Article

DISTINCT POLLINATOR COMMUNITIES PERSIST AMONG CO-FLOWERING SPECIALTY CROPS IN INDIANA

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Abstract—Diverse bee communities pollinate fruits and vegetables, and the composition of these communities has been described for many specialty crops in major production regions. However, pollinator communities in landscapes dominated by agronomic crops may differ in species composition and the contribution of wild bees. With over 4 million ha of maize and soybean, Indiana presents a novel landscape to compare pollinator communities among specialty crops that differ in their use of managed bees and bloom phenology, with potential implications for the composition of wild bee communities and their contributions to flower visitation. We sampled pollinator communities with flower observations and pan traps in spring-blooming apples and blueberries and summer-blooming tomatoes and watermelons, allowing us to compare communities between specialty crops with overlapping and distinct bloom times. Apples, blueberries, and watermelons were stocked with honey bees, and watermelons additionally had managed bumble bees. Across two years of sampling, we observed 1,651 flower visits by 13 taxa, collected 1,967 bees, and identified 84 taxa from collected specimens. Apples and blueberries hosted the richest pollinator communities (34 and 51 taxa, respectively) followed by watermelons (22 taxa), and tomatoes (19 taxa). While 70% of flower visits in apples and blueberries were attributed to honey bees, wild bees accounted for 82% and 99% of flower visits in watermelons and tomatoes, respectively. Our results indicate that distinct pollinator communities persist among co-flowering specialty crops in a landscape dominated by maize and soybean production and underscore the contribution of wild bees for specialty crop pollination, particularly in watermelons and tomatoes.

Keywords—Bee communities, pan traps, pollinator diversity, pollinator observations, wild bees

INTRODUCTION

Specialty crops, which include non-staple fruits and vegetables, are crucial to food security (Eilers et al. 2011) and economically important, generating up to $50 billion in the United States annually (NASS 2017). Production of most specialty crops relies on insect pollination, with visitation by bees improving fruit set and quality (Klein et al. 2006). Managed bees are stocked in a variety of fruit crops to ensure adequate pollination; however, as managed bee health and pollinator populations have declined (Potts et al. 2010; Goulson et al. 2015), there is a growing interest in quantifying and protecting the pollination services provided by wild bees.

Western honey bees (*Apis mellifera*) are a managed species commonly used for specialty crop pollination, providing up to $11 billion annually in pollination services in the United States (Calderone 2012). The contribution of honey bees to pollination varies by crop; for example, they are often responsible for the majority of flower visits in blueberries (*Vaccinium corymbosum*) and apples (*Malus domestica*) (Watson et al. 2011; Mallinger et al. 2021). However, in crops like watermelon (*Citrullus lanatus*) and tomato (*Solanum lycopersicum*), honey bees can comprise less than half of all visits (Greenleaf & Kremen 2006; Winfree et al. 2008; Bloom et al. 2021; Pecenka et al. 2021), while wild bees provide the bulk of pollination services.

Although wild bee visits correlate with increased fruit set in 41 crop systems (Garibaldi et al. 2013), bee community composition, including the relative contributions of wild bees and the species responsible for pollination, is variable among agricultural regions and crops, as well as seasonally (Gibbs et al. 2016; Nooten et al. 2020; Reilly et al. 2020). Floral morphology might contribute to differences in pollinator communities by filtering which species are able to access floral rewards. For example, tomato flowers offer pollen concealed within a hard-to-access anther cone; they may be less attractive to species that have difficulty extracting pollen, compared to flowers that have a more accessible structure or that offer both nectar and pollen (e.g., apples or watermelons) (Toni et al. 2020; Cooley & Vallejo-Marín 2021). In combination with geographic variation, these crop-specific differences necessitate a regional and system-specific approach to describing and protecting pollinator communities.

Indiana is a producer of several specialty crops: namely, spring-blooming perennial fruits like apples and blueberries, as well as summer-blooming annual crops like tomatoes and watermelons. Specialty crops in the state are typically grown at small scales and/or isolated in a field crop-dominated landscape. Indiana is a top producer of maize (*Zea mays*) and soybean (*Glycine max*), with a combined area of 4 million ha per year (NASS 2017). The associated effects of heavy pesticide use, combined with the isolation of specialty crop fields, present a landscape that is hostile to species less adapted to disturbance (Duelli & Obrist 2003; Potts et al. 2010; Kennedy et al. 2013; St. Clair et al. 2020). The landscape may be particularly challenging for oligolectic species with a narrow diet range, whose abundance and diversity is reduced in heavily cultivated areas (Main et al. 2019). While there are a wealth of studies describing pollinator communities in some of the major production regions for specialty crops, the species composition in those regions may not be broadly representative. For example, geographical differences in land use type and intensity, which differ between production regions, influence bee abundance and diversity (Ricketts et al. 2008; Millard et al. 2021). Less attention has been devoted to characterising pollinator assemblages in smaller-scale operations, especially within the Corn Belt region of the Midwestern United States. In Iowa, wild bee community composition does not differ between soybean fields and diversified fruit and vegetable farms, suggesting that large acreage row crops and smaller acreage specialty crops recruit from the same regional pool of pollinators (St. Clair et al. 2020). Although most Indiana specialty crops rely on pollinators, little is known about the community composition of wild bees in these systems and how their flower visitation compares to managed bees. Each crop system is distinguished by unique managed bee stocking practices and bloom phenology, with potential implications for their pollinator communities.

