RESEARCH ARTICLE



Floral identity and availability along with surrounding landscapes affect pollinator communities in eastern Tennessee

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Abstract

Context Anthropogenic land use can significantly alter insect communities and may threaten services provided by beneficial flower-visiting insects. However, the plant community composition may interact with surrounding land use to affect insects in a way that is not well understood.

Objectives Our goal was to disentangle the effect of the background plant community on the flowering visiting insect community composition from the independent effect of surrounding land use.

Methods We planted four fixed community garden plots, three that each contained six species of one plant family (Asteraceae, Fabaceae, Lamiaceae) and one that was a mixed community plot, controlling the number of individuals and species identity of the plants. We then replicated these four fixed plots across five different landscapes in eastern Tennessee and surveyed the insects that visited the flowers for 2 years.

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Department of Plant Sciences, University of Tennessee, Knoxville, TN 37996, USA *Results* Both the identity and abundance of floral resources were strong drivers of flower-visiting insect abundance, with floral display being the single largest driver. Independent of the plant community, specific pollinating insects responded to different types of land use at different radii around each site. Total flower visitor and soldier beetle abundance increased with agricultural land use at 500 and 2000 m, respectively. On the other hand, sweat bee abundance increased with semi-natural land use at 2000 m and honey bee abundance increased with developed land use at 1000 m.

Conclusion Independent of plant community composition, surrounding land use affected the abundance, diversity, and composition of flower-visiting insects. However, there was not one consistent land use effect across all flower-visiting insects.

Keywords Floral resources · Plant community composition · Land use effects · Pollinator community composition

Introduction

Many agricultural crops depend on insect pollination (Klein et al. 2007) and the demand for these insectpollinated crops is increasing at a faster rate than for wind-pollinated crops (Aizen et al. 2008). Although land managers often rent honey bee hives for pollination services, wild pollinators may be able to provide

sufficient pollination (Russo et al. 2017) and have been identified as more efficient pollinators for some crops (Garibaldi et al. 2013; Kennedy et al. 2013). Despite our reliance on insect pollinators, increased agricultural intensification and urbanization have led to a loss of natural habitat, which previously provided crucial resources for a diverse community of pollinators (Kremen et al. 2002; Landis 2017). Moreover, as farm ownership has transitioned from many small farms to fewer larger farms, land coverage has become more specialized, for example to row crop or pasture (Benton et al. 2003). Increased acreage and the removal of nonproductive lands and field boundaries allows for large land parcels to have identical agricultural use (Robinson and Sutherland 2002). Common agricultural practices have shifted toward maximizing yield through modern machinery, leading to simplified crop rotations and overall reduced crop variety (Robinson and Sutherland 2002) promoting spatial and temporal uniformity (Benton et al. 2003).

Land use is commonly defined as the set of activities and management practices humans employ to alter landscapes (Foley et al. 2005). A commonly studied example of land use is agricultural land use because of both the large spatial extent and intensity of agricultural production (Foley et al 2005). Moreover, the spatial extent of the intensive agricultural land use has increased over time (Benton et al. 2003). These historical shifts have led to biodiversity loss and biotic homogenization across the globe (Kremen et al. 2002; Tscharntke et al. 2005; Deguines et al. 2014; Landis 2017). For example, the conversion of landscapes to agricultural use leads to habitat fragmentation that impacts plant species richness across greater spatial and temporal scales, and habitat loss with more immediate and localized effects (Alofs et al. 2014).

There are many threats to pollinators, but among the most critical threats are those that impact habitat quality or extent (Carvell et al. 2007; Alofs et al. 2014). Wild pollinating insects require a variety of floral resources and nesting substrates, adding to the complexity of restoring or supplementing degraded landscapes for pollinator conservation. Native perennials can provide vital resources, such as pollen and nectar, and nesting habitats for native and nonnative insects (Blaauw and Isaacs 2014; Danforth et al. 2019). Native plants are ideal for establishing conservation habitat for pollinating insects because they exhibit adaptations that allow them to thrive within their native regions, including resilience to environmental conditions such as seasonal variation, soil conditions, or pest pressures. Establishing native plantings in agricultural landscapes has been shown to increase pollinator diversity and abundance (Tuell et al. 2008; Tuell and Isaacs 2009; Morandin and Kremen 2013; Morandin et al. 2014; Bennett and Isaacs 2014; Garibaldi et al. 2014). Because of this, recent conservation efforts have been directed at diversifying and supplementing agricultural landscapes with communities of native plant species, with demonstrable increases in pollinator abundance (Pywell et al. 2005; Tuell et al. 2008; Blaauw and Isaacs 2014; Williams et al. 2015; Schulte et al. 2017).

