



# Flower traits associated with the visitation patterns of bees

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## Abstract

Plant-pollinator interactions are partially driven by the expression of plant traits that signal and attract bees to the nutritional resources within flowers. Although multiple physical and chemical floral traits are known to influence the visitation patterns of bees, how distinct bee groups vary in their responses to floral traits has yet to be elucidated. In this study, we used a common garden experiment to test for morphological floral traits associated with pollen quantity at the plant species level, and examined how the visitation patterns of taxonomically and functionally distinct bee groups are related to flower trait characteristics of 39 wildflower species. We also determined how floral traits influence the structure of wild bee communities visiting plants and whether this varies among geographic localities. Our results suggest that floral area is the primary morphological floral trait related to bee visitation of several distinct bee groups, but that wild bee families and functionally distinct bee groups have unique responses to floral trait expression. The composition of the wild bee communities visiting different plants was most strongly associated with variability in floral area, flower height, and the quantity of pollen retained in flowers. Our results inform wildflower habitat management for bees by demonstrating that the visitation patterns of distinct bee taxa can be predicted by floral traits, and highlight that variability in these traits should be considered when selecting plants to support pollinators.

**Keywords** Bees · Traits · Flowers · Conservation · Plant–insect interactions

## Introduction

Recent concern about global declines in pollinator abundance and diversity have led to increased calls to support populations of bees in managed and natural areas

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(Biesmeijer et al. 2006; Potts et al. 2010). Habitat management that increases flower availability is a common method to support bees (Isaacs et al. 2009; Williams et al. 2014), but may disproportionately alter the visitation frequencies of bees if plant selection for habitat management only utilizes plant species that are visited by a subset of the bee community. The wide variation in bee visitation to different plant species (Tuell et al. 2008; Rowe et al. 2018; Lundin et al. 2019) reflects the considerable diversity of bee phenologies, nutritional requirements, and morphological traits that allow bees to access flower resources, as well as the composition of the bee community at the study sites. Since bee species vary considerably in their floral preferences, identifying plants traits that influence the visitation patterns of distinct pollinator taxa will provide insight into how plant trait composition predicts flower visitation for distinct bee groups. Such insight will help to inform plant selection for pollinator habitat management programs and strengthen interpretation of broader plant-pollinator interactions in natural community contexts.

Patterns of bee visitation to flowers is often related to the floral traits that initially attract, and then retain visitors

as they collect floral resources (Conner and Rush 1996; Raguso 2008; Stang et al. 2009; La Rosa and Conner 2017). Floral area is generally considered the strongest and most consistent predictor of bee abundance and species richness, operating from plant to landscape scales (Conner and Rush 1996; Potts et al. 2003; Westphal et al. 2003; Tuell et al. 2008; Kennedy et al. 2013; Blaauw and Isaacs 2014; Lundin et al. 2019). Furthermore, plants that produce taller flowers may be more frequently visited by generalist bees foraging throughout a landscape primarily utilizing visual cues to locate flower patches. Additional flower traits, such as flower color and scent can further aid in flower attractiveness to bees by advertising floral rewards such as pollen and nectar (Gumbert 2000; Reverté et al. 2016; Russell et al. 2017; Bauer et al. 2017; Raguso 2008; Junker and Parachnowitsch 2015; Hetherington-Rauth and Ramírez 2016). Visual flower traits in wildflower species can signal quantity and/or quality of pollen and nectar resources, which have consistently been shown to influence bee visitation (Potts et al. 2003; Vaudo et al. 2016; Nicholls and Hemple de Ibarra 2017; Russell et al. 2017). Importantly, bees often forage for pollen and nectar strategically to meet dietary requirements or maximize nutritional intake, resulting in strong preferences for plants with flower traits that signify high levels of resources (Cnaani et al. 2006; Nicolson 2011; Vaudo et al. 2015, 2016; Somme et al. 2015). The availability of pollen may be particularly important as it provides bees with protein and lipids and is the primary dietary component of developing offspring (Michener 2000; Vaudo et al. 2018).

Plant species can vary greatly in their structural traits, chemistry, and timing of resource availability (Junker and Parachnowitsch 2015; Vaudo et al. 2015). Rather than attracting pollinators independently, multiple flower traits likely interact to affect bee visitation (Leonard and Masek 2014). Since bee species respond uniquely to the quantity, quality, and timing of resource availability (Bosch et al. 1997; Potts et al. 2003), plant trait variability likely influences the composition of bee communities visiting the flowering plant community (Stang et al. 2009; Bartomeus et al. 2013; Urban-Mead 2017). Concurrently, dissimilarity in the ecological and life history traits of bees within a community allows many species to co-exist in the same environment, limiting competition for plant-based resources (Blüthgen and Klein 2011). Two life history traits of bees that may be sensitive to flower trait characteristics are body size (Greenleaf et al. 2007) and diet specialization (Williams et al. 2010), which influence their foraging distance and resource selection, respectively (Öckinger et al. 2010; Williams et al. 2010; Kennedy et al. 2013). Depending on the nutritional requirements and functional/ecological constraints of different bee species, individual species may be limited in their ability to use flowers of certain plant species, resulting in specificity of resource selection (Blüthgen and Klein 2011; Leonhardt and

Blüthgen 2012; Bauer et al. 2017). For this reason, functionally distinct bee species may utilize different floral trait cues to locate floral resources.

Although the relationships between flower traits and bee visitation are generally understood, most studies assessing the effect of flower traits on visitation patterns of bees examine these relationships by either focusing on the relationships between a relatively few species or assessing broad patterns across many different species groups (Conner and Rush 1996; Mitchell et al. 2004; Tuell et al. 2008; Lundin et al. 2019). Furthermore, the majority of these studies assess patterns of bee species' visitation in situ, whereas controlled and direct comparisons of plant species that naturally vary in their floral trait composition are rare. Lundin et al. (2019) used a common garden experiment with single species plots to identify plant traits that positively affect bee abundance, but this study only quantified species found in the Western U.S. and focused solely on broad pollinator groups. A more detailed approach that identifies how these relationships vary by taxonomically and functionally distinct bees is needed to identify the traits of plants that should be used for habitat management projects that target particular groups of bees or alternatively, aim to support broader bee diversity.