This study describes and compares the pollinator communities in Indiana's major specialty crops, including watermelons and tomatoes (produced on a large scale) and blueberries and apples (high value and important for agrotourism). Indiana's landscape serves as a microcosm for production throughout much of the Corn Belt (i.e., isolated pockets of fruits and vegetables within a larger maize and soybean matrix). Using commercial farms, we quantified the proportion of flower visits from managed and wild taxa and compared bee community composition between the four specialty crops. We emphasised comparisons between bee communities in the two spring-blooming perennial crops (apples and blueberries) and the two summer-blooming annual crops (tomatoes and watermelons) because we expected to find more similarities in wild bee community composition between crops that have overlapping bloom phenology. If specialty crops recruit from the same regional pool of pollinators, as in St. Clair et al. (2020), bee communities should be similar in co-blooming systems, although additional crop-specific aspects (e.g., flower morphology) may further filter species composition. We also expected that managed bees would be the most abundant pollinators in crops that stocked them (i.e., apple, blueberry, watermelon). In Indiana, floral resource availability peaks in the summer months, and more bee species are active at that time (Grundel et al. 2011). Consequently, a greater abundance and diversity of wild bees was expected in summer-blooming crops.

MATERIALS AND METHODS

CROP SYSTEMS

I. Spring-blooming crops

Apple and blueberry production is numerous but relatively small scale in Indiana (e.g., often < 2 ha per farm). There are 304 apple and 139 blueberry farms in the state, totalling 586 and 257 ha of production, respectively (NASS 2017). While apple production is spread throughout the state, blueberries are primarily grown in northern counties (NASS 2017). Michigan is the closest major production hub for both crops, which host diverse and unique pollinator assemblages (Tuell et al. 2009; Gibbs et al. 2016; Nooten et al. 2020). Although both crops are spring-blooming, Indiana apples typically begin to bloom in mid to late April, and selected cultivars for this study bloomed several weeks earlier than blueberries, with an approximately one-week window of overlap between crop bloom in early to mid-May. Both crops are stocked with honey bees at a rate of 1-2 hives/acre (0.4-0.8 hives/ha) for apples and 2-3 hives/acre (0.8-1.2 hives/ha) for blueberries, per crop-specific recommendations (Delaplane & Mayer 2000). Because commercial farms were used for this study, stocking rate varied slightly within each crop (Table 1).

II. Summer-blooming crops

Watermelons and processing tomatoes are the top summer-blooming annual crops produced in Indiana. Indiana ranks third in the country for field tomato production, growing 2,878 ha annually and is among the top five U.S. states for watermelon production, totalling about 2,525 ha annually (NASS 2017). Tomatoes are grown primarily in the northern and central regions of Indiana, while watermelon production is concentrated in the southwestern corner of the state. Watermelons are stocked with honey bees (1 hive/acre) and bumble bees (*Bombus impatiens*) (0.5-1 hive/acre) to supplement pollination (Delaplane & Mayer 2000). The watermelon farms in this study utilised both honey bees and bumble bees, while none of the tomato farms stocked managed bees (Table 1). Both crops have a longer bloom period than the spring perennials; differences in bloom time between tomato varieties extend the bloom period in Indiana from mid-June through late July, and watermelons bloom from mid- to late June through early September.

FARM SELECTION

Pollinator communities were sampled on 22 commercial farms in Indiana in 2022 and 2023. In 2022, we recruited five apple, five blueberry, three tomato and two watermelon farms. In 2023, five farms were recruited for each crop, which entailed resampling all 2022 farms (except for two apple farms that were removed and replaced) and

Table 1. Summary of farm characteristics for each crop. Managed bee stocking rates varied between farms and are reported as a range for each crop. For apples and blueberries, which varied in transect length, we report mean ± standard deviation (SD) of all transects.

Crop	Number of fields sampled (sampling year)	Selected cultivar(s) (sampling year)	Plant age (years)	Managed bee stocking rate (hives/ac)	Mean field size (ha) ± SD	Transect length (m) ± SD
Apple	5 (2022-2023)	Gala (2022), Honeycrisp (2023)	6-20	Honey bees: 1-2	14 ± 9.3	119 ± 15.8
Blueberry	5 (2022-2023)	Blue-Ray (2022-2023)	18-50	Honey bees: 2-3	7 ± 3.0	102 ± 13.8
Tomato	3 (2022), 5 (2023)	TSH-4 (2022-2023)	Annual	None	42 ± 15.8	100
Watermelon	4 (2022), 5 (2023)	Blackjack, Captivation, Fascination (2022-2023)	Annual	Honey bees: 1 Bumble bees: 0.5-1	33 ± 24.2	100

adding 2-3 new farms for tomato and watermelon (Table 1). Apple and blueberry farms were sampled in the same location both years. We selected one field to sample per tomato and watermelon farm, except for 2022, when we selected three fields from one of the watermelon farms due to low farm recruitment. Tomatoes and watermelons are rotated annually with maize and soybeans, hence field locations changed year to year. We use the term "field" throughout the paper to refer to the area in which transects were located, as it is the most inclusive term across different crop types. Each field was ≥ 2.5 km apart, outside of the flight range of most bees, ensuring that pollinator observations were independent (Greenleaf et al. 2007). In total cultivated area, apple and blueberry farms were smaller than fields of tomatoes and watermelons (Table 1). All farms used conventional practices typical for the region (i.e., not organic) and did not alter their management practices with regards to pesticide applications or managed bee stocking rates for the duration of the study. The amount of natural and semi-natural vegetation adjacent to the fields was variable, but generally low. Given the low replication of fields per crop (three to five), analysis of vegetative cover was beyond the scope of this study.