Insect pollinators also vary substantially in body size and are capable of foraging at a wide range of distances; thus, many studies have evaluated the effect of surrounding land use on pollinator communities (e.g. Kennedy et al. 2013; Bennett and Isaacs 2014; McKechnie et al. 2017; Cusser et al. 2019) and pollination services (e.g. Klein et al. 2012; Smith et al. 2013; Connelly et al. 2015). An increased proportion of land dedicated agriculture in the landscape has been found to negatively affect bee species richness and abundance (Watson et al. 2011; Connelly et al. 2015), while an increase in the proportion of natural areas in the landscape have been found to have a positive relationship with bee species richness and abundance (Watson et al. 2011; Klein et al. 2012; Smith et al. 2013; Cusser et al. 2016; McKechnie et al. 2017). Crucially, in these studies, the plant community typically varies along with land use, making it difficult to disentangle the effect of plant species composition from the effect of surrounding land use. Land use that causes habitat fragmentation decreases the species richness of herbaceous plant species (Alofs et al. 2014), and pollinators respond strongly to the identity and availability of floral resources (Rowe et al. 2020). Agricultural land use can also shift plant community composition in non-random ways; for example, agriculture has in some cases been associated a decline in the proportion of legumes and insect-pollinated plant species (José-María et al. 2010, 2011; Solé-Senan et al. 2018; Fonderflick et al. 2020). If plant species preferred by flower-visiting insect species are lost differentially from the community, one would expect to see corresponding decreases in pollinator richness and diversity, independent of direct land use effects.

Beyond species specific preferences, plant family identity may relate to nutritional resources provided by plants. For example, legumes in the Fabaceae family are thought to have pollen with high protein levels (Vaudo et al 2020) that may relate to insect fitness (Roulston and Cane 2002). Thus, to evaluate the effect of land use independent of the plant community, it is necessary to replicate a fixed plant community across a gradient of land uses.

To disentangle the effect of plant community and surrounding land use, we established fixed plots of 18 species of native perennials of three plant families, in sets of four plots. We then replicated these sets of four plots across five different landscapes. We used these plantings to characterize pollinator abundance, species richness, and community composition. We also explored the background effects of plant identity and abundance on pollinator visitation. Given the established effects of agricultural intensification and natural areas in the surrounding landscape, we then investigated the potential impacts of land cover on the pollinator community.

Methods

All research sites were located on the University of Tennessee properties in eastern Tennessee (Anderson, Cumberland, and Knox counties). In 2019, we established four sites (1) Urban Gardens, (2) Arboretum, (3) Cattle Pasture, and (4) Mixed Use Agriculture. In 2020, we established a fifth site: (5) Organic Agriculture. At each site, we established four $(3 \text{ m} \times 2 \text{ m})$ plots, one containing six species of each plant family (Asteraceae, Fabaceae, and Lamiaceae) and one featuring two species of each family (Mixed family plot). These plots were planted between 15 and 50 m apart, depending on space availability at each site. Within each plot, we planted four individuals each of six native perennial species, such that the composition of the plots in each site was fixed (Fig. 1). As each site served as a replicate of the four plant plots, there were five replicates for the study in 2020 and four replicates in 2019.

Plot setup

For each plot, we eliminated grass through handweeding and hoeing. Additionally, all sites except the Organic Agriculture site received one application of glyphosate three weeks before planting the study species. We distributed compost and commercially available topsoil throughout each plot before planting the selected native perennials. All plants were purchased as plugs from the same native plant nursery (Overhill Gardens) and placed approximately 50 cm apart within the plots. After planting, we added a soil amendment (compost) and a layer of commercially available mulch to each plot for moisture retention and weed suppression. The plots were enclosed with chicken wire fencing to deter herbivores. The plants were hand-watered regularly during dry periods, and all plots within a site received the same amount of water.

Selected plant families and species

We selected plant families based on specific qualities attractive to pollinators. Asteraceae have an attractive, open flowering display and extended flowering periods (Blaauw and Isaacs 2014). Flowering plants in the Fabaceae family contain high protein pollen (Pywell et al. 2005; Danforth et al. 2019; Vaudo et al. 2020) and Lamiaceae flowers produce significant quantities of nectar (Danforth et al. 2019). Due to variation in pollen protein content among plant species, supplementing habitat with an array of plant species can support the nutritional needs of a diverse community of pollinators. The reported pollen protein to lipid ratio of our selected plant families by Vaudo et al. (2020) is as follows: Asteraceae 1.06 ± 0.1 ug/mg, Lamiaceae ~ 1.2 ug/mg, and Fabaceae 3.8 ± 0.5 ug/ mg. We selected our native perennial study species (Table 1) based on the Lady Bird Johnson Wildflower Center database, the Southeast Region Pollinator Plants List published by The Xerces Society, nutrient content (Vaudo et al. 2020), and plant availability from a local nursery. All plant species used in this study were native to the southeastern United States and were sourced from a native plant nursery that grows native plants from local source populations. The plants in the Mixed plot were



Fig. 1 Heuristic diagram of experimental design showing four plot types (not to scale): L (Lamiaceae), A (Asteraceae), F (Fabaceae), and M (Mixed). Each of the four plot types contains four individuals (a, b, c, d) of six species (1-6) of native

selected from the available plant species based on their commercial availability.

