

More Than Meets the Eye? The Role of Annual Ornamental Flowers in Supporting Pollinators

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Abstract

Ornamental flowers are commonly planted in urban and suburban areas to provide foraging resources for pollinator populations. However, their role in supporting broad pollinator biodiversity is not well established as previous studies have been conducted in urban landscapes with pollinator communities that are distinct from those in natural systems. We observed pollinator visitation patterns to five ornamental annual plant genera and their cultivars over multiple years at two semi-natural sites in Pennsylvania to understand their potential for supporting diverse pollinator communities. There was significant variation in visitor abundance and diversity by season and year for many annual ornamental cultivars. Within some genera, cultivars had similar visitor abundance, diversity, and main visitor taxa, while cultivars in other genera varied greatly in these measures. We observed only polylectic (pollen generalist) bee species visiting annual ornamentals, despite the presence of oligolectic (pollen specialist) bee species in the background population. We conclude that the attractiveness of annual ornamental plants likely depends on both cultivar characteristics and environmental context. While their role in supporting complex pollinator populations is limited both based on the number of and dietary breadth of the species they support, ornamental plants may nonetheless provide long-lasting supplemental foraging resources for the generalist pollinator communities characteristic of urban and suburban environments.

Key words: Anthophila, Lepidoptera, Diptera, Ornamentals, Pollination

Pollinator populations decline due to a number of interacting stressors, including a reduction in food resources, which are the result of agricultural or urban land use patterns (Potts et al. 2010, Winfree et al. 2011). In urban areas, there is interest by landscapers, urban planners, and home gardeners to mitigate these declines by increasing floral abundance and diversity through managed plantings (Campbell et al. 2017). Due to the availability of certain stocks in nurseries and garden centers and demand for a particular landscaping aesthetic (Hooper et al. 2008, Hoyle et al. 2017), these intentional greenspaces are often dominated by ornamental plants (Thompson et al. 2003). With increasing urbanization (McKinney 2002), understanding how these plant stocks can support pollinator species is critical to creating greenspaces that can support thriving urban pollinator communities, which, in turn, promote urban agriculture (Lin et al. 2015), human well-being (Barton and Rogerson 2017), and ecological awareness (McKinney 2002).

Ornamental plant stocks are typically defined as cultivated varieties produced by the floriculture industry for decorative purposes in gardens and aesthetic landscapes (Horn 2002). Many annual species have a long history of selective breeding for human-desirable

plant traits that potentially alter attractiveness and utility to pollinators (Mol et al. 1995, Horn 2002). While each cultivated variety, or ‘cultivar’ has a unique breeding history, there are general patterns to this selection process. To increase attractiveness to consumers, ornamental annuals have been selected for low pollen production, vibrant color, long phenology, shorter stature, and oversized or multiple blooms (Seagraves and Thompson 1999, Wilde et al. 2015, EFSA 2006), all of which could influence the quality of the nutritional reward for pollinators and the detectability and accessibility of the flower to pollinators (Giurfa and Lehrer 2001). The selection on these floral traits can positively affect pollinators, with larger blooms increasing visitation (Bauer et al. 2017) via increased nectar reward (Harder and Cruzan 1990) and more prominent advertisement (Comba et al. 1999), or extended bloom time offering season-long nutritional resources, especially during periods of natural seasonal flowering dearth (Stelzer et al. 2010, Harrison and Winfree 2015). However, alteration of these traits may also reduce plant utility to pollinators, through loss of structural components such as nectar-bearing spurs or ‘doubling’, a process whereby increased ray florets are selected for, replacing or obscuring nectar-producing disc

florets that contain plant reproductive organs (Comba et al. 1999); these structural changes may result in decreasing pollinators' ability to handle flowers (Portlas et al. 2018) or the amount or accessibility of nutritional rewards (Comba et al. 1999). Other alterations can include changes in flower color via altered petal epidermal cell shape (Noda et al. 1994) and pigment deposition (Bradshaw and Schemske 2003, Dyer et al. 2007), which may make the flower more difficult for a pollinator to locate or learn (Chittka et al. 2001, Giurfa and Lehrer 2001).

Artificial breeding also removes ornamental varieties from natural selection by particular pollinator taxa. In many evolved plant–pollinator interactions, floral advertisement and nutritional reward are often linked, with floral traits representing an honest signal of nutritional quality and quantity (Wright and Schiestl 2009). In bred varieties, the floral advertisement may no longer be coupled with the reward, and pollinators would rapidly learn not to visit an unrewarding floral species, regardless of the sensory cues (Smithson and MacNair 1997). Alternatively, pollinators may also use flowers they do not typically visit if there is a nutritional reward present. Since the artificial breeding history of ornamental plants has altered both advertisement and reward, we expect that pollinator attraction will vary significantly across cultivars within a species. Indeed, studies of pollinator visitation to ornamental aster and *Lavendula* cultivars found substantial variation in the abundance and types of pollinator taxa observed to visit different varieties (Garbuzov and Ratnieks 2015).

Typically annual plants complete their life cycle in a single year. They are desirable for use in landscapes due to their average lower price compared with ornamental perennial plants (Hovhannisyan and Khachatryan 2017), reduced risk of invasiveness (Dehnen-Schmutz et al. 2007), suitability for quick and tidy landscape design (Nassauer 1988, Bhatti and Church 2001), and often show colors (Hardy et al. 2000). Sales of annual ornamental plants consistently exceed those of perennial or foliage plants both in quantity and market value (Yue et al. 2011, Hovhannisyan and Khachatryan 2017). Still, there have been few studies to date on how horticulturally selected ornamental annual plants may interact with pollinator taxa, with those that have assessed the attractiveness of ornamental plant stock to pollinators putting greater emphasis on perennial or woody species (Garbuzov and Ratnieks 2014, Garbuzov and Ratnieks 2015, Mach and Potter 2018).