In this study, we identified floral traits related to one floral resource collected by individual bees (pollen) for a set of 39 plant species and used a common garden field experiment to examine how these plant traits influenced the visitation patterns of bees to the plants. Specifically, we determined (1) which morphological flower traits are associated with increased pollen quantity at the plant species level, (2) whether the floral traits that are associated with the visitation patterns of taxonomically and functionally distinct bees vary between bee groups, and (3) which flower traits are most important in the overall structuring of the wild bee community collected from experimental plots. We hypothesize that the floral traits associated with visitation by taxonomically and functionally distinct bees will vary, and that variability in flower traits will influence the bee community.

## Materials and methods

The study was conducted at three Michigan State University research stations in Southwest Michigan (Southwest Michigan Research and Extension Center, 42.085, – 86.358), Mid-Michigan (Clarksville Research Center, 42.870, – 85.256), and Northwest Michigan (Northwest Michigan Horticultural Research Center, 44.882, – 85.674). At each site, single species 1 m<sup>2</sup> plots were arranged in a randomized complete block design, consisting of 4 blocks each of 52 native plant species. Due to logistical constraints, 39 species were used in analyses (see below). Details of these sites and plant species selected are provided in Rowe et al. (2018) and in

Supplemental Table 1. For this study, we selected plant species commonly found in prairie type habitats in Michigan, and species from a range of plant families with considerable variability in flower morphology and timing of bloom.

### Plant traits

In 2016, each plot was visited weekly to assess plant phenology. Data were collected from plant species during their 3 weeks of peak bloom, determined as the 3-week period of peak flower production for each species (See Supplemental Table 1). To determine total floral area ( $\text{cm}^2$ ) in each plot, we conducted flower counts and multiplied the total number of flowers by the area of an individual flower for each species in single species plots. For some species, counting the total number of flowers was not feasible because of extremely high numbers of individual floral units, so for plant species with inflorescences, we first determined the average number of flowers per inflorescence using five representative inflorescences and multiplied by the total number of inflorescences in that plot. To calculate floral area, we first took photos of a single representative flower with a ruler placed adjacent to the flower(s), and determined single flower area by converting flower images into white space (Knoll 2000) and using Adobe Photoshop CS6 and ImageJ software (Abramoff et al. 2004). The average area of an individual flower was multiplied by the number of flowers for each plant species to estimate total floral area within each plot. Chroma of field collected flowers with intact stamens were analyzed using an S2000 fiber optic spectrometer (PX2 pulsed xenon light source, Ocean Optics, Dunedin, FL), which is capable of determining floral reflectance in wavelengths 400–700 nm. To determine the mean maximum flower height (cm) for each plant species, we measured the tallest flower in each plot to the nearest cm. Chroma is broadly defined by the level of saturation of a color. For example, flowers with a higher chroma are darker and more vibrant than flowers with low chroma. Freshly collected petals were placed in a 7-mm diameter circular sample area for measurement. Flower chroma was calculated using formulae modified from Endler (1990) and used in a similar research context by Fiedler (2007).

In addition, we quantified pollen (i.e. the quantity of pollen grains produced) in freshly open flowers of plant species. One day prior to sampling plants, clusters of flowers in each replicate plot were covered using insect exclusion bags to prevent insect visitation. After 24 h, exclusion bags were removed and five newly opened flowers were collected, placed in clear plastic tubes, and kept on ice for later processing. For plant species with very small flowers (< 5 mm diameter), partial inflorescences were placed in tubes. Pollen was isolated from 5, 10, or 20 individually sampled flowers, depending on flower size, by removing

all stamens and placing them in a 60% ethanol solution and lightly dislodging pollen from anthers using a mortar and pestle. Samples were then filtered through a mesh screen to remove plant material, centrifuged at 5000 rpm for 1 min to pelletize pollen, and decanted to remove the ethanol solution from the pelletized pollen sample. We then added 50  $\mu\text{l}$  of a 60% ethanol solution to each sample and lightly homogenized them. For each plant species, a 5- $\mu\text{l}$  subsample of pollen mixture was placed on a slide with fuschin gel and the number of pollen grains were counted. The resulting value was multiplied by 10 to account for the full 50- $\mu\text{l}$  sample. We did this five times for each plant species. To extrapolate to the plot level, pollen per flower was multiplied by the total number of flowers available in each meter square plot divided by the number of flowers used for the 50- $\mu\text{l}$  sample. Data on pollen quantity and flower chroma were only collected at the Clarksville Research Center and applied to plant species from each site.

### Bee data

At each site during the 3 weeks of peak bloom, all non-*Apis* bees were collected from flowers during a 5-min insect sample, conducted once per week on each plot of plants that were in flower, for a total of 15 min per single species plot. Samples were collected using a modified hand-held vacuum (model: 2820GA, Bioquip products Inc, Rancho Domingo, CA) with a clear extension tube in order to minimize the disturbance to pollinators. Honey bees (*Apis mellifera* L.) were counted but not collected, as they could be identified in-field. Bee specimens collected from plots were identified to species using published keys and revisions (Stephen 1954; LaBerge 1967, 1969, 1971, 1980, 1989; Bouseman and LaBerge 1978; Coelho 2004; Packer et al. 2007; Gibbs 2011; Gibbs et al 2013; Williams et al 2014), online keys available through [www.discoverlife.org](http://www.discoverlife.org) (Droege 2016; Larkin et al 2016), and comparison to material in the A.J. Cook Arthropod Research Collection at Michigan State University. For each bee species collected, we classified it by its body size (small, medium, and large) and dietary specialization (polylectic and oligolectic). We calculated mean intertegular (IT) distances of bee species collected by measuring ITs for three individual female bees from each species collected and used the following IT ranges for our classifications and analyses: small = 0.0–1.9 mm, medium = 2.0–3.5 mm, large = 3.5–7.0 mm. For species without dietary specialization information, we used the lowest taxonomic level in which this information was available (Gibbs et al. 2017). Voucher specimens are housed at the A.J. Cook Arthropod Research Collection at Michigan State University.