Cultivars selected for study were standardised where possible in each crop (Table 1). In 2022, Gala cv. trees were used for apples; however, in 2023, due to management changes (e.g., tree age and condition, farm participation), we switched to Honeycrisp cv., which has a similar blooming period to Gala. Watermelon cultivars varied between fields but were standardised within each field, and included Blackjack, Captivation, and Fascination.

SAMPLING DESIGN

Two transects were established along crop rows at every field, with one near the margin and one near the centre of the planted area of the selected cultivar, ensuring that sampled areas included both edges and interiors, which can vary in bee visitation (Garibaldi et al. 2011). Transects ran the entire length of the entire crop row (thus maximising the sampled area) for apples and blueberries (Table 1). In tomatoes and watermelons, where crop rows were significantly longer than apples and blueberries, transects were 100 m long and situated such that the middle of the transect fell near the middle of the crop row.

POLLINATOR OBSERVATIONS

Pollinators were observed in each crop system during timed flower observations. These were repeated in each transect on four separate days during crop bloom both years, except for watermelons, for which observations were only performed in 2022. Flower observations were done on days with weather conditions conducive to bee flight (i.e., no rain, temperature ≥10°C, and wind speeds <2.5 m/s) (Vaissière et al. 2011). Efforts were made to sample on non-consecutive days, but for crops with short bloom periods, sampling occasionally occurred on consecutive days due to a lack of appropriate weather on other days (Table S1). In apples, blueberries, and watermelons, flower observations consisted of 3-minute observation periods in a 1×1 m^2 area of flowers. All flowers in the focal area were counted prior to observation. In apples and blueberries, a square area of flowers was selected at the height of the observer's head (1.5-2 m above ground); in watermelons, a square area on the ground was selected. Bees visiting flowers were identified to the lowest possible taxonomic level, which was often genus or tribe. Non-bees (e.g., syrphid flies) were occasionally observed but not recorded. *Apis mellifera* was identified to species and *Bombus* was identified to species when possible. We recorded the identity of individual bees and the number of flowers visited by each bee. To avoid interference with bee behaviour when recording the number of flowers visited, none of the bees were caught. Observations were repeated at five randomly selected trees or bushes per transect, or in the case of watermelon fields, at five locations in 20 m intervals along each transect, totalling two hours of observation at each field in each sampling year.

Due to the relatively low abundance of pollinators in tomatoes compared to other crops (Greenleaf & Kremen 2006; Winfree et al. 2008), observations in tomatoes consisted of timed transect walks, to cover a greater area during each observation period and avoid excessive zeroes in the dataset. Prior to observation, flowers were counted on five random plants, averaged, and multiplied by the number of plants per transect to obtain an estimate of flowers per observed area. Each transect was walked at a constant pace in one direction for 15 minutes each sampling day to observe and record pollinator identity, totalling two hours of observation at each field during each sampling year. The number of sampling hours were held consistent in each system, allowing us to calculate bee visitation rates similarly for each crop. Increasing the sampled area in tomatoes allowed us to detect more individual bees and accurately describe the bee community.

PAN TRAPS

Pollinators were caught in each crop system in both 2022 and 2023 for species-level identification using pan traps. Each pan trap array consisted of one white, one blue, and one yellow plastic bowl (355 ml) attached to a wooden stake and filled to just below the rim with a solution of water and dish soap. The three different pan trap colours attract more diverse pollinator communities, and attractiveness of different bowl colours changes throughout the growing season (Heneberg & Bogusch 2014; Nooten et al. 2020). Arrays were placed at the height of crop flowers (Fig. S1). Six pan trap arrays were deployed for a period of 24 hours twice per field each year during crop bloom. Pan traps were placed along both transects (three arrays each), with an array located at the middle of the transect and one at each end. After 24 hours, all bees in each bowl were transferred to vials containing 70% ethanol.

Specimens were processed, pinned, and identified. All non-bee bycatch was either discarded or pinned and left unidentified. Bees were identified to species when possible, using Discover Life (Ascher & Pickering, 2020) and Mike Arduser's online keys to bees of the Tallgrass Prairie Region (2020). Specimens for which species-level identification was difficult (e.g., *Nomada* spp., *Lasioglossum (Dialictus)* spp.) were left at the genus or subgenus level. A subsample of specimens is vouchered in the Purdue Entomological Research Collection.

DATA ANALYSIS

Analysis and data visualisation were performed in R version 4.3.0 (R Core Team, 2023) with packages 'vegan' (Oksanen et al., 2022), 'pairwiseAdonis' (Arbizu, 2017), and 'ggplot2' (Wickham, 2016). Flower visitation rates, richness, and diversity were qualitatively compared between crops. Visitation rates (bee visits/crop flower/hour) were calculated by dividing the total number of flower visits during an observation period by the number of flowers in the observed area. These values were multiplied by 20 in apples, blueberries, and watermelons and by 4 in tomatoes to obtain an estimate of visits/flower/hour (3-minute observation period × 20 = 1 hour; 15-minute observation period × 4 = 1 hour). Visitation rates were averaged within each crop across both years of data collection. Inverse Simpson's indices were calculated using pan trap data from each crop as a measure of diversity. Pollinator community composition from pan traps and flower observations was visualised with stacked bar charts, allowing for qualitative comparisons of taxa identity and proportions between crop systems and sampling methods. For these comparisons, pan trap data were simplified to genus to match flower observations. Since bees from the tribe Augochlorini could not reliably be identified to genus in the field, pan trap records for these genera were simplified to tribe.