As ornamental varieties as a whole are commonly planted in urban and suburban landscapes, most studies of their attractiveness to pollinators have been conducted in these areas. These studies have found that many horticulturally produced ornamentals to attract only low numbers of pollinators, and these are exclusively dietary generalist pollinator species (Frankie et al. 2005, Garbuzov and Ratnieks 2014, Garbuzov et al. 2017). However, because of their climate (Sukopp 1998, Hamblin et al. 2018) and heterogeneous habitat (Hamblin et al. 2018), urban areas tend to support predominantly generalist foragers that are more resilient to habitat fragmentation and urbanization (Aizen and Feinsinger 1994, McFrederick and LeBuhn 2006, Baldock et al. 2015). Thus, if we rely exclusively on these studies, our understanding of the ability of cultivated ornamental plants to support diverse pollinator communities will be limited. To fully understand the potential of ornamental plants for supporting pollinators, it is important to also assess their attraction in the context of a diverse plant and pollinator community.

Here, we evaluated the relative attractiveness of five annual ornamental plant genera to insect pollinators at two ex-urban (or semi-natural, outer suburban) study sites that were historically found to have a high diversity of bee species and support a nested

plant–pollinator community (Russo et al. 2013). By observing the plants at these sites, we could evaluate the functional significance of annual ornamental plants in a semi-natural community context. To determine if artificial selection has impacted pollinator attraction, we selected five cultivars within each genus that varied in traits such as color and shape (Table 1). Since it is well established that plant–pollinator networks are greatly influenced by spatial and temporal parameters (Eckhart 1991, Thompson 2001, Wolfe and Barrett 2008), we compared patterns of visitation throughout the growing season across two independent sites and years. Understanding this system will not only provide insights into how plant–pollinator communities are organized, but can also inform design of urban and suburban landscapes to support pollinators.

Materials and Methods

Plant Selection

Plants were selected from a 2014 National Agricultural Statistics Service (USDA-NASS 2014) survey of top grossing ornamental plant stock. We identified five annual genera that had been described to attract pollinators (Schemske 1976, Bosch et al. 1997, Yeagan and Colvin 2009, Binoy et al. 2014, Shilpa et al. 2014) and grow well in the Northeastern region of the United States. To include a range of pollinator types, we selected genera with varied floral morphology. The taxa selected for this study were *Tagetes* spp. (marigold), *Zinnia* spp. (zinnia), *Pentas lanceolata* (Forssk.) Deflers (Egyptian starcluster), *Lobularia maritima* (L.) Desv. (sweet alyssum), and *Lantana camara* (L.) (lantana). To test within taxa variation, five cultivars of each flower taxa were selected. When the option was available, cultivars were selected to be within series (a group of cultivars based on an ideotype that differ from each other in one or only a few characters – generally color, size, or stature) (see Table 1) (Brickell et al. 2009).

Plants were grown in 18.9-liter plastic pots using Metro Mix 830 potting medium (Sun Gro Horticulture, Agawam, MA) and fertilized with Osmocote 15-8-11 (Everris Americas ICL Group, Tel Aviv, Israel), in levels specific to the requirements of each genus. Separate sets of plants were purchased in 2016 and 2017 and used for field observations. Plants were purchased as 7.6 and 12.7 cm (4" and 5") starter pots from Quality Greenhouses (Dillsburg, PA). In 2017, the following plants were grown from seed in a greenhouse due to limited supplier availability: *P. lanceolata* 'Graffiti Red Lace' and *T. patula* 'Alumia Flame'. The plants that were purchased as starter pots from Quality Greenhouses were treated as seedlings by the grower with chemical controls (see Supp Materials [online only] for details). Otherwise, plants were not chemically treated throughout the study period.

Plot Design

Observations were conducted at two sites on the Pennsylvania State University Russell E. Larson Agricultural Research Center in Pine Grove Mills, PA (Site 1: 40.704960, –77.973650; Site 2: 40.712323, –77.933606). Plots were arranged in a randomized complete block design with four blocks per plot and one replicate of each cultivar per block. Plants were kept in pots for the duration of the study and placed on top of the soil. The plots were regularly mowed so vegetation would not obscure the plants. The sites were 3.5 km apart. Honey bees will regularly forage further than 5 km from their hive (Beekman and Ratnieks 2000), thus, foragers from the same colony could potentially be present at both sites. Bumble bees and solitary bees are described to have much smaller foraging ranges

Table 1. Estimated Marginal Means \pm SE of total visitor abundance (A) and diversity (B) and the significance of the interaction effect between the cultivar and the independent variable listed on the dependent variable