## Data analysis

For each plant species assessed, we calculated plot level mean values for floral area (cm<sup>2</sup>), height of the tallest flower (cm), flower chroma, pollen quantity, and the week of peak bloom. Mean values were determined by combining data for each plant species across sites and generating a single value for each plant species-trait combination assessed. Due to variable plant establishment, short bloom periods, and/or no blooming plants, 13 of the 52 plant species produced incomplete plant trait data at one or more sites, and therefore were excluded from our analyses. Prior to analyses, we z-transformed numeric plant trait data to standardize each of the variables to the same scale and normalize their distribution. This standardization allowed us to directly compare the strength of influence of plant traits relative to one another, regardless of measurement scale. We used variance inflation factors (VIF) to assess the correlation between plant trait variables, and to assess for multicollinearity between plant traits used to construct models. We did not find high correlation between variables (see Supplemental Table 3 for VIF scores), and therefore each measured plant trait was included in final models.

To determine the relationship between pollen quantity per plot and other measured flower traits, we used a generalized linear model (glm, R version 3.4.0, R Core Team 2017) with mean pollen quantity (z-transformed) as the response variable and mean floral area, flower height, flower chroma, and week of peak bloom, (all z-transformed) as predictor variables.

We ran generalized linear models with the mean (log  $x + 1$  transformed) number of bees collected during 5-min sampling periods as response variables, and mean plot-level flower traits as predictor variables. Response variables included different groupings of collected bees: broad (honey bees, bumble bees (*Bombus* spp.), and non-*Bombus* wild bees), individual wild bee families (Apidae, Halictidae, and Megachilidae) and shared ecological traits (body size: small, medium, or large; and diet specialization: polylectic and oligolectic). We also ran a similar analysis with species richness of wild bees collected from plant species as a response variable. Predictor variables included floral area, flower height, flower chroma, pollen quantity, and the week of peak bloom. We ran our models independently on each bee group in order to identify the specific plant traits that are related to the visitation frequency of species within that group.

To determine how plant traits influence the structure of bee communities, we used the metaMDS function in *vegan* to construct a bi-plot with the Bray–Curtis dissimilarity matrix based on wild bee community data collected from each site (function: *rda*, package: *vegan*, version 1.12) (Oksanen et al. 2013). Flower trait data from each

site were then fitted onto the bi-plot in order to assess the relative influence of different plant traits on wild bee community structure. Permutational analysis of variance (PERMANOVA, function: *adonis*, package: *vegan*) was used to determine which plant traits had the greatest influence on wild bee community structure at the genus level based on environmental fitting of the measured flower traits at each site: floral area, flower height, flower chroma, week of peak bloom, and pollen availability. Data for this analysis were summed between repetitions of a single flowering species to eliminate zero bias, and then analyses were conducted at each site independently to assess for site level differences. However, we did not conduct this analysis on data from NWMHRC, due to a low sample size of bees at this site. All statistical analyses were conducted in R (version 3.4.0, R Core Team 2017).

## Results

A total of 3705 bees visited the 39 wildflower species planted in single-species plots at the Southwest Michigan Research and Extension Center, the Clarksville Research Center, and the Northwest Michigan Horticultural Research Center. Non-*Bombus* wild bees represented the greatest percentage of these bees ( $n = 1634$ , 44%), followed by honey bees ( $n = 1520$ , 41%) and bumble bees ( $n = 551$ , 15%) (Table 1). Of the wild bees collected, individuals within the Halictidae ( $n = 1056$ ) and Apidae ( $n = 885$ ) families represented the majority of collected specimen. Plant species attracted a broad range of different sized bees, and the majority of visitors had either polylectic or oligolectic diet types (Table 1).

### Relationships between pollen availability and floral traits

The abundance of pollen retained within a plant species was positively associated with floral area ( $F_{1,34} = 23.42$ ,  $p < 0.001$ ). However, pollen abundance was not associated with flower height ( $F_{1,34} = 1.22$ ,  $p = 0.277$ ), flower chroma ( $F_{1,34} = 1.51$ ,  $p = 0.228$ ), or week of peak bloom ( $F_{1,34} = 0.46$ ,  $p = 0.502$ ) (Fig. 1).

### Predictors of plant species attractiveness to bees

Visitation of bumble bees and non-*Bombus* wild bees, as well as wild bee species richness were positively associated with floral area (bumble bees:  $F_{1,33} = 4.50$ ,  $p = 0.04$ ; non-*Bombus* wild bees:  $F_{1,33} = 10.99$ ,  $p = 0.002$ ; species richness:  $F_{1,33} = 15.54$ ,  $p < 0.001$ ). However, visitation by of honey bees was not associated with any measured flower trait (Fig. 2, Table 2). Visitation by Apidae and Halictidae

**Table 1** Bees sampled from 39 native wildflower species blooming at research sites in Michigan during 2016

Bee classification	Individuals ( <i>n</i> )	Prop. of total
<b>Broad</b>		
Honey bees	1520	0.41
Bumble bees	551	0.15
non- <i>Bombus</i> wild bees	1634	0.44
<b>Wild bee family</b>		
Apidae	885	0.41
Andrenidae	66	0.03
Halictidae	1056	0.48
Megachilidae	149	0.07
Colletidae	29	0.01
<b>Functional group</b>		
<b>Body size</b>		
Small	576	0.26
Medium	1060	0.49
Large	549	0.25
<b>Diet</b>		
Polylectic	1957	0.90
Oligolectic	209	0.10
Kleptoparasitic	19	<0.01

Plant species were established as seedlings in 2014 in replicated meter square common garden plantings at three locations. Functional groupings of bees do not include honey bee observations. A total of 3705 bees were observed (honey bees only) or collected (all other wild bees, including *Bombus*)

were both positively associated with flora area (Apidae:  $F_{1,33} = 10.26, p = 0.003$ ; Halictidae:  $F_{1,33} = 8.17, p = 0.007$ ) whereas visitation by Megachilidae was negatively associated with both pollen availability and week of peak bloom (pollen:  $F_{1,33} = 9.43, p = 0.004$ ; week of bloom:  $F_{1,33} = 4.14,$