Pollinator community composition was visualised in each crop and year with an NMDS (non-metric multidimensional scaling) ordination using a Bray-Curtis dissimilarity index of pan trap specimens identified to species or subgenus. Species counts from pan traps were averaged between sampling dates within a year at each field prior to analysis, allowing for comparisons between fields despite unequal sampling effort. Counts were also log-transformed to control for overabundance of several taxa.

Pollinator communities were quantitatively compared between crops using PERMANOVA analysis of the pan trap specimens; the response variable was a Bray-Curtis dissimilarity index of taxa with crop type, year, and their interaction included as fixed effects. To account for the potential influence of geographical variation on pollinator communities, we partitioned our fields based on three latitudinal tiers (lower, middle, upper) in Indiana, as defined by Jean, 2010. Due to the highly localized nature of watermelon production in the state, this crop type was confounded with latitudinal tier; all watermelon farms were located in the lower tier, where no other farms were located. Thus, we were unable to test the effect of latitudinal tier vs. crop type for watermelons. Latitudinal tier was included as a fixed effect in a separate model excluding watermelons, and the results of the PERMANOVA including watermelons (but lacking latitudinal tier) are interpreted with caution. Limitations of the pairwise.adonis function used for analysis precluded the inclusion of random effects. SIMPER analysis was used to describe which taxa were the main contributors to differences between crop pollinator communities.

RESULTS

In total, 1,651 bees from 13 taxa were observed visiting flowers and 1,967 bees from 84 taxa were caught in pan traps across the two years of sampling. Dominant taxa in flower observations and pan traps varied between crop systems and sampling methods. Only three taxa were detected in pan traps for all four crops: *A. mellifera*, *L. (Dialictus)* spp., and *Augochlorella aurata* (Fig. 1; Table S2). Based on pan trap data, the spring blooming crops were far more taxa rich than summer blooming crops, with an average of 43 and 21 taxa, respectively (Fig. 1). Bee diversity in apples was approximately twice as high as that of watermelons and blueberries, and four times higher than in tomatoes (Table 2). Visitation rate was highly variable between crop systems. Watermelons had the highest visitation rate, over three times as high as apples and seven times higher than blueberries, while tomato visitation rates were over 100 times lower than any other crop (Table 2).

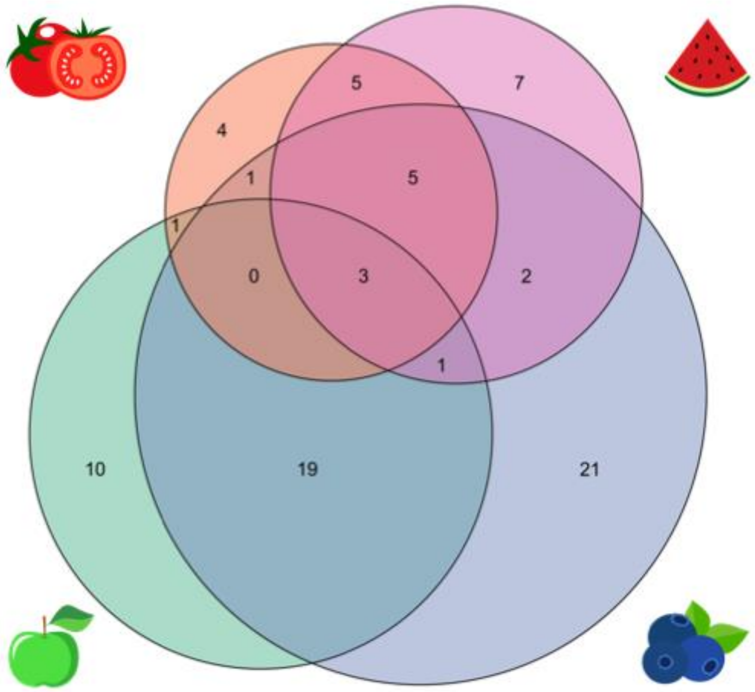

Figure 1. Venn diagram describing similarities in taxa caught in pan traps between each crop community. Numbers reflect the number of species found exclusively in the crop system(s) corresponding to the area of overlap across both sampling years, 2022 and 2023.

Table 2. Wild bee, managed bee, and overall average bee visitation rate (visits/flower/hour), species richness, and Simpson's inverse diversity in crop systems. Visitation rates are calculated from flower observations, while species richness and diversity are based on specimens caught in pan traps.

Crop	Wild bee visitation rate ± SE	Managed bee visitation rate ± SE	Average bee visitation rate ± SE	Species richness	Diversity
Apple	0.3 ± 0.03	0.8 ± 0.07	1.1 ± 0.07	34	8.00
Blueberry	0.2 ± 0.02	0.3 ± 0.02	0.5 ± 0.03	51	4.11
Tomato	0.0030 ± 0.00050	0.0001 ± 0.00010	0.0030 ± 0.00050	19	2.32
Watermelon	2.7 ± 0.3	1.1 ± 0.25	3.7 ± 0.39	22	4.24

SPRING BLOOMING CROPS

In apples and blueberries, flower observations resulted in pollinator communities that were similar at the genus/tribe level. Overall, 600 flower visits were observed in apples, while 496 were observed in blueberries. Honey bees were the most common visitor in both crops, accounting for 70% of visits (Fig. 2). The most abundant wild bee was *Andrena*, which contributed 20% of visits in apples and 10% in blueberries.