A	Species	Cultivar	Average abundance (SE)	Area, <i>P</i>	Year, <i>P</i>	Site, <i>P</i>	Week, <i>P</i>
A	<i>Lantana camara</i>	'Citrus'	1.66 (0.29)	0.16	0.00	0.13	0.01
		'Rose Glow'	1.83 (0.27)	0.00	0.00	0.79	0.00
		'Sunrise Rose'	1.33 (0.21)	0.00	0.00	0.10	0.00
		'Peach Sunrise'	1.11 (0.16)	0.00	0.04	0.85	0.00
		'Yellow'	1.33 (0.22)	0.01	0.00	0.08	0.02
	<i>Lobularia maritima</i>	'Easter Bonnet Violet'	1.35 (0.22)	0.00	0.00	0.38	0.07
		'Snow Princess'	7.52 (0.83)	0.06	0.00	0.00	0.05
		'Frosty Knight'	5.06 (0.60)	0.00	0.00	0.75	0.41
		'Wonderland Deep Purple'	0.48 (0.14)	0.02	0.46	0.14	0.93
		'Clear Crystal Mix'	1.71 (0.27)	0.03	0.00	0.27	0.81
	<i>Pentas lanceolata</i>	'Graffiti Red Lace'	0.65 (0.18)	0.65	0.32	0.96	0.00
		'Graffiti White'	0.28 (0.09)	0.62	0.32	0.06	0.00
		'Starcluster Lavender'	0.84 (0.17)	0.07	0.02	0.00	0.00
		'Starcluster Red'	0.28 (0.09)	0.54	0.00	0.00	0.03
		'Starcluster White'	1.43 (0.26)	0.33	0.17	0.10	0.00
	<i>Tagetes</i> spp.	'Alumia Deep Orange'	1.33 (0.19)	0.21	0.04	0.05	0.02
		'Alumia Flame'	1.71 (0.24)	0.00	0.77	0.04	0.00
		'Alumia Red'	1.13 (0.18)	0.02	0.52	0.46	0.03
		'Taishin Orange'	1.32 (0.20)	0.00	0.75	0.74	0.01
		'Alumia Yellow'	1.04 (0.16)	0.00	0.00	0.15	0.00
<i>Zinnia</i> spp.	'Profusion Cherry'	1.67 (0.22)	0.00	0.00	0.00	0.04	
	'Zahara Raspberry'	1.20 (0.17)	0.00	0.13	0.03	0.01	
	'Zahara Starlight Rose'	1.32 (0.21)	0.01	0.75	0.37	0.01	
	'Zahara Sunburst'	2.20 (0.30)	0.00	0.00	0.53	0.00	
	'Zahara Red'	0.43 (0.09)	0.00	0.42	0.61	0.20	
B	Species	Cultivar	Average diversity (SE)	Area, <i>P</i>	Year, <i>P</i>	Site, <i>P</i>	Week, <i>P</i>
		<i>Lantana camara</i>					
	<i>Lantana camara</i>	'Citrus'	1.50 (0.25)	0.08	0.00	0.79	0.03
		'Rose Glow'	1.40 (0.19)	0.71	0.00	0.81	0.00
		'Sunrise Rose'	1.75 (0.20)	0.36	0.02	0.82	0.70
		'Peach Sunrise'	1.37 (0.16)	0.92	0.09	0.98	0.48
		'Yellow'	1.33 (0.20)	0.31	0.05	0.62	0.36
	<i>Lobularia maritima</i>	'Easter Bonnet Violet'	1.27 (0.23)	0.39	0.64	0.15	0.82
		'Snow Princess'	1.92 (0.15)	0.88	0.00	0.01	0.60
		'Frosty Knight'	2.27 (0.18)	0.18	0.00	0.69	0.67
		'Wonderland Deep Purple'	1.13 (0.28)	0.01	0.00	0.18	0.83
		'Clear Crystal Mix'	1.62 (0.20)	0.03	0.00	0.90	0.54
	<i>Pentas lanceolata</i>	'Graffiti Red Lace'	1.58 (0.37)	0.19	0.44	0.32	0.04
		'Graffiti White'	1.21 (0.29)	0.20	0.19	0.20	0.00
		'Starcluster Lavender'	1.80 (0.22)	0.72	0.13	0.17	0.76
		'Starcluster Red'	1.51 (0.31)	0.86	0.02	0.39	0.15
		'Starcluster White'	1.87 (0.26)	0.64	0.02	0.32	0.05
	<i>Tagetes</i> spp.	'Alumia Deep Orange'	1.53 (0.17)	0.21	0.09	0.40	0.17
		'Alumia Flame'	1.46 (0.16)	0.70	0.25	0.15	0.12
		'Alumia Red'	1.52 (0.20)	0.08	0.01	0.24	0.73
'Taishin Orange'		1.67 (0.18)	0.00	0.09	0.23	0.02	
'Alumia Yellow'		1.45 (0.16)	0.40	0.05	0.14	0.31	
<i>Zinnia</i> spp.	'Profusion Cherry'	1.61 (0.16)	0.91	0.00	0.10	0.37	
	'Zahara Raspberry'	1.41 (0.16)	0.95	0.01	0.59	0.87	
	'Zahara Starlight Rose'	1.55 (0.17)	0.44	0.00	0.47	0.53	
	'Zahara Sunburst'	2.00 (0.19)	0.87	0.00	0.04	0.71	
	'Zahara Red'	1.33 (0.22)	0.18	0.16	0.42	0.79	

Area = Floral display area (cm²), Year = 2016/2017, Site = Site 1/Site 2, Week = Time of year (early, mid, and late).

Significance of area and week were calculated using Pearson's rank correlation test.

Significance of year and site were calculated using a Tukey's HSD post-hoc test.

from 150–1,200 m, dependent on body size (Osborne et al. 1999, Gathmann and Tscharrntke 2002, Greenleaf et al. 2007). Therefore, we do not expect individual foragers or nestmates from these species to be present at each site and so we treated each site independently. The general area of collections had been previously surveyed by Russo et al. (2013) and hosts a diverse bee community and a

nested plant-pollinator network. Additionally, each site was supplemented with a single nucleus honey bee colony placed ~400 m away from the plot.

Both sites were on a forest edge at a working research and production farm. Site 1 was positioned in a floodplain, and the soil was a Chagrin Silt Loam (an inceptisol with alluvium parent material;

SoilWeb). The unmanaged vegetation at this site was predominantly grasses, clovers, vetches, *Asclepias* spp. and *Solidago* spp., as well as trees and shrubs (neither of which were in bloom during the sampling periods). Site 2 was located on a northwest facing slope between a production corn field and a multi-year native meadow study. The soil at this site was a Murrill Channery Silt Loam (a utisol derived from sandstone and limestone characterized by over 15% rock content by volume; SoilWeb). The background vegetation was characterized by crown vetch and clovers early in the season and *Daucus* spp., *Plantago* spp., and *Cirsium* spp. in the mid-late season. The surrounding agricultural fields at both sites were primarily no-till corn, soybean, hay, and oats managed in a yearly rotation.