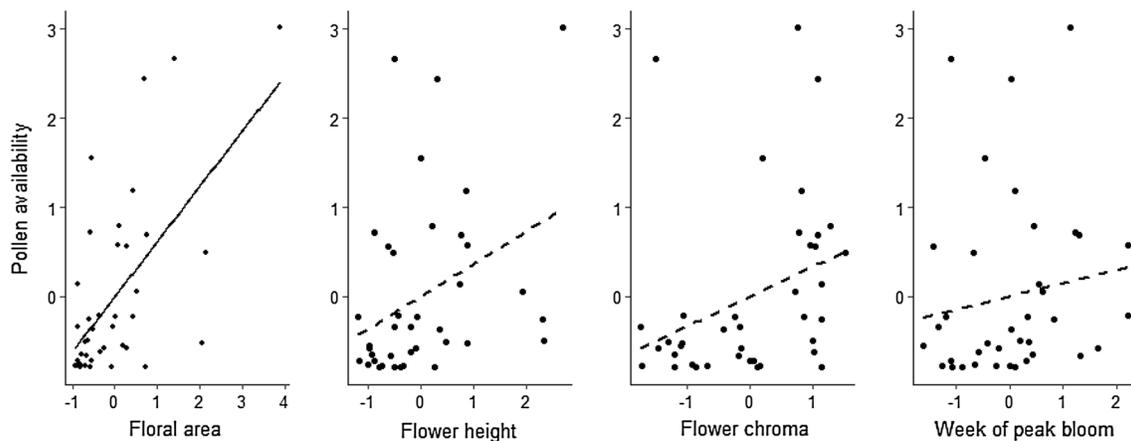
$p < 0.050$ ) (Fig. 3, Table 2). Visitation by small, medium and large bees were all positively associated with floral area (small:  $F_{1,33} = 6.91, p = 0.013$ ; medium:  $F_{1,33} = 4.17, p = 0.049$ ; large:  $F_{1,33} = 4.51, p = 0.041$ ). In addition, visitation by small bees was also associated with pollen availability ( $F_{1,33} = 4.95, p = 0.033$ ) and visitation by medium and large bees was positively associated with flower height (medium:  $F_{1,33} = 4.17, p = 0.035$ ; large:  $F_{1,33} = 4.95, p = 0.033$ ). Both polylectic and oligolectic visitation frequencies were positively related to floral area (polylectic:  $F_{1,33} = 19.30, p < 0.001$ ; oligolectic:  $F_{1,33} = 5.28, p = 0.028$ ), and polylectic bee visitation also increased with week of bloom ( $F_{1,33} = 7.53, p = 0.01$ ) whereas oligolectic bee visitation increased with flower height ( $F_{1,33} = 16.20, p < 0.001$  and chroma ( $F_{1,33} = 8.79, p = 0.006$ ) (Fig. 4, Table 3).

**Wild bee community response to flower traits**

The strongest influence on wild bee community structure was seen in response to variation in plot floral area ( $F_{1,29} = 2.93, p = 0.002$ ), average flower height ( $F_{1,29} = 2.81, p = 0.004$ ), and pollen availability at the plot level ( $F_{1,29} = 2.43, p = 0.009$ ) (Fig. 5, Table 4). In addition, variation in flower chroma had a non-significant, but positive, association with the structure of the wild bee community.