Land use

The five sites we chose represented varying proportions of three land use types common to the region:

perennials. The mixed plot contains two species of each plant family. We then evaluated the effect of land use at three radii: 500 m, 1000 m, and 2000 m

urban, semi-natural, and agricultural. The Urban Gardens (1) represented the urban landscape for our study, comprising roughly 4 hectares of native and non-native plants, shrubs, and tree species surrounded by the Tennessee River, highways, buildings, and parking lots, near downtown Knoxville, TN. The Arboretum (2) comprised approximately 100 hectares

Order in plot	Asteraceae	Fabaceae	Lamiaceae	Mixed
1	Helianthus occidentalis, Riddell	Amorpha herbacea, Walter	Conradina verticillata, Jen- nison	Helianthus occidentalis
2	Coreopsis lanceolata, L	Senna marilandica, L	Pycnanthemum muticum, Pers	Senna marilandica
3	Eurybia saxicastelli, Newsom	Baptisia albescens, Small	Lycopus virginicus, L	Conradina verticillata
4	Stokesia laevis, Greene	Lespedeza hirta, Hornem	Physostegia leptophylla, Small	Baptisia albescens
5	Helianthus hirsutus, Raf	Baptisia tinctoria, L	Blephilia subnuda, Simmers & Kral	Coreopsis lanceolata
6	Verbesina occidentalis, L	Thermopsis villosa, Fer- nald & B.G. Schub	Collinsonia canadensis, L	Pycnanthemum muticum

Table 1 The perennial species used in the experiment, including their family and their order within the plot, or their spatial position within each plot, from left to right (Fig. 1)

of semi-managed forests and woody plants, with a high diversity of protected natural habitat and native plant species in Oak Ridge, TN. To assess pollinator communities in agricultural land, we selected three sites that represented common cropping systems and land uses in the region: organic agriculture, conventional row crops, and cattle pasture. The Cattle Pasture (3) and Mixed-Use Agriculture (4) sites were both located in Crossville, TN, approximately 1.6 km apart on an over 800 hectare conventional farm used for cattle, cash crops, and horticulture research. The Organic Agriculture (5) site was located 12.9 km south of Knoxville on roughly 36 hectares dedicated to organic horticulture and field crop research surrounded by residential housing and some small-scale independent farm operations.

The community of the flowering plants immediately surrounding the plots at each site varied from frequently mown, short cut grasses (Cattle Pasture), to managed gardens with a high diversity of native (Arboretum) and ornamental (Urban Gardens) flowering beds. Both the Mixed-Use Agriculture and Organic Agriculture sites comprised a mixed community of taller grasses and some common nonnative flowering weeds, that were mown twice a summer, alongside a mixture of research crops including blueberries, apples, and switchgrass (Mixed-Use Agriculture) and lettuce, squash, and mint (Organic Agriculture).

We used ArcGIS and the US National Land Cover Database (NLCD) (Dewitz 2019), to classify the land cover surrounding each of our research sites at 500 m, 1000 m, and 2000 m with the Asteraceae plots as the center. These three radii were chosen based on differences in forage distances for pollinators, specifically bees, as there is some correlation with body size and forage distance capabilities (Greenleaf et al. 2007). Smaller bodied, solitary bees have an estimated forage range of 150 to 600 m for some bee species (Gathmann and Tscharntke 2002), while large body bees such as *Bombus* spp. have been documented to forage well over 2000 m (Rao and Strange 2012; Redhead et al. 2016).

The NLCD has more than 20 different land cover classifications, including categories for vegetation, and various land-use densities. In our analysis, we detected 14 land cover classifications that we aggregated into four general land-use types: water (Open Water), developed (Developed High Intensity, Developed Low Intensity, Developed Medium Intensity, Developed Open Space), agriculture (Cultivated Crops, Grassland/Herbaceous, Pasture/Hay), and semi-natural (Deciduous Forest, Emergent Herbaceous Wetlands, Evergreen Forest, Mixed Forest, Shrub/Scrub, Woody Wetlands) (Table S1). The NLCD defined developed land as constructed materials and impervious surfaces such as commercial and residential housing, roadways, and lawn grasses. Areas classified as water included open water and areas with minimal soil and vegetation. Semi-natural land use included different forest types, wetlands, shrubland, and non-grassland herbaceous land cover. Agricultural land use comprised pastureland, cultivated crops, or grasslands. We calculated the proportion of each land cover classification for each radius. We used semi-natural habitat as a proxy for suitable pollinator habitat in the surrounding landscape because of previous research showing a relationship between pollinator abundance and diversity and seminatural land use (e.g. Cusser et al. 2016). We then estimated the relationship between land cover type and pollinator abundance and richness across the sites. We hypothesized that landscape context would have an effect on pollinator diversity or abundance; specifically, that greater proportions of semi-natural land cover in the landscape would correlate with pollinator abundance and diversity.

