0.13	0.20	0.06	**0.92**	**0.99**									
4	250	0.19	0.10	0.17	0.07	0.74	**0.97**	**0.92**								
1	500	0.37	0.15	-0.08	-0.09	0.66	0.51	0.60	0.37							
2	500	0.37	0.11	0.06	-0.02	0.65	0.77	0.79	0.72	0.77						
3	500	0.37	0.11	0.03	-0.04	0.67	0.72	0.76	0.63	**0.88**	**0.97**					
4	500	0.33	0.08	0.12	0.04	0.55	0.77	0.74	**0.80**	0.49	**0.92**	**0.80**				
1	750	0.30	0.16	-0.13	-0.12	0.43	0.25	0.34	0.11	**0.89**	0.53	0.68	0.22			
2	750	0.45	0.25	0.05	0.03	0.52	0.58	0.62	0.52	0.79	**0.87**	**0.88**	0.73	0.71		
3	750	0.40	0.19	-0.03	-0.05	0.50	0.46	0.53	0.35	**0.89**	0.78	**0.86**	0.53	**0.91**	**0.93**	
4	750	0.43	0.31	0.15	0.14	0.47	0.63	0.62	0.66	0.44	0.79	0.69	**0.85**	0.24	**0.84**	0.59

Appendix 8.

Model estimates and AICc values obtained from best models for bee visits in late-spring, early-summer, mid-summer, and late-summer sampling periods for all bee taxa. Generalized linear mixed models were run, with a zero-inflated negative binomial distribution and log link function. Floral resource (FR) terms in models represent the median floral volume per 1 m^2 of a land type, weighted by the proportion of visits to each flowering species by a given bee taxon. Spatial scale indicates the radius distance (250, 500, or 750 m) of floral resources surrounding a sampling location, with local spatial scale including only floral resources per 1 m^2 in the transect used for observation. Unknown areas within a given radius of a sampling location were either assigned the minimum estimate of the weighted floral resource volume of all land types during a given sampling period (0 cm^2) or the maximum estimate of the weighted floral resource volume of all land types during a given sampling period, and used in calculations for FR values. Significant FR coefficients are indicated with * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$. Shaded grey areas in table represent which past FR were not included in models of bee visits from a given sampling period.

Table A8.1. Weighted floral resource models with minimum estimates for unknown areas.

Sampling period	Bee taxon	Spatial scale	Log_{10} Local FR	Log_{10} Present FR	Log_{10} Past FR			AICc
					Late-spring	Early-summer	Mid-summer	
Late-spring	All bees	750	0.17*	0.62				340.4
	Honey bees	All models failed to converge						
	Bumble bees	250	0.024	0.83				153.1
	Halictidae	250		0.52				239.2
	Andrenidae	Local	1.00*					113.3
	Megachilidae	500	0.82**	−5.10***				46.8
Early-summer	All bees	750	0.36*	−1.94				344.2
	Honey bees	Local	1.06***					177.5
	Bumble bees	250			0.22			212.4
	Halictidae	250			−0.36			256
	Andrenidae	750		0.49	1.90***			138.2
	Megachilidae	500	0.69**		−2.82**			82.4
Mid-summer	All bees	750	0.51**	−0.22				385
	Honey bees	Local	0.78*					214.9
	Bumble bees	Local	0.56***					239.5
	Squash bees	250		−1.11				167.3
	Halictidae	Local	0.96***					204.8
	Andrenidae	Local	1.04***					118.7
	Megachilidae	Local	0.87**					77.7
Late-summer	All bees	750			−0.68*			411.5
	Honey bees	750		−25.3*		7.48	16.5	200.6
	Bumble bees	250				1.87*		306.6
	Squash bees	250	1.08***	0.75			−0.65	200.4
	Halictidae	Local	0.40*			−2.39		130.9
	Andrenidae	Local	0.77*					72
	Megachilidae	500			1.59*			43.4

Table A8.2. Weighted floral resource models with maximum estimates for unknown areas.

Sampling period	Bee taxon	Spatial scale	Log_{10} Local FR	Log_{10} Present FR	Log_{10} Past FR			AICc
					Late-spring	Early-summer	Mid-summer	
Late-spring	All bees	750		0.75				342.4
	Honey bees	750		384				460.9
	Bumble bees	Local	0.77***					172.1
	Halictidae	250	0.13***	0.44*				234.7
	Andrenidae	Local	1.00*					113.3
	Megachilidae	500		-5.64***				50.3
Early-summer	All bees	750	0.36	−1.26				344.1
	Honey bees	Local	1.06***					177.5
	Bumble bees	250		−0.36				212.8
	Halictidae	Local	0.051					256.6
	Andrenidae	750		−2.47**	2.98***			136.6
	Megachilidae	500	0.84*		−3.15*			83.3
Mid-summer	All bees	750	0.53**		−1.08			383
	Honey bees	750			−2.41*			213.7
	Bumble bees	Local	0.56***					239.5
	Squash bees	250		−14.5*		11.5*		165.3
	Halictidae	Local	0.96***					204.8
	Andrenidae	Local	1.04***					118.7
	Megachilidae	Local	0.87**					77.7
Late-summer	All bees	750			−0.83			414.3
	Honey bees	750	1.02*		4.87	−1.06		242.6
	Bumble bees	250				1.55		309.2
	Squash bees	250	1.08***			1.03		196.9
	Halictidae	Local	0.40					130.9
	Andrenidae	Local	0.77*					72
	Megachilidae	500			2.19*			43.4

Appendix 9.

Sample calculation of weighted floral resources for honey bees (*Apis mellifera*) in the cucumber (*Cucumis sativus*) land type during the late-summer sampling period. Note that only one transect with cucumber was sampled during late-summer.