More specimens were caught in blueberry pan traps (*N = 705*) than in apple pan traps (*N = 306*) (Fig. 2, Table S2). Honey bees constituted a far lower proportion of the total sample in pan traps compared to observations for both crops (only 4% in apples and 17% in blueberries) (Fig. 2). *Andrena* were overrepresented in the apple pan traps, accounting for 87% of the specimens. *Lasioglossum* were overrepresented in blueberry pan traps, accounting for 49% of the specimens (Fig. 2).

Pan trap communities showed little similarity at both the genus/tribe and subgenus/species levels for apples and blueberries (Figs. 2 and 3). PERMANOVA analysis found that apple and blueberry pollinator communities were significantly different in pan trap samples and communities also differed by sampling year, but not latitudinal tier (Table 3). SIMPER analysis of pan trap data found that *L. (Dialictus)* spp. were important for differentiating the crop bee communities, contributing to 18% of the difference between apples and blueberries (Table S3).

SUMMER BLOOMING CROPS

In tomatoes and watermelons, flower observations resulted in pollinator communities that were distinct at the genus/tribe level. In tomatoes, a total of 88 individual flower visits were recorded across two years, and in only one year of observation in watermelon, 136 visits were recorded. *Bombus* spp. were the dominant pollinators in tomatoes, responsible for 62% of flower visits (Fig. 2). *Bombus griseocollis* was particularly abundant, accounting for 49% of all flower visits (Table S4). In watermelons, *Lasioglossum* spp. were the most numerous, comprising 65% of visits while managed honey

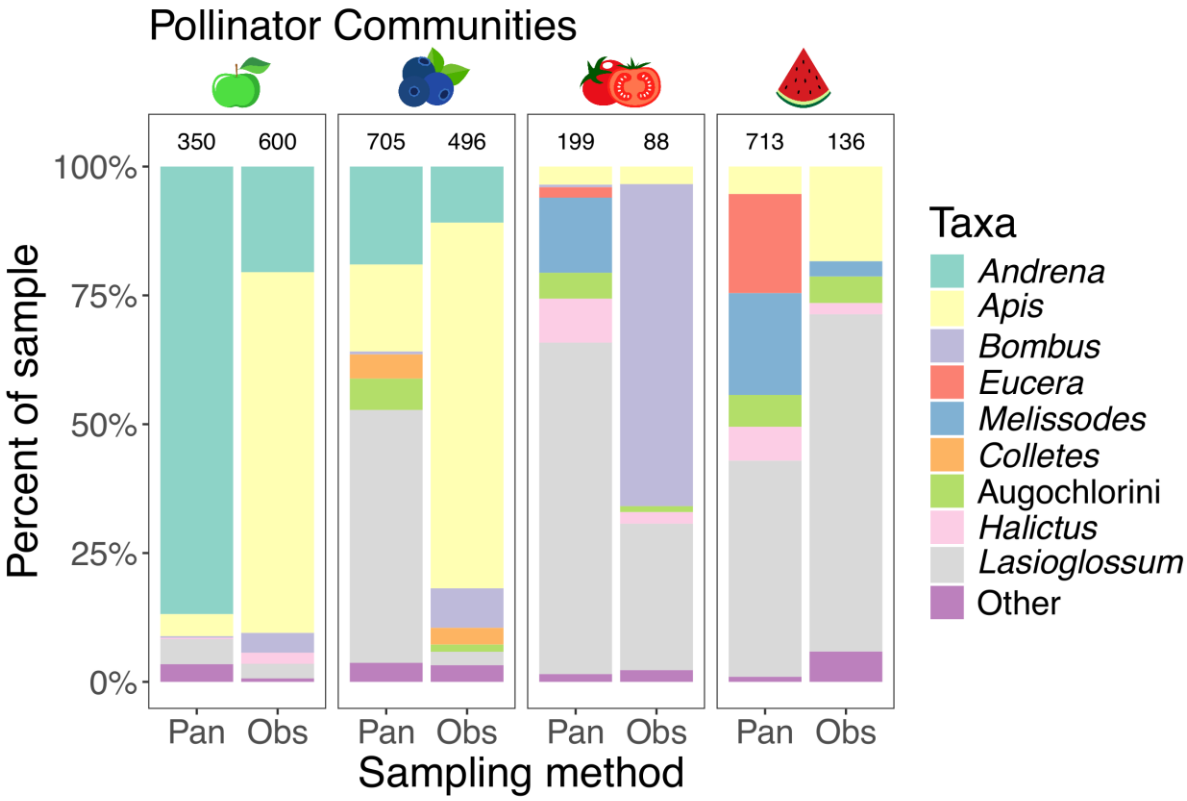

Figure 2. Relative proportions of taxa caught in pan traps (Pan) and observed visiting flowers (Obs) for each crop type, combined across sampling years. Numbers above bars refer to the number of specimens caught/observed in that crop system with each method. Taxa that contributed <1% of the sample for each crop are grouped and classified as "Other".