Background Insect Community

We measured the background insect community at both sites in 2017 using bee bowls and blue vane traps, using protocols modified from Droege (2015). Vane traps were hung from a post at 1 m. Blue, yellow, and white 29.5-ml (3.25 oz) bowls (New Horizons Supported Services, Inc., Upper Marlboro, MD) were mounted on specialized adjustable stands so each bowl was raised to the height of the grass and was easily visible to insect visitors. Bowls were placed in triangular sets of three, with each color represented, and each bowl 1 m apart. Two sets of bowls and two vane traps were located at the perimeter of the study sites within 1 m from the outer plant every other week for 24 h on days with low wind, full to partial sun, and peak daytime temperatures of at least 21°C. There were six collection periods total from early July to mid-September 2017. Traps were filled with soapy water, and samples were collected in the field and stored in alcohol in Whirl-Paks (Nasco, Fort Atkinson, WI) for later identification.

Observations

Each plant was observed for 10 min between the hours of 9:00 to 12:00 (AM) and 13:00 to 16:00 (PM), with each site visited at least once in the morning and once in the afternoon each week. As with trap collections, observations were conducted on days with peak daytime temperatures of at least 21°C, with low wind and full to partial sun. Observations were conducted from the start to end of bloom of each plant from early July 2016 to early September 2016 and early July 2017 to late-September 2017. For starter plants that already had flowers when purchased from the supplier, we began observations upon transplanting in early July. Observations were conducted by three individuals and Observer was included in the statistical models.

Only pollination visits were tallied: a pollination visit was defined as an insect observed to be actively collecting pollen and/or nectar or coming in contact with the anthers or stigma of the plant. Each visitor was identified in the field to morphotaxa and then classified broadly to functional group as bees (Anthophila), moths and butterflies (Lepidoptera), and flies (Diptera) for analysis (For morphotaxa and functional groups see [Supp Table 1 \[online only\]](#)). In addition, all visiting insects were collected from each plant for 10 mins by net and aspirator, once in July 2017 and once in August 2017. The bee specimens in these collections as well as those from background collections have been identified to species or genus with assistance from Sam Droege (USGS Native Bee Inventory and Monitoring Lab, Laurel, MD) and are stored in the Penn State Frost Entomological Museum (University Park, PA) as a reference collection. We classified these species as oligolectic or polylectic using data sets and species descriptions from previous studies ([Robertson 1925](#), [Maier 2009](#), [Bartomeus et al. 2013](#), [Fowler 2016](#), [Normandin et al.](#)

[2017](#), [Ascher and Pickering 2018](#), [Wood et al. 2018](#)). All specimens were sorted into morphotaxa and functional groups (Anthophila, Diptera, Lepidoptera) used for the observational data set and included in the statistical analyses (see [Supp Table 2 \[online only\]](#) for species identification and sources).

Floral Display Area

Floral area is a major driver of visitation rates for certain pollinator species ([Thompson 2001](#), [Vaudo et al. 2016](#)). Therefore, we controlled for display size of each plant. The area in bloom was documented weekly using photos of each potted plant with a measuring stick held at the level of bloom. The images were then processed manually in Photoshop (Adobe 18.1.1), with a custom measurement scale set for each image according to the measuring stick. Total bloom area (cm²) was recorded and included in the statistical models. For the GLMMs, only weeks with floral area records from both sites were used.

Quantitative Analysis

Observations for the first year were divided into ‘Early’, ‘Mid’, and ‘Late’ season periods. These periods, as well as the start and end of yearly observations, were then standardized across years using accumulated growing degree days (Base 10°C). The accumulated GDDs for periods and span of observations in 2016 were matched to the accumulated GDDs for 2017 and the data from 2017 was subset and divided accordingly.

All statistical analyses were done in R 1.0.136 ([R Core Team 2019](#)). Generalized Linear Mixed Effects Models (GLMMs) were used to model the fixed effects of cultivar, year, site, observer, time of day (categorical), seasonal period (categorical), and floral display area (continuous), the interaction effects of cultivar and year, cultivar and site, and cultivar and time of day, and the random effect of individual plant identifier, on the response variables ‘total visitor abundance’. To avoid issues of model convergence, ‘abundance of visitors within a functional group’ was modelled with fewer predictor variables. This model included the fixed effects of cultivar, pollinator functional group, the interaction of cultivar and functional group, and the random effect of individual plant identifier. Both models were fit to a Poisson distribution and offset for the minutes of sampling per week to account for unequal sampling effort. The best fit, biologically relevant, model for each response variable was selected based on weight and AIC delta and assessed for multicollinearity using the VIF function ([Bates et al. 2015](#), [Bolker 2017](#)). Estimated Marginal Means and Tukey post-hoc tests on interaction effects were calculated using the emmeans package ([Lenth 2019](#)). The effects of floral display area and time period (expressed as the continuous variable ‘week’) were tested for significance of effect size using the model, and then the interaction of these variables with individual cultivars was tested using the Pearson’s correlation coefficients.

Visitor diversity was calculated for each individual observation using the inverse of Simpson’s Diversity index (1/D), which accounts for both species richness and evenness ([Mach and Potter 2018](#), [Simpson 1949](#)). As we used morphotaxa groups for these calculations, we anticipate diversity estimates to be lower than if we had used species information, but comparable within this study.

Diversity was analyzed using two separate models to account for the data being zero-inflated non-integer. First, the data was converted to presence/absence and the fixed effects of cultivar, week, and floral area were modelled on the response variable of ‘presence/absence of visitors’, and fit to a binomial distribution to determine

the probability of encountering a non-zero value. Then, the non-zero calculated diversity values (i.e., given a visitor) were modeled with the same fixed effects as the total abundance model, except for the time of day and cultivar interaction effect, and fit to a gamma distribution and offset for sampling effort. The diversity model with the lowest AIC value was selected, similarly to abundance. The Estimated Marginal Means and standard error of visitor diversity as well as Tukey's HSD post hoc site and year comparisons were calculated from the gamma model and Pearson's rank correlation coefficient was used to evaluate the effect of floral display area and week on diversity. See [Supp Material \(online only\)](#) for models.