Percent of honey bee visits to *C. sativus*

= 100 × (29 visits to *C. sativus* / 2455 visits to all flowering species)

= 1.18%

Weighted floral volume of *Cucumis sativus*

= percent of visits × average volume of *C. sativus* flower

= 1.18 × 19.5mm^3

= 23.01mm^3

Average unweighted volume of *C. sativus* per 1m^2 of transect

= [floral volume × (number of flowers in 3 quadrats of 1.5m × 1m)] / 3

= [19.5mm^3 × (11 flowers/1.5m^2 + 19 flowers/1.5m^2 + 35 flowers/1.5m^2)] / 3

= 281.67mm^3/m^2

Average weighted volume of *C. sativus* per 1m^2 of transect

= [weighted floral volume × (number of flowers in 3 quadrats of 1.5m × 1m)] / 3

= [23.01mm^3 × (11 flowers/1.5m^2 + 19 flowers/1.5m^2 + 35 flowers/1.5m^2)] / 3

= 332.36mm^3/m^2

Weighted value of cucumber land type for honey bees

= median weighted floral volume per 1m^2 / median unweighted volume per 1m^2

= (332.36mm^3/m^2) / (281.67mm^3/m^2)

= 1.18

Appendix 10.

Model estimates and AICc values obtained from best models for bee visits in early-summer, mid-summer, and late-summer sampling periods for all bee taxa, when areas with soybean were assigned the median floral resource volume of all land types during a given sampling period. Generalized linear mixed models were run, with a zero-inflated negative binomial distribution and log link function. Floral resource (FR) terms in models represent the median floral volume per 1 m^2 of a land type, weighted by the proportion of visits to each flowering species by a given bee taxon. Spatial scale indicates the radius distance (250, 500, or 750 m) of floral resources surrounding a sampling location, with local spatial scale including only floral resources per 1 m^2 in the transect used for observation. Land area with soybean crops and unknown areas within a given radius of a sampling location were assigned the median floral resource value from all land types during a given sampling period, and used in calculations for FR values. Significant FR coefficients are indicated with * for $p < 0.05$, ** for $p < 0.01$, and *** for $p < 0.001$. Models and AICc values in bold indicate that “best” models differed from analyses where soybean area was assigned zero floral resource values, and had lower or equal AICc values; FR coefficients in bold indicate which terms in the model differed (compare to Table 3). Shaded grey areas in table represent which past FR were not included in models of bee visits from a given sampling period.

Sampling period	Bee taxon	Spatial scale	Log$_{10}$ Local FR	Log$_{10}$ Present FR	Log$_{10}$ Past FR			AICc
					Late-spring	Early-summer	Mid-summer	
Early-summer	All bees	Local	0.18					344.3
	Honey bees	Local	1.06***					177.5
	Bumble bees	**250**		**0.501**				**212.9**
	Halictidae	Local	0.05					256.6
	Andrenidae	**750**		**−0.486**	2.02***			**138.2**
	Megachilidae	500	0.73**		−2.937**			82.3
Mid-summer	All bees	750	0.51**		−0.324			384.7
	Honey bees	Local	0.78*					214.9
	Bumble bees	Local	0.56***					239.5
	Squash bees	250		-1.411				166
	Halictidae	Local	0.96***					204.8
	Andrenidae	Local	1.04***					118.7
	Megachilidae	**500**	1.05			**−3.13**		**77.6**
Late-summer	**All bees**	**750**					**−1.094***	**411.4**
	Honey bees	All models failed to converge						
	Bumble bees	250				2.86**		304.5
	Squash bees	**250**				**−0.472**		**227.9**
	Halictidae	Local	0.40					130.9
	Andrenidae	**750**			**1.549**	**−0.864**		**62**
	Megachilidae	500			1.68*			43.5

Appendix 11.

The five species most visited by all bees compared to the five most abundant species in floral counts within quadrats across all sampling locations during late-spring, early-summer, mid-summer, and late-summer sampling periods. “All species” refers to the sum total of bee visits and floral counts across each sampling period.

Sampling period	Most-visited species	Bee visits	Most abundant species	Floral counts
Late-spring	*Malus pumila*	501	*Malus pumila*	6568
	Taraxacum agg.	393	*Taraxacum* agg.	616
	Rubus allegheniensis	197	*Erigeron philadelphicus*	426
	Fragaria × ananassa	154	*Glechoma hederacea*	266
	Fragaria virginiana	89	*Fragaria × ananassa*	266
	All species	1659	All species	9352
Early-summer	*Rubus* sp. (raspberry)	575	*Vicia cracca*	1499
	Trifolium repens	472	*Galium mollugo*	1483
	Vicia cracca	280	*Cerastium fontanum*	1264
	Asparagus officinalis	101	*Trifolium repens*	1205
	Leucanthemum vulgare	85	*Asparagus officinalis*	1180
	All species	1946	All species	11031
Mid-summer	*Cucurbita* spp.	775	*Trifolium repens*	1131
	Trifolium repens	481	*Medicago sativa*	830
	Echium vulgare	176	*Erigeron* sp.	436
	Leucanthemum vulgare	134	*Leucanthemum vulgare*	434
	Anthemis arvensis	111	*Vicia cracca*	310
	All species	2211	All species	5768
Late-summer	*Cucurbita* spp.	1475	*Medicago sativa*	1464
	Medicago sativa	283	*Lotus corniculatus*	1147
	Solidago spp.	222	*Erigeron* sp.	923
	Lotus corniculatus	156	*Cucurbita* spp.	378
	Trifolium pratense	92	*Solidago* spp.	309
	All species	2618	All species	5097