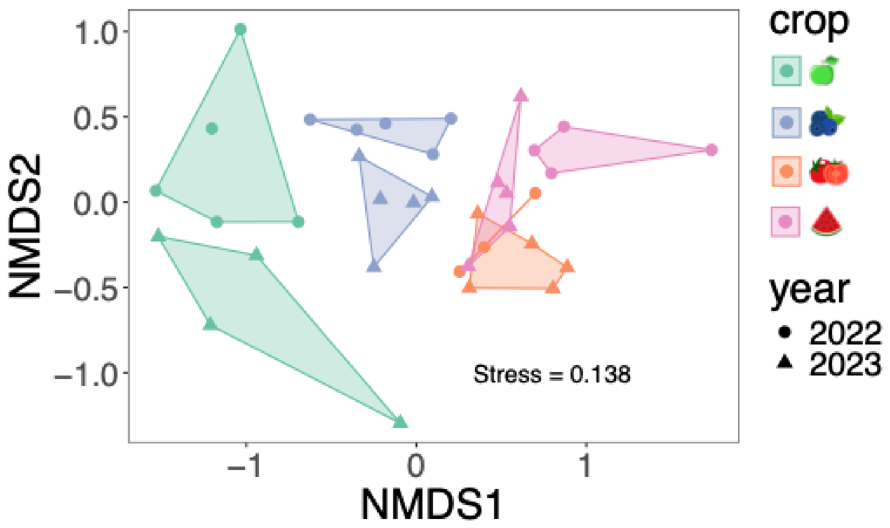

Figure 3. An ordination of pan trap data reflects trends in crop pollinator communities at the species level, showing differences in pollinator communities between crop systems and sampling years. Each data point represents the pollinator community at an individual farm for a given sampling year.

bees and bumble bees were responsible for 18% and 1% of visits, respectively (Fig. 2).

Tomato pan traps yielded 199 specimens, and 713 specimens were caught in watermelon (Fig. 2, Table S2). *Lasioglossum* spp. were the most abundant specimens in both crops (64% of specimens in tomatoes and 42% in watermelons) (Fig. 2). Several pronounced differences in pollinator communities occurred between sampling methods in the same crop system. In tomatoes, *Melissodes* spp. comprised 15% of specimens in pan traps but were not observed visiting flowers; conversely, *Bombus* were underrepresented in the tomato pan traps (only 1% of specimens), despite comprising a majority of flower visits (Fig. 2). In watermelon pan traps, *Melissodes* spp. and *Eucera (Peponapis) pruinosa* were more abundant than in flower observations (20% and 19% of specimens, respectively), while honey bees were less abundant (5% of specimens) (Fig. 2).

Pan trap samples were more similar between tomatoes and watermelons at the genus/tribe level than flower observations and overlapped to some extent at the species/subgenus level on the NMDS ordination (Figs. 2 & 3). However, PERMANOVA analysis found that tomato and watermelon pollinator communities sampled in pan traps were significantly different (Table 3). SIMPER analysis of pan trap data indicated that *M. bimaculatus* and *L. (Dialictus)* spp. were important for differentiating the crops, each contributing to 15% of the difference between tomato and watermelon fields (Fig. S3).

DISCUSSION

Indiana specialty crops host unique assemblages of wild and managed pollinators, which vary across cropping systems, throughout the growing season, and between sampling methods. Spring communities were dominated by honey bees and early-flying wild taxa, while summer-blooming crops had a larger proportion of visits attributed to wild bees. Interestingly, these seasonal crop abundance patterns were the opposite from pollinator diversity, i.e., summer crops had substantially lower diversity of wild bees compared to spring crops.

FLOWER OBSERVATIONS

The highly variable flower visitation rate across crop systems was due to differences in both floral densities and the abundance of pollinators, both managed and wild. While the largest number of flower visits were recorded in apples and blueberries, both crops had lower visitation rates than watermelons because of their higher floral densities, which averaged 106 and 201 flowers/m^2 in apples and blueberries, respectively, compared to 8 flowers/m^2 in watermelons. A combination of high floral densities (12,427 flowers/100 m) and low pollinator abundance in tomatoes resulted in a very low visitation rate. Comparing our results to the suggested visitation rates in a review of pollination requirements for each crop, Garibaldi et al. (2020) showed differences across crops in pollination thresholds. In Indiana apples (110 visits/100 flowers/hour) and watermelons (370

Table 3. Results of PERMANOVA pairwise tests between crop pollinator communities, based on specimens caught in pan traps in 2022 and 2023. Comparisons between watermelons and other crops are from a model excluding latitudinal tier.

Comparison	Explanatory variable	df	Sum of squares	F	R^2	p
Apple x Blueberry	crop	1	1.318	7.000	0.26	< 0.001
	year	1	0.630	3.348	0.123	0.003
	crop:year	1	0.239	1.271	0.047	0.232
	latitude tier	1	0.312	1.658	0.061	0.103
	Residual	14	2.635		0.513	
	Total	18	5.134		1.000	
Apple x Tomato	crop	1	2.130	10.105	0.389	< 0.001
	year	1	0.366	1.736	0.067	0.111
	crop:year	1	0.198	0.939	0.036	0.402
	latitude tier	1	0.239	1.136	0.044	0.290
	Residual	12	2.530		0.463	
	Total	16	5.464		1.000	
Apple x Watermelon	crop	1	2.241	11.486	0.390	< 0.001
	year	1	0.504	2.584	0.088	0.031
	crop:year	1	0.274	1.405	0.048	0.182
	Residual	14	2.731		0.475	
	Total	17	5.750		1.000	
Blueberry x Tomato	crop	1	1.071	7.148	0.295	< 0.001
	year	1	0.332	2.221	0.091	0.036
	crop:year	1	0.160	1.067	0.044	0.362
	latitude tier	1	0.124	0.827	0.034	0.587
	Residual	13	1.947		0.536	
	Total	17	3.634		1.000	
Blueberry x Watermelon	crop	1	1.193	8.604	0.301	< 0.001
	year	1	0.502	3.624	0.127	0.003
	crop:year	1	0.186	1.340	0.047	0.199
	Residual	15	2.080		0.525	
	Total	18	3.961		1.000	
Tomato x Watermelon	crop	1	0.531	3.705	0.187	0.003
	year	1	0.219	1.525	0.077	0.154
	crop:year	1	0.228	1.590	0.080	0.139
	Residual	13	1.864		0.656	
	Total	16	2.842		1.000	