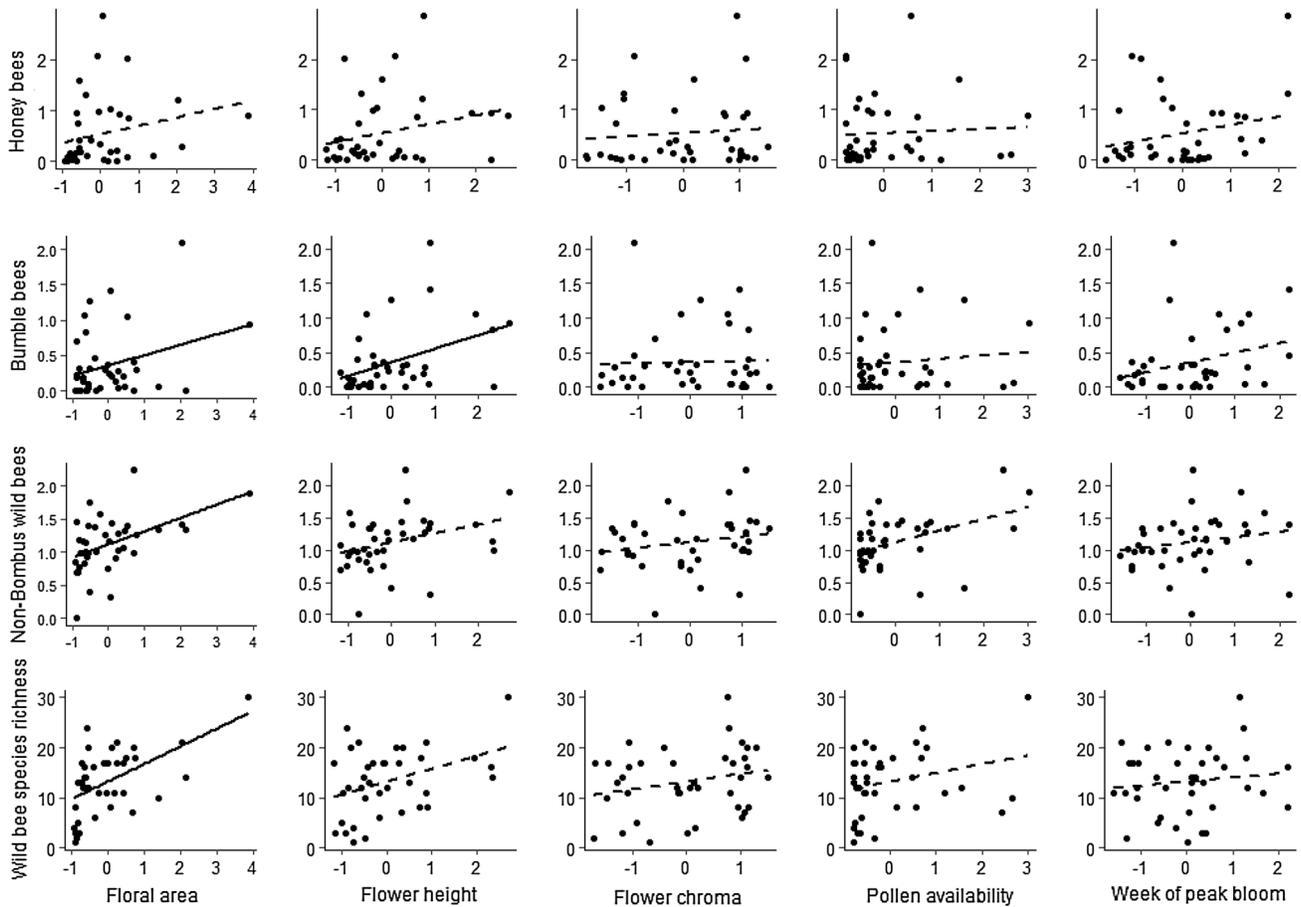
**Discussion**

Supporting a diverse assemblage of bees in human-dominated landscapes requires effective management of plant communities that increase bee visitation frequencies. Although research has demonstrated distinct variation in plant attractiveness to bees (Tuell et al. 2008; Rowe et al.



**Fig. 1** Relationships between pollen availability on floral area (cm<sup>2</sup>), flower height (cm), flower chroma, and week of peak bloom. Data represent the z-transformed mean values calculated from single spe-

cies plots. Significant slopes are represented by solid lines, while non-significant slopes are represented by dashed lines

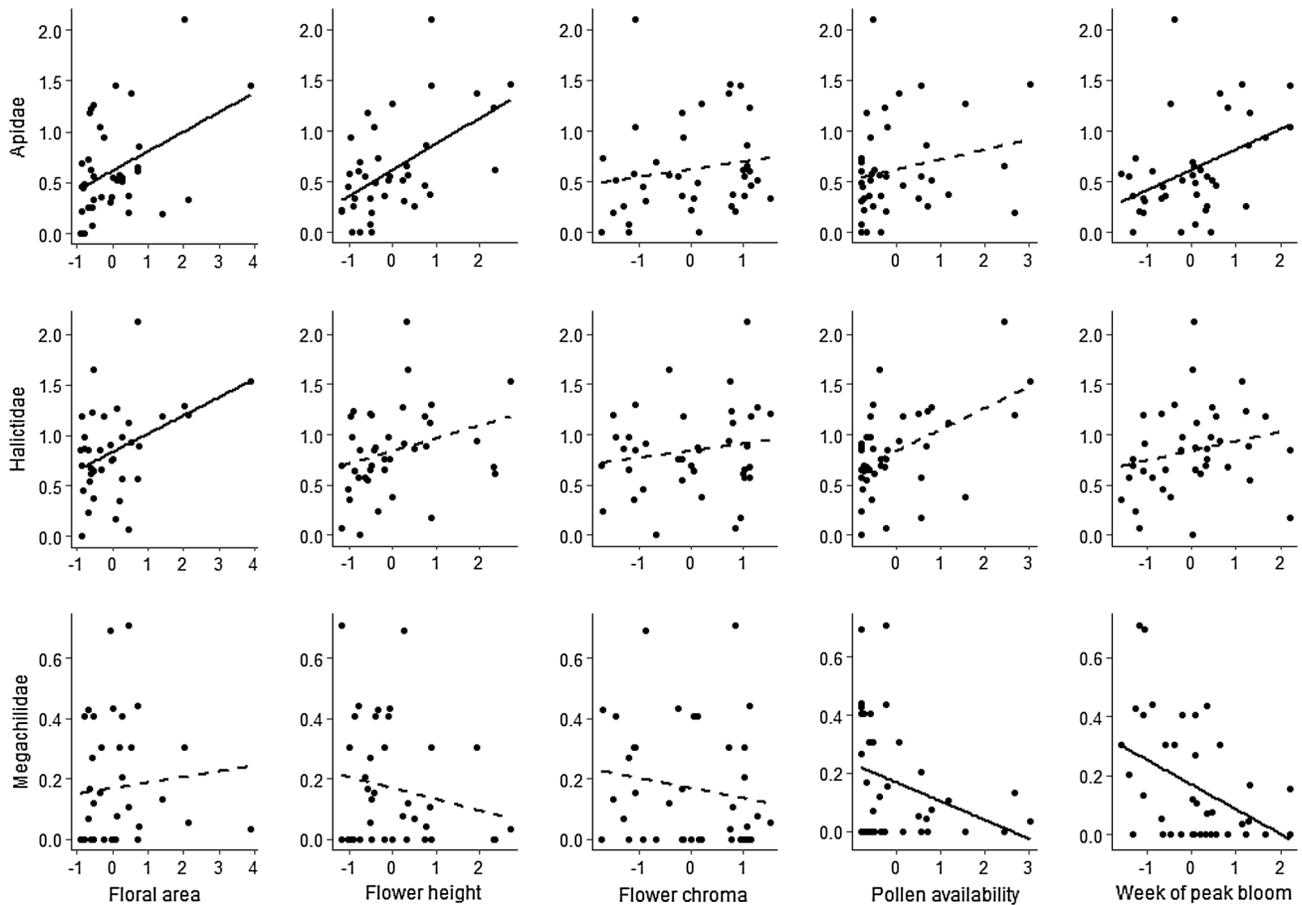


**Fig. 2** Relationships between log ( $x + 1$ ) transformed mean visitation frequencies of broad bee groups (honey bees, bumble bees, and non-*Bombus* wild bees), as well as wild bee species richness and mean  $z$ -transformed floral traits collected from 39 plant species. Significant slopes are represented by solid lines, while non-significant slopes are represented by dashed lines

**Table 2** Results from generalized linear models to assess the influence of plot-level mean flower traits on the log transformed abundance (log  $x + 1$ ) broad bee groups and wild bee families collected from wildflower plots during 2016. Broad pollinator groups include honey bees, bumble bees, non-*Bombus* wild bees and wild bee species richness