Data collection

We conducted pollinator collections weekly at each site throughout the flowering season in 2019 and 2020. For each pollinator collection, we recorded the date, time, site location, plot name, cloud cover, sun, temperature at the time of collection, number of inflorescences per plant, and the collector. We conducted pollinator collections between the hours of 0900 h to 1600 h, as this is when most pollinators are active (Danforth et al. 2019). We did not conduct collections during times of rain or excessive cloud cover.

Pollinator collections began each season (2019/2020) as the first plants began to bloom. We monitored all individuals of a given plant species within a plot for 5 min and collected any insects seen touching the reproductive parts of the flowers using a handheld insect-collecting vacuum. We repeated the same procedure for each plant species until all flowering plant species within a plot were sampled for five minutes. The specimens were stored in a freezer and later pinned, labeled, and sorted taxonomically. We used voucher specimens to identify the specimens and our identifications were verified by a taxonomist (Sam Droege, USGS).

We calculated floral display as the number of open inflorescences in a given collection event multiplied by the average size of the inflorescence (length and width) for each plant species. We calculated the average size of the inflorescences by randomly selecting 10 to 20 different inflorescences per plant species, and measuring them to the nearest tenth of a millimeter with a digital caliper (Russo et al. 2019).

Data analysis

Because the study plants were perennials, their flowering was inconsistent in their first year (2019); therefore, we conducted data analysis primarily with the 2020 data, including 2019 data only for analyses of sampling completeness and species richness at the different sites.

Floral display is a strong determinant of pollinator visitation (Williams et al. 2015; Russo et al. 2019, 2020). To determine the background statistical relationship between floral display and flower-visitor abundance, we created a generalized linear mixed effects model with floral display as the fixed effect and site as a random effect, using the lme4 package in R (Bates et al. 2014). We log-transformed both floral display and abundance to normalize their distributions. We then calculated the conditional and marginal coefficient using the r.squaredGLMM function from the MuMIn package (Barton 2018).

To better determine the relative attractiveness of individual plant species, we also calculated the visitation rate to their flowers. The visitation rate of floral visitors acts as a proxy for pollinator forage preferences (Rowe et al. 2020). We calculated the visitation rate using the total number of insects collected during a 5 min sample, divided by the size of the floral display (number of inflorescences multiplied by average inflorescence size) during the sample for each plant species. We separately calculated the visitation rate of bee specimens only. We used a GLMM to test for differences between the average visitation rate across the four plot types (Asteraceae, Fabaceae, Lamiaceae, and Mixed). We did not perform a statistical test to compare visitation rates among the individual plant species because there were too many pairwise comparisons, which may have increased our risk of type 1 error.

In addition to flower-visitor abundance, we calculated species diversity using Hill numbers with the iNEXT package in R (Chao et al. 2014), accounting for both species richness and evenness in the pollinator community. We used a rarefaction analysis to establish sampling completeness at each site and to compare the pollinator diversity of the sites to one another (Chao et al 2014). We determined significant differences between Hill numbers when their 95% confidence intervals were not overlapping. We separately conducted rarefaction analyses for all insect visitors and just bee visitors. We used a non-metric multidimensional scaling (NMDS) analysis to compare the community composition among the sites for all visitors and just bees separately (Oksanen et al. 2011).

To determine the effect of land use, and because the land use variables were correlated with one another, we used a model selection process with GLMMs to test the relationship between pollinator abundance and richness and the major land cover classes (agriculture, developed and semi-natural) at the three different radii with floral display as a covariate and plot as a random effect (Barton 2018). We excluded water cover from this analysis because we did not consider it a land use type. We repeated this process with the following subsets of the flowervisitor community: (1) the most abundant non-bee insect (Chauliognathus pensylvanicus, Cantharidae), (2) honey bees (Apis mellifera, Apidae), (3) the most abundant bee species (here Halictus ligatus/poeyi, Halictidae), (4) the most abundant bee genus (here Lasioglossum spp., Halictidae), and (5) the summed abundance of all the specialist bee species found in our study (Andrena placata, A. asteris, A. simplex, Pseudopanurgus labrosus, P. rugosus, P. compositarum, Andrenidae; Melissodes boltoniae, M. dentiventris, M. trinodis, M. druriella, M. denticulatus, Melitoma taurea, Svastra obliqua, Apidae; Megachile xylocopoides, Paranthidium jugatorium, Megachilidae; Lasioglossum lustrans, Halictidae). For these subsets, we also tested the significance of the plot types (Asteraceae, Fabaceae, Lamiaceae, or Mixed plot). We used an ANOVA to compare the models and selected the model with the lowest AICc for each comparison (total flower-visitor abundance and species richness, bee abundance and species richness, and the abundance of each of the subsets of flowervisiting insects).