visits/100 flowers/hour), our visitation rates fell above those suggested for adequate pollination (55 visits/100 flowers/hour and 64-96 visits/100 flowers/hour, respectively). Blueberry visitation rates (50 visits/100 flowers/hour) fell towards the middle of the estimated requirements, which ranged from 8-160 visits/100 flowers/hour. Tomatoes had a much lower visitation rate (0.3 visits/100 flowers/hour) compared to the recommended 10 visits/100 flowers/hour (Garibaldi et al. 2020), indicating they may be receiving inadequate pollination. Target values are based on greenhouse tomato studies and may be unrealistic for a field tomato setting. However, our preliminary data suggest that supplemental pollination improves fruit set and weight of field-grown tomatoes, lending support to indications of pollen limitation (Stroh et al., unpublished data). These results indicate that some Indiana specialty crops receive inadequate pollination as a result of low pollinator visitation.

Although visitation data offer lower taxonomic resolution than pan trap data, crop-specific differences still emerged. Both spring-blooming crops were dominated by honey bees, which are often the most abundant pollinator in other apple and blueberry production regions (Watson et al. 2011; Gibbs et al. 2016; Reilly et al. 2020). Given the use of commercial hives, their dominance is best explained by the sheer abundance of honey bees present in the area during bloom. Indiana blueberry pollinator communities exhibited honey bee dominance at levels similar to studies in other homogenous, intensively managed landscapes (Eeraerts et al. 2023). Studies also identify *Andrena*, along with *Bombus* and *Lasioglossum* as important wild taxa for apple and blueberry pollination, which aligns with the results of our study (Watson et al. 2011; Nooten et al. 2020; Kline et al. 2023; Eeraerts et al. 2023). Some Midwestern studies also note the presence of Ericaceae specialists in blueberries (e.g., *Andrena carolina*, *Colletes validus*) (Tuell et al. 2009), both of which were present exclusively in blueberry systems in our study, indicating that specialist species persist even in small production regions.

The suite of flower visitors markedly shifted in the summer-blooming crops, with a higher proportion of visits performed by wild bees than honey bees in both tomatoes and watermelons, even though watermelons were stocked with managed pollinators. Several studies have described watermelon pollinator communities in Indiana, identifying *Melissodes* and *Lasioglossum* as the most abundant wild bee genera (Bloom et al. 2021; Pecenka et al. 2021; Leach & Kaplan 2022), while in Florida and California, a greater portion of flower visits are attributed to honey bees (Campbell et al. 2019; Reilly et al. 2020). In our study, we found that *Lasioglossum* spp. performed more flower visits than honey bees, and while *Melissodes* spp. were abundant in pan traps, they only performed about 3% of flower visits in watermelons. Despite stocking with bumble bees and honey bees, it appears that wild bees are important pollinators for Indiana watermelons.

The dominance of *Lasioglossum* spp. and *Melissodes* spp. in watermelon is striking, given that the annual nature of watermelon production necessitates regular tillage. *Lasioglossum* and *Melissodes* are predominantly ground-nesting genera. Although deep tillage can negatively impact ground-nesting species (Ullmann et al. 2016), other factors including distance from field edges and soil characteristics may be more consequential for occurrence of ground-nesting taxa (Tschanz et al. 2023). Other studies have demonstrated that the ground nesting bees found in our study, including *Lasioglossum* spp. and *Eucera pruinosa,* are able to persist in highly disturbed agricultural landscapes (Julier & Roulston 2009; Kratschmer et al. 2018). Our results concur that ground nesting taxa can be found even in environments with regular soil disturbance.

Tomatoes exhibited a contrasting community of flower visitors, dominated by *Bombus* spp. Tomato pollinator records in the US are limited, especially outdoors (i.e., non-greenhouse production) and within large monoculture fields (e.g., processing tomatoes), for which there are virtually no data published. Available information suggests that wild bees, particularly large-bodied taxa like *Bombus* provide the majority of pollination services to fresh market tomatoes on small, diversified farms in Pennsylvania and California, while managed honey bees contribute little (Greenleaf & Kremen 2006; Winfree et al. 2008). In our study, flower visits were heavily dominated by the species *B. griseocollis* (Table S4). Visitation by *Bombus* spp. and other wild taxa is particularly important for tomatoes because of the ability of these species to buzz pollinate, a behaviour that dislodges pollen grains and increases pollination success in plants like tomatoes that have poricidal anthers (King & Buchmann 2003). Recent climate and population modelling suggests that Indiana may be at risk of decline or loss of several tomato-pollinating species, including *Bombus* spp. and other buzz pollinating taxa (Carrasco et al. 2021). In this context, description of current Indiana tomato pollinator communities is crucial to monitoring future declines.