Results

Abundance

Average abundance values are based on the total number of visitors and the number of visitors in the pollinator functional groups (Anthophila, Diptera, Lepidoptera) that made a pollination visit to each plant during the 10-min observation periods. The results of the statistical analyses are presented in [Table 2](#) and summarized below. All data are reported as means and \pm SE. We examined the variables time of year ('Week'), year (2016/2017), site, time of day (AM/PM), and floral display area ('Area'). Average visitor abundance per 10 min across both years and sites ranged from 0.28 ± 0.09 to 7.52 ± 0.83 ([Fig. 1](#), [Table 2](#)). We found an effect of week on visitation rates for 20 out of 25 of the cultivars studied. Week was strongly correlated to floral display area ($P < 0.001$, Pearson Correlation test), with a predictable increase in floral display size later in the growing season. In 17 out of 25 of the cultivars in our study, floral area was significantly correlated with pollinator visitor abundance ([Fig. 2](#)). The exception to this trend is with the *P. lanceolata* cultivars, which had no effect of floral display size on visitor abundance, likely due to low visitation rates. Time of day also had a significant effect on observed visitor abundance for 14 of the 25 cultivars, more visits in the morning for the cultivars within *P. lanceolata*, *Lo. maritima*, and *Zinnia* spp., and more visits in the afternoon for *La. camara* and *Tagetes* spp. (see [Supp Fig. 2 \(online only\)](#))

For 15 out of 25 cultivars, there was significant effect of year on visitor abundance. There was a significant effect of site for seven of 25 cultivars (cultivars with Tukey's HSD $P < 0.05$).

Next, we evaluated the abundance of individuals within functional groups visiting each cultivar ([Fig. 1](#)). When we use a threshold Estimated Marginal Mean for each pollinator group of 0.05 visitors/10 min (a low estimate), all cultivars attracted at least two pollinator taxonomic groups. When the threshold is 0.50 visitors/10 min (a moderate estimate), 7 cultivars attract no visitors, 15 attract one taxonomic group, and 3 attract two groups (see [Supp. Table 3 \(online only\)](#)). Notably, a few cultivars attracted different dominant taxa compared to the other cultivars of their species. *Zinnia* 'Zahara Sunburst' and 'Zahara Red' and *Lo. maritima* 'Wonderland Deep Purple' were mainly visited by Anthophila spp. (Hymenoptera), while other cultivars within their species were visited by Lepidoptera and Diptera, respectively.

Diversity

The probability of recording a pollination visit during a 10-min observational period ranged from 0.13 ± 0.04 for *P. lanceolata* 'Starcluster Red' to 0.54 ± 0.06 for *Lo. maritima* 'Snow Princess' (see [Table 2](#)). There was significant variation for only a few cultivars within genera but notable differences between genera in the probability of a non-zero observation. Both floral area ($P < 0.01$) and

week ($P < 0.01$) were significant positive predictors of probability of recording a non-zero observation.

Insect visitor diversity values fit to the gamma model ranged from 1.13 ± 0.28 to 2.27 ± 0.18 ([Fig. 1](#), [Table 2](#)). There was no significant difference in 1/D within the cultivars of all genera with the exception of *Lo. maritima*, which had two cultivars deviating from the rest. The inverse Simpson Diversity was more consistent than abundance across sites, with only 2 out of 25 cultivars showing an effect, but was similarly variable with time, with 16 cultivars showing a significant effect of year ($P < 0.05$). In total, 6 out of 25 cultivars had an effect of week, and 3 out of 25 had an effect of floral display area.

Background Diversity and Snapshot Collections

Within two time points in 2017, we collected (with nets) 305 specimens visiting the study flowers. Of these, 66 specimens were within the Anthophila clade representing 16 unique species and 8 genera. All were polylectic (see [Supp Table 2 \(online only\)](#) for references). We verified sample completeness using species accumulation curves (see [Supp Materials \(online only\)](#)).

Comparatively, we trapped 274 Anthophila specimens belonging to 35 species and 16 genera in the background using passive bowl traps. Six of these species were classified as oligolectic or exhibiting specialized preferences, while 40 were polylectic ([Supp Table 2 \(online only\)](#)). Three of the species collected in the background (*Melissodes trinodis* (Robertson), *M. agilis* (Cresson) and *Lasioglossum trigeninum* (Gibbs)) were either specialists on or have been described as having a strong preference for Asteraceae pollen ([Robertson 1925](#), [Mitchell 1962](#), [Gibbs et al. 2017](#), [Ascher and Pickering 2018](#)), and yet they were not observed to be foraging on the two studied plant genera (*Zinnia* and *Tagetes*) in this family.

Discussion

Our results reveal striking variation in visitor abundance and identity among annual ornamental plant species and among cultivars within a species, which provides insights into how variation in floral cues and rewards may influence pollinator attraction, and how artificial breeding of ornamentals could alter pollinator attraction. This information can be utilized to examine the detailed mechanisms shaping the attraction of different functional groups of pollinators and can be used to improve breeding practices to generate plants that are more attractive and nutritionally rewarding for pollinators. Additionally, the correlation between floral display area, week, and visitor abundance, and significance of these factors on the probability of encountering non-zero observations support findings that floral display size is a strong predictor of pollinator visitation, and, predictably, that floral display size is linked to phenology ([Ashman and Stanton 1991](#), [Cohen and Shmida 1993](#)).