Results

Summary of data

For two field seasons combined (2019/2020), we collected 7294 insects during a total of 101.33 h of sampling. Most (5108, 70%) of our collected specimens were bees and 2186 (30%) were non-bee flower-visiting insects. The most abundant non-bee species was the soldier beetle (*C. pensylvanicus*) (843). Over our two-year study, we collected 4563 wild bees and 545 honey bees (*Apis mellifera*). These individuals represented 28 different bee genera, with a majority from *Lasioglossum* (1374), *Halictus* (1096), *Augochlorella* (493), Ceratina (434), and Bombus (417) (Table S2). We collected a total of 99 different bee species and 53 non-bee families (Tables S3, S4). Seven of the bee species we collected were previously unreported in Tennessee and were considered new state species records: Andrena placata, Ceratina cockerelli, Heriades leavitti/variolosa, Lasioglossum lionotum, L. pruinosum, L. rozeni, and Sphecodes heraclei (pers. comm. S. Droege, J. Ascher).

The plant species varied in their average floral display. All species in the Asteraceae and Lamiaceae families flowered, but none of the individuals of *Thermopsis villosa* (Fabaceae) flowered at any site (Fig. S1). Asteraceae species had larger floral displays compared to Fabaceae and Lamiaceae. There was a significant positive relationship between the log-transformed floral display and insect abundance (effect size=0.33, N=5, P<0.001, marginal $R^2=0.35$, conditional $R^2=0.38$, Fig. S2).

Insect visitation

Pycnanthemum muticum had the highest visitation rate of any plant species in 2020 across all flower-visiting insects (Fig. 2A), and the second highest visitation rate when including only bee visitors (Fig. 2C). The plant with the highest bee visitation rate was *Lespedeza hirta* (Fig. 2C). At the plot level, visitation rates were similar between all visitors and just bees. Across the plot types, the Asteraceae had the lowest visitation rates overall, despite high abundances of flower-visitors, due to large floral displays (Fig. 2B, D). The Lamiaceae had the highest visitation rate overall, but did not differ significantly from the Mixed plot (Fig. 2B, D).

Across all flower-visitors, the Organic Agriculture site had the highest abundance and the Urban Gardens the lowest with overlapping relationships among the other sites (Fig. 3A, Table S5). On the other hand, the bee abundance did not differ significantly among the sites (Fig. 4A). The sites did not differ significantly from one another in terms of species richness of all flower-visitors or just bees (Figs. 3B, 4B). The Mixed-Use Agriculture site had a significantly higher, and the Organic Agriculture site significantly lower, Shannon diversity for all flower-visitors (Fig. 3B). For bee visitors, the Shannon diversity was highest in the Cattle Pasture site, followed by the Mixed-Use Agriculture



Fig. 2 The log-transformed visitation rates of all insect visitors (\mathbf{A}, \mathbf{B}) and just bees (\mathbf{C}, \mathbf{D}) to the 17 perennial species that bloomed in our experimental plots (\mathbf{A}, \mathbf{C}) and among the four plot types (\mathbf{B}, \mathbf{D}) . Species represent three plant families: Asteraceae (purple), Fabaceae (green), and Lamiaceae (blue). We

also include visitation rates to species in a Mixed composition plot comprising two species of each plant family (brown). Species names are abbreviated to the first three letters of the genus and species names. Significant differences among plot level visitation rates are indicated by differing letters above the bars

and Arboretum sites (which did not differ significantly), then the Urban Gardens, and finally the Organic Agriculture site (Fig. 4B). For the Simpson diversity of all insects, the Mixed-Use Agriculture site was significantly higher than all other sites, followed by the Arboretum, which was also higher than the Urban Gardens and Cattle Pasture sites, with the Organic Agriculture site again having the lowest diversity (Fig. 3B). For just bees, the Simpson diversity was highest at the Arboretum, Mixed-Use Agriculture, and Cattle Pasture sites (which did not differ significantly), followed by the Urban Gardens, which was significantly higher than the Organic Agriculture site (Fig. 4B).

The NMDS analysis showed that the sites overlapped in the composition of the pollinator community, both for all flower-visiting insects (Fig. 3C) and for just bees (Fig. 4C).