Pollinator group	Flower traits ( $z$ -transformed)									
	Floral area (cm <sup>2</sup> )		Flower height (cm)		Flower Chroma		Pollen quantity		Week of peak bloom	
	$F_{1,33}$	$P$	$F_{1,33}$	$P$	$F_{1,33}$	$P$	$F_{1,33}$	$P$	$F_{1,33}$	$P$
<b>Broad group</b>										
Honey bees	2.29	0.14	1.28	0.266	0.01	0.909	0.89	0.352	1.77	0.193
Bumble bees	<b>4.51</b>	<b>0.041</b>	<b>4.97</b>	<b>0.033</b>	0.91	0.346	1.10	0.301	2.65	0.113
non- <i>Bombus</i> wild bees	<b>11.00</b>	<b>0.002</b>	1.33	0.258	0.12	0.734	0.91	0.346	0.74	0.398
Species richness	<b>15.54</b>	<b>&lt;0.001</b>	2.27	0.141	0.14	0.714	1.06	0.311	0.23	0.632
<b>Wild bee family</b>										
Apidae	<b>10.26</b>	<b>0.003</b>	<b>11.03</b>	<b>0.002</b>	0.20	0.656	0.97	0.331	<b>6.47</b>	<b>0.016</b>
Halictidae	<b>8.17</b>	<b>0.007</b>	1.01	0.323	0.02	0.877	3.66	0.064	1.12	0.298
Megachilidae	0.44	0.514	2.84	0.102	0.88	0.354	<b>9.43</b>	<b>0.004</b>	<b>4.14</b>	<b>0.05</b>

Wild bee families include Apidae, Halictidae, and Megachilidae. Colletidae and Andrenidae are excluded from analyses due to too few specimen collected. Flower traits that were significant ( $p < 0.05$ ) in individual GLM are bolded



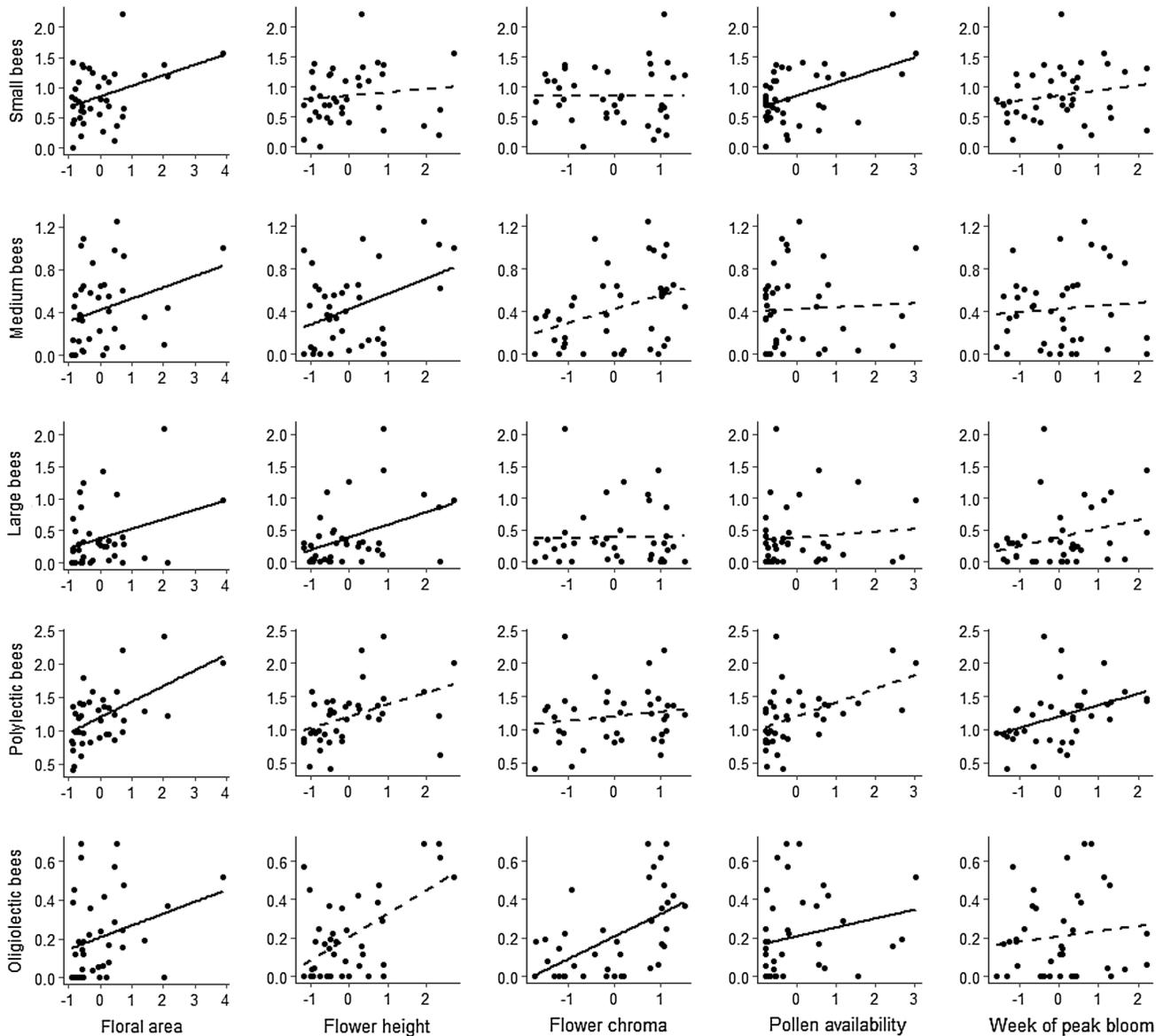
**Fig. 3** Relationships between log ( $x + 1$ ) transformed mean visitation frequencies of bees from wild bee families (Apidae, Halictidae, and Megachilidae) and mean  $z$ -transformed floral traits collected from 39

plant species. Significant slopes are represented by solid lines, while non-significant slopes are represented by dashed lines

2018; Lundin et al. 2019), the mechanisms that influence a plant’s attractiveness to bees remains unclear (but see Lundin et al. 2019 for a similar exploration of bee response to wildflowers in California). By determining the flower traits associated with visitation by distinct bee groups to plants in a common garden planting design, we fill this important information gap in two main ways: (1) we show predictable relationships between increased bee visitation frequency and flower traits, providing a mechanism associated with realized variability in plant attractiveness to bees, and (2) we demonstrate that multiple plant traits related to the structure of wild bee communities.