There were several examples of variation in the abundance and types of floral visitors to different cultivars within taxa, which may fuel future studies to investigate how variation in floral traits may influence pollinator attraction. For example, despite significant variation in color, the cultivars of *La. camara* did not differ in abundance or diversity of visitors ([Fig. 1](#), [Table 1](#)). *Lantana* spp. are specialists of lepidopteran visitors, and this relationship in its native and naturalized range is driven by floral color signaling ([Mohan Ram et al. 1984](#)). Our study suggests that in cultivars of this species, traits such as floral nutritional reward may be driving pollinator attraction more than color. Some pollinators learn to associate complex floral signals with nutritional reward ([Ings et al. 2009](#), [Riveros and Gronenberg 2009](#)), and this can

Table 2. The 25 ornamental annual plant varieties included in this study

<i>Lantana camara</i>	<i>Lobularia maritima</i>	<i>Pentas lanceolata</i>	<i>Tagetes</i> spp.	<i>Zinnia</i> spp.
'Citrus'	'Easter Bonnet Violet'	'Graffiti Red Lace'	'Alumia Deep Orange'	'Profusion Cherry'
				
'Rose Glow'	'Snow Princess'	'Graffiti White'	'Alumia Flame'	'Zahara Raspberry'
				
'Sunrise Rose'	'Frosty Knight'	'Starcluster Lavender'	'Alumia Red'	'Zahara Starlight Rose'
				
'Peach Sunrise'	'Wonderland Deep Purple'	'Starcluster Red'	'Taishin Orange'	'Zahara Sunburst'
				
'Yellow'	'Clear Crystal Mix'	'Starcluster White'	'Alumia Yellow'	'Zahara Sunburst'
				

override innate preferences (Blarer et al. 2002, Riffell et al. 2008, Schiestl and Johnson 2013). In contrast, the white *Lo. maritima* 'Snow Princess' and 'Frosty Knight' cultivars attracted a higher abundance of visitors than the other three purple cultivars (Fig. 1, Table 1). These two cultivars closely resemble both the wild type (Rohrig et al. 2014) and fit the myophilous pollination syndrome (Willmer 2011) indicating that in this species floral color may modulate attractiveness. The *P. lanceolata* cultivars attracted a low insect visitor abundance and varied little in attractiveness. As a group, they varied the least based on spatial and temporal

context. However, this is likely based on low visitation rates (Figs. 1 and 3). The cultivars of *Tagetes* spp. also varied little in abundance and diversity of visitors, which is surprising since 'Taishin Orange' is a doubled variety (Fig. 1, Table 1). However, in our study a visit simply represents a foraging attempt, and future assays are needed to determine if visitors were able to obtain rewards from these flowers. Finally, zinnia 'Zahara Sunburst' and 'Zahara Raspberry' differ outwardly only in color and pattern and are from the same series (Fig. 1, Table 1). However, they attract different pollinator taxa and in very different abundances,

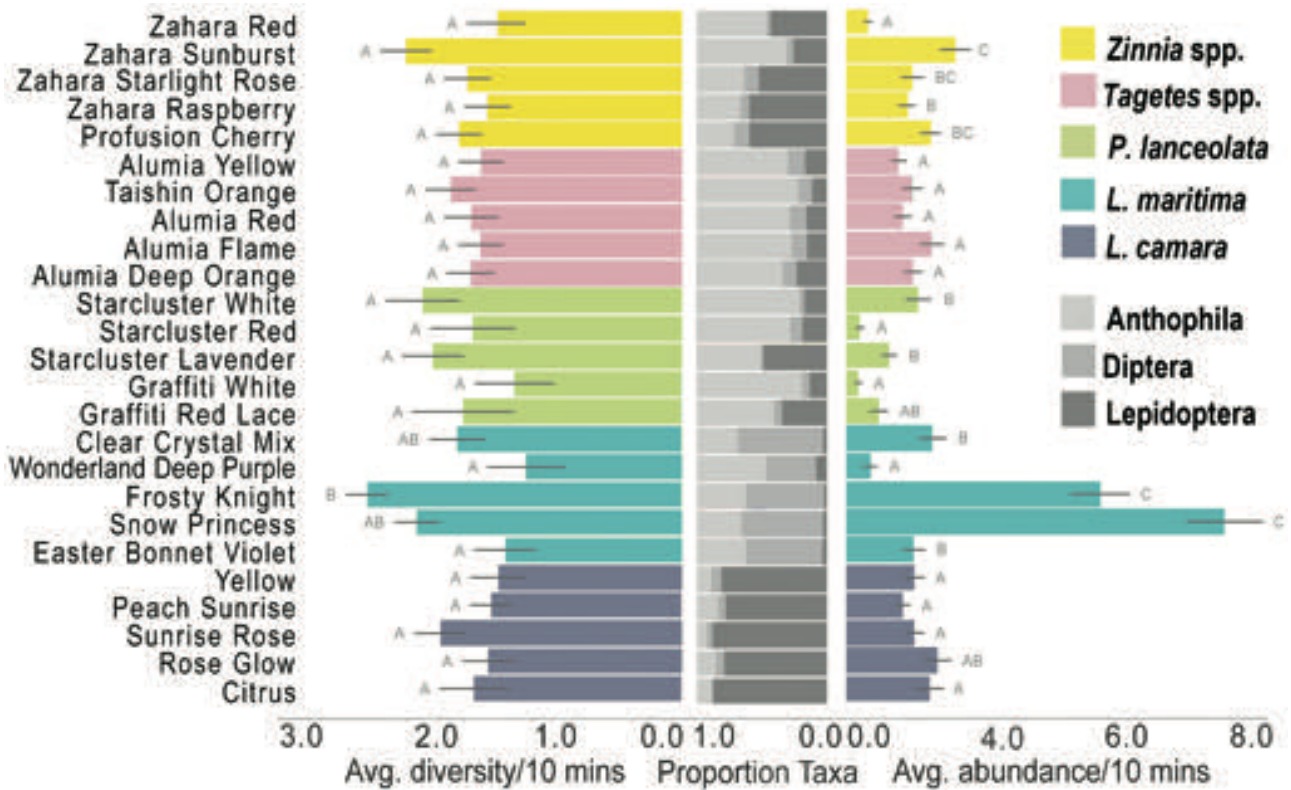


Fig. 1. Estimated Marginal Means of total visiting pollinator abundance and the inverse Simpson's Diversity Index, and the proportional abundance of pollinator functional groups visiting observed cultivars. Values were extracted from the mixed effects models and letters indicate differences between cultivars within genera based on a Tukey post-hoc test. Most cultivars had few visitors, but some were especially attractive. There is significant variation in visitor abundance to cultivars within some plant taxa (e.g., *Lobularia maritima*) and non-significant differences in cultivar attractiveness for others (e.g., *Lantana camara*). Most cultivars attracted at least two pollinator functional groups. Cultivars within plant taxa were predominantly visited by the same pollinator functional groups; however some were preferred by a functional group that was not the main visitor to that taxa. While there is some variation in diversity between cultivars within genera, most are not significantly different from each other, and diversity values are much less variable between cultivars than abundance values. These patterns may be explained by overall low visitor abundance and a generalized pollinator community visiting plants.