Fig. 3 Differences among the sites in terms of abundance (**A**), diversity (**B**), and species composition (**C**) of all visitors. The sites are (1) Urban Gardens (red), (2) Cattle Pasture (yellow),

(3) Mixed-Use Agriculture (green), (4) Arboretum (blue), and (5) Organic Agriculture (purple)



Fig. 4 Differences among the sites in terms of abundance (A), diversity (B), and species composition (C) of bees only. The sites are (1) Urban Gardens (red), (2) Cattle Pasture (yellow),

(3) Mixed-Use Agriculture (green), (4) Arboretum (blue), and (5) Organic Agriculture (purple)

Spatial analysis results

The Urban Gardens had the highest proportion of developed land coverage at any given radius (Table 2). The Arboretum had the highest proportion of seminatural land cover at the smallest radius, 500 m, but equal semi-natural cover as the Organic Agriculture site at 1000 m and the Mixed-Use Agriculture site at 2000 m, respectively. The Arboretum had the second highest proportion of land cover classified as developed land at any scale. For the agricultural sites, in general, as the analyzed radius of land use increased, the percentage of land classified as agriculture decreased, while the percentage of land classified as semi-natural increased. The Mixed-Use Agriculture site had the most land cover classified as semi-natural Table 2Land use in threeradii around each site(centered on the Asteraceaeplot), categories determinedby the National Land CoverDatabase (ESRI 2016)

	Radius (meters)		
Land cover class	500 m (%)	1000 m (%)	2000 m (%)
Site 1, UT gardens			·
Agriculture	0.9	5.6	5.9
Developed	68.8	63.4	60.3
Semi-natural	6.4	18.4	23.2
Water	23.7	12.2	10.5
Site 2, Cattle pasture			
Agriculture	59.4	47.3	50.9
Developed	16.1	12.4	5.8
Semi-natural	21.6	39.0	40.8
Water	2.0	0.1	0.8
Site 3, Mixed use agriculture			
Agriculture	64.0	67.8	37.7
Developed	5.2	5.5	5.0
Semi-natural	30.3	25.6	55.1
Water	0.6	1.1	0.6
Site 4, Arboretum			
Agriculture	10.3	10.9	12.3
Developed	26.1	26.5	29.2
Semi-natural	63.6	62.2	55.4
Water	_	_	2.6
Site 5, Organic agriculture			
Agriculture	64.4	39.9	32.3
Developed	11.5	18.3	15.3
Semi-natural	24.1	41.8	49.0
Water	-	-	3.4

at both the 500 m and 2000 m scale and had the lowest percentage of developed at any scale as compared to the Cattle Pasture and Organic Agriculture.

Our model selection process identified the best model for overall flower-visitor abundance with the fixed effects of floral display and proportion of agriculture at a 500 m radius around each site. The agricultural land use at that scale had a significant positive association with overall flower-visitor abundance (effect size = 0.59, T value = 2.73, P value = 0.006, Fig. 5A, Table 3). A similar model was selected for overall species richness and had similar results (effect size = 0.41, T value = 3.39, P value < 0.001, Table 3). The best models for the flower-visitor subsets were: (1) soldier beetles: agricultural land use at 2000 m (Fig. 5B), (2) A. mellifera: developed land use at 1000 m (Fig. 5C), (3) H. ligatus/poeyi: seminatural land use at 2000 m (Fig. 5D), (4) Lasioglossum spp.: semi-natural land use at 2000 m (Fig. 5E),

(5) specialist bees: semi-natural land use at 500 m (Fig. 5F). For these subsets, the land use effect was significantly positive for soldier beetles, honey bees, and *Lasioglossum* spp. The land use effect was not significant for specialist bees or *H. ligatus/poeyi*. Plot type was a significant fixed effect for soldier beetles, specialist bees, *H. ligatus/poeyi*, and *Lasioglossum* spp (Fig. 5, Table 3).

Discussion

Anthropogenic land use is a major driver of ecological change, and can affect both the abundance and composition of insect communities (Kennedy et al. 2013). However, the effect of surrounding land use and local flowering resources can be difficult to disentangle from the composition of the surveyed plants, which are likely primary drivers of the flower-visiting



Fig. 5 Linear relationships between land use and the abundance of all flower visiting insects (A), as well as subgroups of interest, including the most abundant non-bee visitor, soldier beetles (*Chauliognathus pensylvanicus*, Cantharidae) (B), honey bees (C), the most abundant bee species (*Halictus ligatus/poeyi*) (D), the most abundant bee genus (*Lasioglossum* spp.) (E), and the sum of the specialist bee species (F).

insect diversity and abundance that is collected. In this experiment, we carefully controlled the species composition and abundance of the plant species, and therefore floral resources, available to insects in fixed experimental plots, allowing land use and flowering plants in the local area around each site to vary. As we show here, different floral visitors may respond

The *x*-axis has the proportion of the land use type and radius that had the lowest AICc in a model selection process for each group of insects. The colors refer to the plot type: Asteraceae (red), Fabaceae (green), Lamiaceae (blue), or the Mixed Plot (purple), which had two species of each of the three plant families. The "ns" denotes a non-significant land use effect

differently to land use change, and at different scales. Moreover, the identity and availability of the plant species these insects are using for floral resources is an important driver of their abundance, above and beyond the role of land use.