First, we determined the visual floral traits associated with the availability of pollen, the primary diet of most bee species (Michener 2000). We found a significant relationship between floral area and the quantity of pollen retained within the flowers of plant species in common garden plantings, where in general, plant species with greater floral area had more pollen resource available for collection. These results are consistent with other research that has demonstrated

similarly positive relationships between floral area and resource availability at the flower, plant, and landscape levels (Potts et al. 2003; Hicks et al. 2016). This relationship between floral area and pollen quantity is particularly important because it suggests that floral area is a simple floral trait that may be used to gauge the nutritional benefit of a plant species. In experiments that manipulate the quality and quantity of pollen resources, bees show predictable responses in foraging behavior to optimize nutritional intake, ultimately maximizing fitness of individual bees or colonies (Pellmyr 1988; Potts et al. 2003; Muth et al. 2016; Kriesell et al. 2017; Vaudo et al. 2018). In general, our study suggests that bees (primarily generalist foragers) that forage to maximize resource intake may utilize floral area to select between co-blooming plant species. In addition to pollen, nectar (quantity or quality) is a second resource collected by foraging bees that is known to influence their visitation to flowers (Silva and Dean 2000; Mallinger and Prasifka 2017). In this study we were unable to accurately measure nectar availability in our experimental plant species, which



**Fig. 4** Relationships between  $\log(x+1)$  transformed mean visitation frequencies of bees from distinct functional groups (body size: small, medium, large; dietary preference: polylectic, oligolectic) and

$z$ -transformed floral traits collected from 39 plant species. Significant slopes are represented by solid lines, while non-significant slopes are represented by dashed lines

may have limited our interpretation of the importance of this trait for bee visitation. Studies that include nectar in a multi-trait approach will be crucial to better understand the role of nectar in maximizing resource availability to foraging bees (Pamminger et al. 2019). Since we focused on natural assemblages of bees and did not manipulate floral traits directly, future research to determine how different bee taxa respond to manipulated floral traits such as floral area and resource quantity and quality could improve our understanding of how floral traits interact to influence visitation of bees.

Species richness of wild bees, as well as the visitation frequencies of bumble bees and non-*Bombus* wild bees

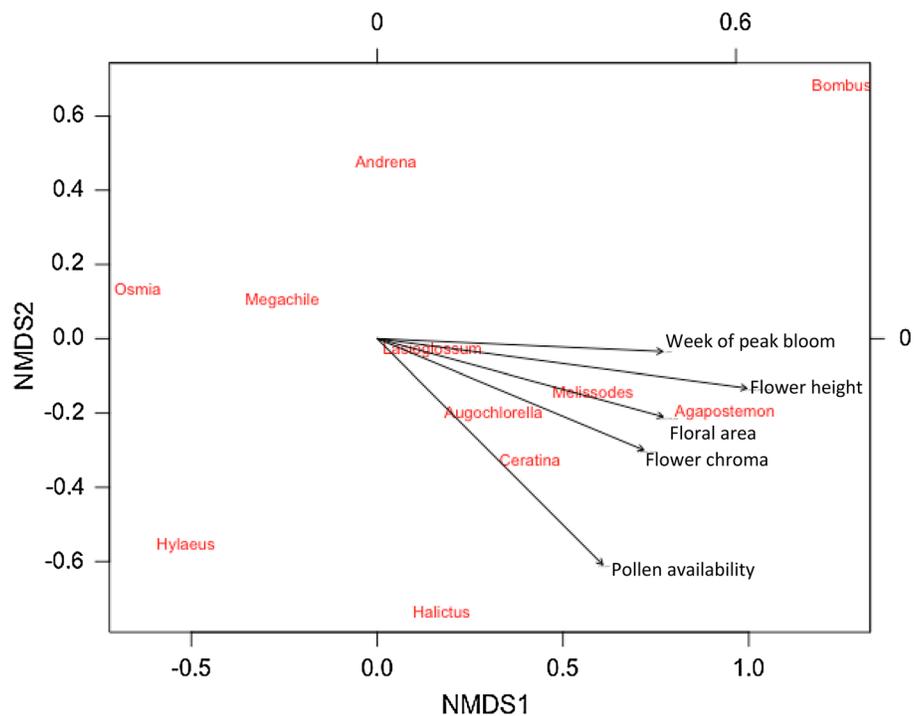
were associated with floral area in single species plots, but this was not the case for honey bees. Instead, we found no significant relationship between honey bees visitation frequency and measured floral traits. Honey bees may have been responding more strongly to plant traits we were unable to measure, such as nectar quantity/quality (Seeley et al. 1991; Mallinger and Prasifka 2017), or they may have been foraging at a larger landscape scale rather than the scale of our common garden experiment (Dornhaus et al. 2006) (i.e. making foraging decisions on flower patches greater than  $1\text{m}^2$ ). When we assessed individual wild bee families, the positive association between floral area and bee visitation

**Table 3** Results from generalized linear models to assess the influence of plot-level mean flower traits on the log transformed abundance (log  $x + 1$ ) of wild bees classified by body size (small, medium, and large) and dietary specialization (polylectic and oligolectic) collected during 2016