with 'Zahara Sunburst' receiving a high number of visits, mostly by *Anthophila* spp., and 'Zahara Raspberry' receiving comparatively few visits, mostly by *Lepidoptera* spp., suggesting that they may vary in nutritional reward, other traits related to floral advertisement, or accessibility (Briscoe and Chittka 2001, Garbuzov and Ratnieks 2015). Overall our results suggest that in some plant genera, floral visual traits such as color may be important predictors of pollinator visitation, while other factors, such as nutrition or floral volatile organic compounds (Hirota et al. 2012, Vaudo et al. 2016) may have a greater influence on visitation in other genera. We have confirmed that all varieties provided nectar and/or pollen resources and had measurable differences in visual traits (Erickson et al. unpublished data). It is, therefore, likely that multiple traits such as color, shape, and odor (see Table 1), together with nutritional quality and quantity, are influencing the attractiveness of the plants in this study to pollinators. Further mechanistic studies on the influence of floral traits and nutritional reward on attraction to ornamental annual plants are needed.

Although our study was limited in numbers of years and sites to test the consistency of pollinator attraction to ornamental annuals, the significant levels of spatial and temporal variability in visitor abundance observed in this study suggest that the attractiveness of these plants depends on their environmental context (Fig. 3). Because ornamental plants are generally clonal or inbred (Tay 2007), the differences we observe cannot be explained by genetics to any great

degree. Additionally, plants were potted in standard medium, and sites were located close enough to have similar climates. Therefore, the observed variation in visitor abundance and taxonomic identity is likely due to other factors, such as differences in pollinator community, differences in background floral communities, landscape characteristics, and environmental stochasticity. These patterns can give us important insights into species interactions. For example, the cultivars of *La. camara* were predominantly visited by butterfly species at Site 2 and *Hemaris* spp. (Sphingidae) at Site 1 (Fig. 3). This pattern may be shaped by the background plant and insect community, with hawk moth (*Hemaris* spp.) foraging potentially displacing other *Lepidoptera*s. Additionally, most cultivars of some species, such as *Tagetes* spp. and *Zinnia* spp., varied consistently in visitor abundance between sites (Fig 3). This suggests that the response to changing background community may be similar in most varieties within these species. Alternatively, within *P. lanceolata*, there was substantial variation in how individual cultivars behaved in different environmental contexts, suggesting cultivar-specific response to changes in the background community (Schlichting and Pigluicci 1998). Finally, most cultivars within *La. camara* and *Lo. maritima* did not vary significantly in abundance between sites, which could indicate that the overall attractiveness of these varieties is not as context dependent. Future work should consider these interactions and the implications of spatial and temporal variability when using ornamentals to support pollinator communities.

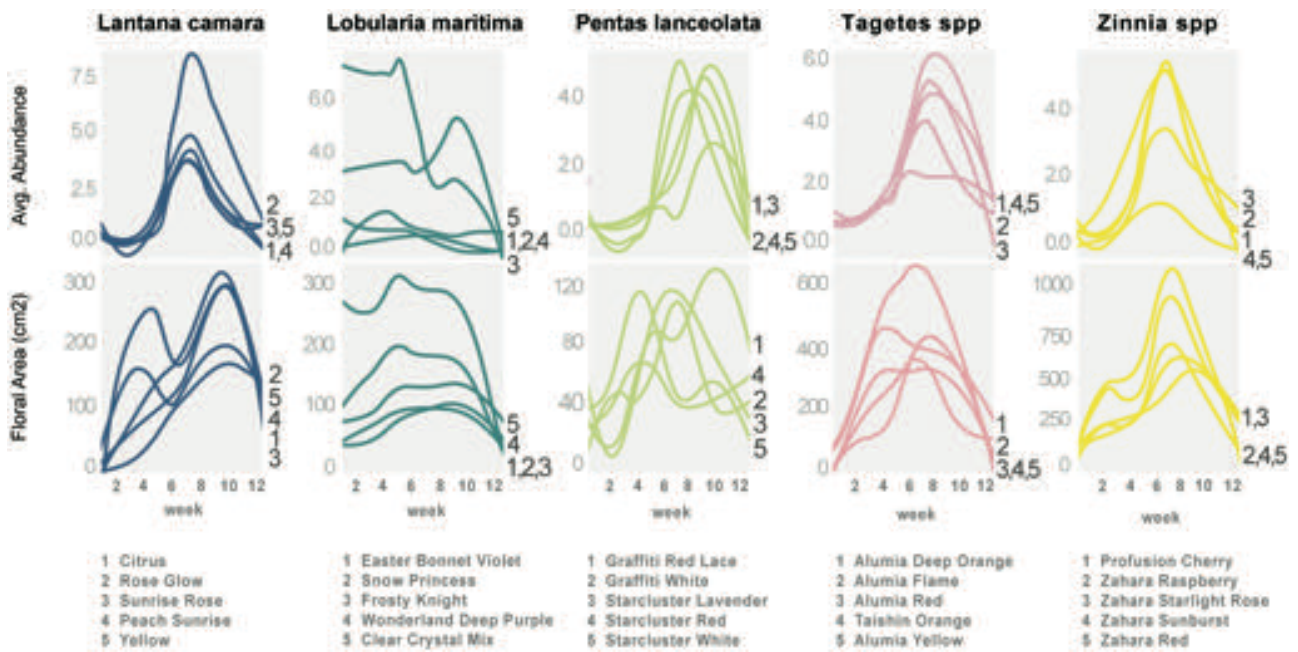


Fig. 2. Mean visitor abundance and floral display area for each cultivar throughout the whole observation averaged across years and sites and visualized using local regression with an unbounded distribution. All floral area data from the observation season was analyzed, including the incomplete data sets not used in the GLMMs. Numbers on the right side of each graph correspond to the cultivars listed below. For most cultivars in this study, visitor abundance tracks floral display size (see Results for quantitative analysis).