First, we illustrated the effect of plant identity and availability on floral visitors, showing significant

Response	Fixed Effect	Contrast	Random Effect	Family	Groups	Effect size	T value	P value	$\mathbb{R}^{2}\mathrm{m}$	$\mathbb{R}^{2}\mathbb{c}$
og abundance (all insects)	Log display	Continuous	Site	Gaussian	890 obs, 5 sites	0.33	22.37	< 0.001	0.36	0.37
	500 m Ag	Continuous				0.59	2.73	0.006		
og species richness (all insects)	Log display	Continuous	Site	Gaussian	890 obs, 5 sites	0.22	21.54	< 0.001	0.35	0.35
	500 m Ag	Continuous				0.41	3.39	0.0007		
og soldier beetle abundance	2000 m Ag		Plot ID	Gaussian	96 obs, 20 plots	3.27	3.87	< 0.001	0.25	0.32
	Family	A-F				- 1.21	- 2.94	0.003		
		A-L				- 0.71	-2.02	0.04		
		A-M				- 0.3	- 0.8	0.42		
og specialist bee abundance	500 m Nat	Continuous	Plot ID	Gaussian	96 obs, 20 plots	- 0.46	- 1.89	0.06	0.02	0.31
	Family	A-F				- 0.79	-5.2	< 0.001	0.36	0.36
		A-L				- 0.75	- 6.21	< 0.001		
		A-M				- 0.67	- 5.1	< 0.001		
log honey bee abundance	1000 m Dev	Continuous	Plot Type	Gaussian	96 obs, 4 plot types	1.83	3.27	0.001	0.1	0.13
og H. ligatus/poeyi abundance	2000 m Nat	Continuous	Plot ID	Gaussian	96 obs, 20 plots	0.52	0.57	0.57	0.004	0.41
	Family	A-F				- 2.5	- 7.08	< 0.001	0.48	0.48
		A-L				- 2.25	- 8.06	< 0.001		
		A-M				-0.86	- 2.83	0.005		
og Lasioglossum abundance	2000 m Nat	Continuous	Plot ID	Gaussian	96 obs, 20 plots	2.06	1.94	0.05	0.14	0.14
	Family	A-F				- 0.24	- 0.56	0.57		
		A-L				0.88	2.68	0.007		
		A-M				0.59	1.64	0.1		

Table 3 Results from the generalized linear mixed effects models with the lowest AICc for each response variable (abundance of all insects, soldier beetles, honey bees, H. liga-

0 $(\mathbf{R}^2\mathbf{c})$ \mathbf{R}^2 for each model

Ag agricultural land use, Dev developed land use, Nat semi-natural land use, A Asteraceae, F Fabaceae, L Lamiaceae, obs observations Significant (P < 0.05) fixed effects are highlighted and in bold variation in the rate of visitation (number of visits per unit floral area per unit time) among plant species and plot types. It is important to use the size of the floral display when comparing floral visitor preferences because there is a strong background effect of the size of the floral display on abundance (Rowe et al. 2020). We demonstrated that here, and it has also been demonstrated in other studies (Tuell et al. 2008; Williams et al. 2015). Using this measure of visitation, the Asteraceae plots were shown to be less preferred than the other plot types, despite their high raw abundances. This was because the Asteraceae had large floral displays relative to the number of visits they received. This analysis also illustrated the attractiveness of P. muticum. The mountain mints (Pycnanthe*mum* species) are widely regarded as valuable pollinator plants, and across all insect visitors this plant had the highest visitation rate. Bees had a similar visitation pattern, but their highest visitation rate was to a Fabaceae species, L. hirta. Many Fabaceae flowers restrict their floral visitors with floral morphology, and bees are among the few insects that can access their potentially high-quality floral rewards. One of our Fabacaeae species (T. villosa) did not bloom during the study duration, but we observed comparable abundance and visitation rates among the Fabaceae, Lamiaceae, and Mixed plot types. It's possible that the difference in visitation rate between Asteraceae and Fabaceae is due to pollen quality, as some studies have suggested that Fabaceae have pollen with high protein content than Asteraceae (Vaudo et al 2020). On the other hand, the high visitation rate of the Lamiaceae may be due to abundant nectar resources (Danforth et al 2019). Future research could explore the drivers of floral preference in this system.