Pollinator group	Flower traits (z-transformed)									
	Floral area (cm <sup>2</sup> )		Flower height (cm)		Flower Chroma		Pollen quantity		Week of peak bloom	
	<i>F</i> <sub>1,33</sub>	<i>P</i>	<i>F</i> <sub>1,33</sub>	<i>P</i>	<i>F</i> <sub>1,33</sub>	<i>P</i>	<i>F</i> <sub>1,33</sub>	<i>P</i>	<i>F</i> <sub>1,33</sub>	<i>P</i>
Body size										
Small	<b>6.91</b>	<b>0.013</b>	0.03	0.862	0.34	0.566	<b>4.95</b>	<b>0.033</b>	1.88	0.18
Medium	<b>4.17</b>	<b>0.049</b>	<b>4.17</b>	<b>0.035</b>	4.82	0.139	2.30	0.059	3.83	0.779
Large	<b>4.51</b>	<b>0.041</b>	<b>4.95</b>	<b>0.033</b>	1.11	0.3	1.28	0.265	2.47	0.126
Dietary specialization										
Polylectic	<b>19.30</b>	<b>&lt;0.001</b>	3.41	0.074	0.11	0.738	1.65	0.208	<b>7.53</b>	<b>0.01</b>
Oligolectic	<b>5.28</b>	<b>0.028</b>	<b>16.20</b>	<b>&lt;0.001</b>	<b>8.79</b>	<b>0.006</b>	0.90	0.349	0.84	0.365

Cleptoparasitic bees are not included in analyses due to too few collected specimen. Flower traits that were significant ( $p < 0.05$ ) in individual GLM are bolded

**Fig. 5** NMDS bi-plot of flower traits and the wild bee community (genera) visiting 39 plant species established in 1m<sup>2</sup> monospecific plantings in Southwest Michigan, Mid-Michigan, and Northwest Michigan. The length and direction of arrows represent that strength and direction of flower trait effect on the wild bee community. Collected bee genera are represented by their genus names



was found within Apidae and Halictidae, and not Megachilidae, for which visitation frequency was instead negatively related to week of peak bloom and pollen availability. Not surprisingly, we found that floral area was associated with increased visitation frequency of bees with small, medium, and large body sizes, as well as both polylectic and oligolectic foragers. These results support the findings of others, which demonstrate strong associations with bee visitation and floral display (Eckhart 1991; Makino et al. 2007) and show increased bee abundance and diversity associated with habitat patches containing higher levels of floral resource availability (Tuell et al. 2008; Blaauw and Isaacs 2014; Williams et al. 2014). Here, we demonstrate that positive relationships between floral area and bee visitation are

significant when assessing visitation patterns to single plant species. We found that distinct assemblages of bees respond similarly to floral area at the plant species scale, and provide evidence that utilizing plant species that maximize floral area in wildflower habitat may attract the greatest number of bees regardless of body size or dietary specialization. Coupling floral area with additional flower traits known to influence bee visitation may provide the greatest benefit to the wild bee community.

In addition to floral area, we identified unique floral traits that contribute to the visitation frequency of specific groups of bees, while not being related to the broader classifications of bees. For example, medium and large bees, oligolectic foragers, and bumble bees also preferred

**Table 4** PERMANOVA results assessing the influence of plot-level mean flower traits on the genus level wild bee community structure at SWMREC (Southwest Michigan Research and Extension Center), CRC (Clarksville Research Center), and a combination of sites

Site	Flower traits ( $z$ -transformed)				
	Floral area (cm <sup>2</sup> )	Flower height (cm)	Flower Chroma	Pollen quantity	Week of peak bloom
SWMREC					
F	<b>2.05</b>	<b>3.10</b>	<b>1.95</b>	1.38	1.25
P	<b>0.026</b>	<b>0.001</b>	<b>0.040</b>	0.187	0.246
CRC					
F	<b>2.41</b>	1.39	<b>2.27</b>	<b>2.49</b>	1.33
P	<b>0.013</b>	0.218	<b>0.016</b>	<b>0.010</b>	0.215
All sites					
F	<b>2.93</b>	<b>2.81</b>	1.86	<b>2.44</b>	1.19
P	<b>&lt;0.002</b>	<b>0.004</b>	0.062	<b>0.009</b>	0.285

Flower traits that were found to be significant ( $p < 0.05$ ) in each analysis are bolded

plant species with taller flowers. Species with taller flowers may be easier to locate by bees that are able to fly greater distances across the foraging landscape. Visitation by oligolectic foragers was also predicted by flower chroma, which may indicate an increasing use of floral color or color saturation by bees with more specialized diets. In fact, the majority of oligolectic bee species in this study foraged from flowers in the Asteraceae and showed a strong preference in general for species with highly saturated yellow flowers. Overall, this variability in bee response to trait expression is likely due to the differences in life histories of individual taxa, including diverse foraging strategies, nutritional requirements, and morphological characteristics for collecting plant-based resources (Harder 1985; Minckley and Roulston 2006; Praz et al. 2008; Gibbs et al. 2017). Differences in which traits were predictive for more specialized groups of bees may reflect competition for plant-based resources leading to resource partitioning, thereby allowing more species to exist within a broader community (Blüthgen and Klein 2011; Schiestl and Johnson 2013; Venjakob et al. 2016).

The community analyses revealed that plot floral area, flower height, and pollen quantity are the three most important traits influencing the wild bee community structure at the genus level. Although not significant when sites were combined, flower chroma also played an important role at individual study locations. The fact that these traits influenced the structure of wild bee communities suggests they are important in maintaining a diverse assemblage of bees and may aid in buffering the community against the consequences of species loss (Blüthgen and Klein 2011), while also promoting co-existing functionally and ecologically distinct bee species. Since our community analyses focused on bees visiting mono-specific plantings in a general area, similar experiments conducted on mixed wildflower species plots would identify whether these relationships between

visitation frequency and plant traits hold true in a more realistic community context.

Building a mechanistic understanding of the relationships between floral traits and patterns of bee visitation will lead to better informed pollinator conservation efforts in managed landscapes, with value for plant selection to support diverse bee communities. This is particularly important for pollinator conservation in geographic regions that lack intensive comparisons of plant attractiveness to bees. However, similar experiments in different geographic regions, utilizing different flower species will allow for generalization of relationships across geographic boundaries.

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**Author contribution statement** RI, DA, LR, and DG conceived and designed the experiments. LR and DG performed the experiments. CB provided expert statistical advice. JG and LR identified species used for analyses. LR performed statistical analyses and wrote the manuscript. All authors reviewed the manuscript and provided editorial advice.

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