Fig. 3. Site variation in visitor abundance to each cultivar. Visitor abundance for nearly all cultivars differs between the sites and the rank order of attractiveness is often different as well suggesting community specific interactions define attractiveness as opposed to cultivar traits alone. Means are pooled across years. Asterisks indicate cultivars with significant ($P < 0.05$) site effect from Tukey's post-hoc test on the estimated marginal means extracted from the abundance model.

Our results indicate that the ornamental plants in this study can attract a diversity of visitors from two to three functional groups of pollinators (Anthophila, Diptera, and Lepidoptera). While all cultivars are capable of hosting multiple types of pollinators, there are still distinct patterns. Most cultivars within genera attracted the same dominant pollinator taxa – in many cases these patterns corresponded

to historical records of pollinator visitation to the plants' wild or naturalized type (Schemske 1976, Yeagan and Colvin 2009, Binoy et al. 2014). However, when compared qualitatively to similar studies of attractiveness on native and perennial plants (Frankie et al. 2005, Tuell et al. 2008), most of the cultivars included in our study were poorly attractive despite placement of plants in natural landscapes

that support a pollinator community, which is consistent with findings from similar studies (Garbuzov et al. 2017). Annual ornamental plants may attract fewer pollinators than perennial flowers due to reduced reward as a result of reproductive trade off (Corbet 1994, Hicks et al. 2016), and a longer history of artificial selection on some species in the horticulture industry (Criley 2017, Wilkins and Anderson 2017). Additional studies are needed where attraction to horticulturally produced ornamental plants are compared directly to attraction to native or perennial plant species, or comprehensive meta-analysis should be conducted. A challenge in the current approaches used to select plants that can support pollinators is a lack of consistent definition of attractiveness (how many pollinators should visit a plant in what amount of time), and the assumption that a visit by a pollinator indicates the value of a plant (Williams and Lonsdorf 2018). Moreover, our study suggests that attractiveness is complex and dynamic and depends on environmental context as well as floral traits. Thus, under conditions of low surrounding plant diversity, ornamental plants may exhibit higher attractiveness.

Earlier studies found that horticulturally produced ornamental plants attract generalist species, but these studies were conducted in urban areas, which host a unique and often limited pollinator community comprised primarily of generalists (McKinney 2002). In stable mutualistic systems, plant–pollinator communities represent complex networks composed of specialist and generalist species interacting in a nested and modular fashion (Bascompte et al. 2003, Montoya et al. 2006, Olesen et al. 2007). Nested networks are more resilient to perturbations (Lever et al. 2014) and are comprised of a diverse plant and pollinator community (Bascompte et al. 2003). Our data indicate that even in the context of a complex, stable community (Russo et al. 2013), annual ornamentals nonetheless attract a limited number of solely polylectic species and, thus, have a unique, functionally specialized role in a pollinator community. Therefore, we predict that their role in a nested community is limited and they likely contribute little to broad network stability. A community of only these plants would support a simplified homogeneous population of generalist pollinators, such as those common in urban environments, but would likely not support even moderately oligolectic species.

Given these results, one consideration for developing urban landscapes for pollinators is whether the prominence of ornamental flora in urban landscapes drives homogenization of pollinator communities. Urban greenspaces are capable of supporting diverse pollinator communities, and some authors suggest that the lack of oligolectic species is the result of their host plant not being present (Tonietto et al. 2011). Indeed, oligolectic bees may be present in tandem with their hosts in these landscapes (Cane et al. 2006, Matteson et al. 2008), although in lower abundance, with certain species being disproportionately affected. Thus, while floral resource availability influences species composition, it is likely that urban pollinator communities are also shaped by anthropogenic habitat and climatic factors that limit restoration of stable ecological networks.

Our results suggest that the utility of annual ornamental plants for supporting pollinator communities varies based on their environmental context. The annual ornamental plant species that we used in our study are insufficient for supporting a diverse pollinator community alone and are likely redundant in a broad nested community. However, in generalized urban environments, where the goals for supporting pollinator populations are different due to the biotic and abiotic factors shaping a unique ecosystem, ornamental plants may play a more significant role in supporting pollinator communities than they would in a wild system. Many ornamental flowers are selected for an extended bloom time (Horn 2002), and those in our study flowered continuously from early June to late September,

with visits throughout the season. Annual ornamentals may provide a season-long food source to generalist pollinators and particularly attractive cultivars should be considered as an option in urban areas to fill temporal gaps in floral resource availability. Furthermore, floral display size was correlated with visitor abundance for most cultivars. Many ornamentals are bred for large showy blooms with many flowers per plant, and our results suggest that this selective pressure could positively influence the attractiveness of ornamentals to pollinators. In situations where aesthetics and landscape requirements are best fulfilled by ornamental annual plants, selection of attractive, rewarding, long-blooming cultivars, perhaps supplemented with flowering trees or shrubs (Mach and Potter 2018), can support core generalist pollinator populations and, therefore, add stability to urban pollinator communities.

Data Accessibility

Data will be archived in Dryad Digital Repository upon acceptance of the manuscript for publication (doi:10.5061/dryad.jsxksn05d).

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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