Next, we compared pollinator community abundance, diversity, and composition among the research sites. Though some differences were present, the sites tended to be more similar than different across these measures. Overall, we did not see strong negative effects of increasing agriculture, or strong positive effects of increasing semi-natural area, in the surrounding landscape. Abundance is important as common species may be the drivers of ecosystem services, as compared to species richness (Winfree et al. 2015). However, species richness provides a key component for biodiversity metrics (Hillebrand et al. 2018) and the diversity of pollinating insects has been repeatedly linked to crop yield and quality (Garibaldi et al. 2013; MacInnis and Forrest 2019). Interestingly, the Mixed-Use Agriculture site had the highest Shannon and Simpson diversity indices for all insects, while the Urban Gardens site had consistently the lowest diversity across all indices. Finally, when looking at pollinator community composition, none of the sites were shown to be particularly different from the others, and all shared a core set of abundant pollinator species.

Finally, we tested the effect of surrounding land use on the abundance of groups of pollinating insects. We measured land use in four categories (semi-natural, agricultural, developed, and water), and at three radii (500 m, 1000 m, and 2000 m). Using a model selection process to identify the best model, we found that the best model varied depending on the insect identity. Across all flower visitors, and for soldier beetles (C. pennsylvanicus, the most abundant nonbee insect), surrounding agricultural land use was included in the best model, but the radius for these two groups differed (500 m for all insects and 2000 m for soldier beetles). For Lasioglossum, semi-natural land use around the site was included in the best model, at a 2000 m radius. Finally, for honey bees, the best land use variable was developed land use at 1000 m. It seems likely that each different insect group tested here was sensitive to different aspects of land use, and that the varying radii might reflect their foraging ranges or reliance on additional habitat and alternative floral hosts. For example, most bees are central place foragers (Michener 2000; Danforth et al. 2019), and foraging range likely varies with body size (Greenleaf et al. 2007). In the case of honey bees, which were actively managed in the study region, the proximity of developed land use might also relate to the presence of hives. Moreover, for soldier beetles, H. ligatus/poeyi, Lasioglossum, and specialist bees, the plot type (here related to plant family) was a significant predictor of abundance. In most cases, the Asteraceae are clearly distinct from the other plot types. This could be due to the fact that the family Asteraceae supports more specialist bee species than any other plant family, or simply because the flowers of that family produced such large and attractive displays (Fowler 2016).

Although not typically considered "pollinators", the soldier beetles were an extremely abundant component of the floral visitor community in this study. They have been observed on a large number of flowering plants (Williams 2006) and are sometimes referred to as "beneficial insects" (Isaacs et al. 2008). Their role as pollen predators and their effect on pollination efficacy could be the source of future research, especially given their relationship to surrounding agricultural land use. Beyond the soldier beetles, our study illustrates the sheer diversity of insects that use floral resources, as we collected 53 non-bee families on just the 17 plant species included in the experiment. The role of these non-bee insects as pollinators is often overlooked, but they represent a significant component of the pollinator community (Rader et al. 2009, 2016, 2020).

Our study was limited in the breadth of the gradient of land use types. The highest proportion of agricultural land use at our largest radius (2000 m) was 48% (Cattle Pasture) while the highest proportion of semi-natural land use was 55% (Mixed-Use Agriculture and Arboretum). It is possible that further extremes of land use would have different effects on these pollinator communities or that there are nonlinear effects of increasing anthropogenic land use (Renaud et al. 2022). However, the land use included in this study was a fair representation of the study area, Eastern Tennessee, which is largely represented by a heterogenous matrix of mixed land use types, and the responses of the pollinator community here were likely representative of broader patterns in the region.

Both competition and magnet effects have been demonstrated in areas of high floral availability (Molina-Montenegro et al. 2008; Grab et al. 2017). In our study, the flowering community in the area immediately surrounding the research plots varied from highly mown and lacking in alternative floral resources (Cattle Pasture) to diverse highly managed flowering gardens (UT Gardens) with abundant floral resources. This local availability may have influenced the insects we observed visiting flowers in our research plots by supporting larger populations of flower-visiting insects or by reducing overall visitation through competition for visitation. In this case, we did not see any clear differences among sites in terms of their pollinator communities, in spite of a wide range of different locally available floral resources. However, it is possible that these effects were temporally transient and that we lacked the resolution to detect them (Grab et al 2017). Future work may conduct time-coupled floral surveys in the areas immediately surrounding such research plots to assess the impact of local floral resource availability.

Overall, we did not see strong, consistent effects of land use surrounding our research plots. Instead, we found that floral identity and availability were the strongest drivers of insect visitation rate, abundance, and diversity. Furthermore, subgroups of the whole pollinator community (soldier beetles, honey bees, and *Lasioglossum*) did respond to surrounding land use, but responded at varying radii and to different land use types. These results are encouraging for those wishing to provide pollinator habitat in landscapes that are highly modified, suggesting that increasing the availability and diversity of floral resources is the most important driver of total flowervisiting insect abundance.

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Declarations

Competing interests The authors declare no competing interests.

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