PAN TRAPS

Differences in pollinator communities between sampling methods within each crop reveal strong biases in pan trap samples towards smaller-bodied bees, a phenomenon that is well-documented (Roulston et al. 2007; Prendergast et al. 2020). This bias is attributed to the fact that larger-bodied bees are more likely to escape the traps without drowning. Although most visits to apple and blueberry flowers were performed by honey bees, pan trap samples for these crops were dominated by smaller-bodied *Andrena* spp. and *Lasioglossum* spp., respectively. *Lasioglossum* spp. were also the most abundant taxa in pan traps for summer-blooming crops. Other studies report high numbers of *Lasioglossum* spp. in pan traps (Tuell et al. 2009; Nooten et al. 2020; Boyer et al. 2020), and in the context of our study, the lack of taxonomic resolution in the subgenus *L. Dialictus* likely influenced the results of subsequent analyses. *Lasioglossum (Dialictus)* spp. specimens were treated as the same "species" in PERMANOVA and SIMPER analyses, and as a result, some of the true species diversity in each system is obscured. The bias in pan traps underscores the need for using diverse sampling techniques when describing pollinator communities.

COMPARING POLLINATOR COMMUNITIES

Despite the isolation of specialty crops within a homogenous, maize and soybean-dominated landscape, unique communities of wild bees were present in all crops. PERMANOVA analyses indicated that pollinator communities were significantly different in each crop system, and there was no latitudinal effect on bee communities for the crops where we were able to test for it. The fact that watermelon farms and the lower latitudinal tier were confounded presented a limitation for interpreting the impact of crop type versus geographic location. Additionally, although apple and tomato farms were spread across two latitudinal tiers, all of the blueberry farms were located in the top latitudinal tier. Despite the confounding effect of latitude, the SIMPER analysis indicated that the top three wild taxa for differentiating watermelon farms from co-blooming tomatoes were *M. bimaculatus*, *Lasioglossum (Dialictus)* spp., and *E. pruinosa*, while the top three taxa for differentiating blueberries from apples were *Lasioglossum (Dialictus)* spp., *Andrena imitatrix*, and *A. perplexa*. All of these taxa are widespread in Indiana, with a distribution throughout the entire state (Jean, 2010). Thus, the effect of geographical location, particularly concerning the most abundant pollinators in these crops, may be negligible.

Pollinator communities also differed between years in pairwise comparisons. Temporal separation in bloom time plays a role in shaping the composition of pollinator communities on a landscape, acting as a selective filter to determine which species are available to pollinate a crop (Ogilvie & Forrest 2017). Interannual differences between pollinator communities in the same crop fit with a general trend of interannual variability in bee communities (Williams et al. 2001), and may also be related to slight differences in bloom time and/or duration (Lázaro et al. 2010; Ogilvie et al. 2017). In the spring-blooming crops, the primary contributor to differences between pan trap communities was a higher abundance of *L. (Dialictus)* spp. in blueberries, a subgenus that peaks in abundance later in the season than the early-flying *Andrena* spp. that dominated apple pan traps (Grundel et al. 2011). Not all taxa are restricted by short activity periods; *Bombus* spp., which are active from early spring through autumn, were observed in all crop systems—queens foraged early in the year on apples and blueberries, and workers later in the summer on watermelons and tomatoes.

Additionally, crop-specific factors likely drive differentiation in pollinator communities between co-flowering crops. Differences in bee communities from flower observations in tomatoes and watermelons could be partly attributed to flower morphology; bumble bees were able to utilize tomato flowers as a pollen sources because of their ability to buzz pollinate, extracting pollen that may be inaccessible to other taxa (King & Buchmann 2003). The open structure of watermelon flowers, combined with the additional attractiveness of a nectar reward, could have contributed to the higher incidence of small-bodied bees (e.g., *Lasioglossum* spp.) observed visiting those flowers. *M. bimaculatus* and *L.(Dialictus)* spp. were important for differentiating tomato and watermelon pollinator communities in our study, and although they were both found in tomato pan traps, neither taxon was observed buzz pollinating tomato flowers. Even if these bees are present in the area (thus appearing in pan traps to some extent), they may not be capable of easily accessing pollen in tomato flowers, and subsequently less likely to visit them.

CONCLUSION

These results indicate that distinct pollinator communities persist among co-flowering crops produced in a landscape dominated by field crop production, emphasizing the role that phenology and other crop-specific factors play in shaping pollinator communities even for small-scale or isolated specialty crop production. Our results indicate that Indiana apples and blueberries are reliant on honey bees for the majority of flower visits, but also host a diverse community of wild bees that contribute up to 30% of all flower visits. Wild bees additionally comprise over 80% of flower visits to watermelons and tomatoes. Given that some wild pollinators are more effective than honey bees on a per-visit basis (Rader et al. 2016; Page et al. 2021), the value of these taxa is potentially even higher, justifying a growing call among pollination researchers to consider the wellbeing of wild bees in crop management decisions (Pecenka et al. 2021; Lundin et al. 2021; Leach et al. 2022). Regionally specific information about pollinator community composition is valuable to specialty crop growers seeking to evaluate or improve pollination services. For growers wishing to bolster pollination from wild bees, knowing which taxa are most abundant in their crop system and region facilitates management decisions informed by the life history of the taxa in question.

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AUTHOR CONTRIBUTION

Concept and design IL, AL, & ES, data collection ES & ZMF, data analysis ES, writing ES, edits and approval for publication IK, AL, ZMF, & ES.

DISCLOSURE STATEMENT

No potential conflict of interest was reported by the authors.

DATA AVAILABILITY STATEMENT

The data used to write this article are available online via the Purdue University Research Repository: https://purr.purdue.edu/publications/4597/1

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix I. Photograph of pan trap setup.

Appendix II. Flower observation dates.

Appendix III. List of taxa caught in pan traps.

Appendix IV. Results of SIMPER analysis.

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