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Pollinator Ecology and Management

Native Flowering Border Crops Attract High Pollinator Abundance and Diversity, Providing Growers the Opportunity to Enhance Pollination Services

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Abstract

Over the past century, habitat loss from agricultural intensification has contributed to pollinator decline. One way to mitigate the harmful effects of agricultural intensification is through the re-introduction of native flowering plants as border strips that provide supplemental floral and nesting resources to pollinators. However, border crop species vary in bloom period and flower densities, and are thus likely to attract different suites of pollinator species. Resulting differences in pollinator community composition are likely to affect their ability to provide pollination services to adjacent crop habitat. To address these issues, we implemented a two-year study on the impact of different flowering border crops on pollinator abundance, richness, and community composition. We also examined which crop features (bloom duration, number of flowers, floral area) were most likely to affect pollinator densities. We found that native flowering plant border crops of diverse prairie mix and monocultures of silflower (*Silphium integrifolium* Michx.) and cup plant (*Silphium perfoliatum* L.) attracted the highest abundance and species richness of bees and pollinator groups combined, while alfalfa (*Medicago sativa* L.) attracted the highest lepidopteran abundance and species richness. We also found a significant, positive relationship between pollinator abundance and floral resource amount and bloom duration. These findings offer valuable insight into the impacts of different land management strategies on different pollinator groups, and thus provide landowners with management options for attracting specific pollinator groups and species.

Key words: border crop, hedgerow, pollinator, sustainable agriculture, floral resource

Some land management practices are eliminating natural habitat, imperiling native insect pollinators and their ecosystem services (Cardoso et al. 2020). Agricultural expansion is currently the main component of land use change, increasing the amount of homogenized land and arthropod habitat loss (Kremen et al. 2002, Williams et al. 2010, Calderone 2012, Lark et al. 2015). Greater chemical input, physical disturbances, and loss in plant biodiversity have all contributed to biodiversity declines, particularly of beneficial insects such as wild pollinators (Cardoso et al. 2020). With thirty percent of the world's food supply relying on pollination services (Klein et al. 2007), it is clear that new and sustainable agricultural practices need to be implemented to support beneficial insects, and maintain important ecosystem services such as pest control, pollination, and decomposition.

The introduction of noncrop perennial plant species in heavily farmed areas can mitigate landscape homogenization resulting from agricultural practices, and can provide an environment in which landowners can benefit from ecosystem services (Bianchi et al. 2006). One way to integrate these plant species more seamlessly into current land use is through their implementation on marginal cropland, such as grass waterways and buffer regions that are unfit for cultivation. These noncrop plantings, also called border crops, hedgerows, buffer strips, or crop strips, diversify landscapes and can provide semi-natural and relatively undisturbed habitat in heavily farmed landscapes. Flowering border strips can provide floral resources to beneficial insects when native sources are scarce, or when the primary crop is not in bloom (Winfree et al. 2007). Border crops have the potential to provide a plethora of additional benefits, such as increasing soil health, reducing erosion and runoff, and providing a secondary crop with minimal cost to yields (Pywell et al. 2015).

The addition of perennial border crops can provide supplementary food and nesting resources year-round for beneficial insects such as pollinators and natural enemies (Winfree et al. 2007). This can reduce pest damage and improve yields in adjacent crop fields through the spillover of ecosystem services such as pollination and pest predation (Bianchi et al. 2006, Kim et al. 2006, Wratten et al. 2012). When given ample natural habitat near farming operations, native pollinators can provide up to 100% of pollination services for crop fields (Klein et al. 2007, Winfree et al. 2007, Blaauw and Isaacs 2014), and can even improve the fruit set of crops that are able to self-pollinate (Klein et al. 2003). Because providing highly diverse flowering strips can further increase pollination and biocontrol services within adjacent field crops, implementing border crops that are different from the main crop and provide floral resources may be an effective way to support a diverse set of beneficial insects (as reviewed by Albrecht et al. 2020).

Despite the potential benefits, many farmers are reluctant to plant border crops from fears of economic loss and a general lack of knowledge (Morandin and Kremen 2013). Not only do natural border crops require upfront costs from the landowner, but in some cases the landowner may wait for a number of years until the border crops establish to begin receiving benefits that 'pay back' the cost of implementation (Morandin et al. 2016). Also, if the border crop or hedgerow is planted in a polyculture, such as the standard prairie mix offered by the Natural Resources and Conservation Service (NRCS), they can be difficult to harvest and may be ineffective as a livestock forage crop or highly variable in forage quality (Jefferson et al. 2004, Willand and Baer 2019). Therefore, selecting border crops that provide direct benefits to farmers, such as secondary forage and grain crops, or low-maintenance plantings such as perennial mixes, may encourage the adoption of this conservation practice. Perennial border crops that establish quickly, and are effective in pollinator attraction as a single species, rather than in a polyculture planting, would be highly desirable as well, as they would better fit traditional farming equipment and management practices and may therefore encourage implementation.

Determining the ability of border crops to support pollinators is imperative to taking the next step towards a more healthy and diverse agricultural landscape, as this equips growers and conservationists with information on practices that can serve both farming and conservation interests. Implementing crops that can utilize marginal land, provide a secondary harvest, and support native insect biodiversity could help offset the negative effects of intensified agriculture, leading to more effective and sustainable agricultural practices.

In this study, our objectives were to 1) measure the ability of flowering, perennial, border crops to attract and support a high species richness and abundance of pollinators, and 2) determine how different groups of pollinators (wild bees vs. lepidopterans) respond to the different border crop types. We investigated six candidate border crops to determine which is most likely to attract and support the highest abundance and diversity of pollinators: 1) a diverse prairie mix (see Supp Table 1 [online only]), 2) alfalfa (*Medicago sativa* (L., Fabales: Fabaceae)), 3) sainfoin (*Onobrychis viciifolia* (Scop., Fabales: Fabaceae)), 4) cup plant (*Silphium perfoliatum* (L., Asterales: Asteraceae)), 5) silflower (*Silphium integrifolium* (Michx.)), and 6) Kernza (*Thinopyrum intermedium* (Host., Barkworth and D.R. Dewey, Poales: Poaceae)). We hypothesized that border crops containing the most diverse and long-lasting floral resources would attract the most abundant and diverse set of pollinator species (Potts et al. 2003). Therefore, we predicted that the native prairie mix (native to the location of our study: Kansas, USA) would perform the best overall, as this mix contains nine different native prairie species with an array of bloom times, resulting in this mix having a long bloom period.

We hypothesized that native planting treatments including the prairie mix treatment and the two sunflower treatments (cup plant and silflower) would attract the highest abundance and diversity of bees, as there are several bee species in Kansas, USA, that have long evolutionary histories with these flowering plants, with some being sunflower obligates (Parker 1981, Mallinger et al. 2018). We also expected Kernza, a wind-pollinated small grain species, to attract the least pollinator abundance and diversity.

Methods

Site Description and Plot Design

We conducted the experiment at The Land Institute located in Salina, Kansas, USA (38°46′6.3″N 97°33′58.9″W). The Land Institute is a nonprofit research organization with the mission of advancing perennial and biologically diverse cropping systems. Most of the surrounding landscape is typical of central Kansas, consisting of alfalfa, wheat, and pasture fields, with natural surrounding areas consisting of woodlands and native prairie. This makes it an ideal research area for testing new crops in an agricultural landscape (see Fig. 1).

During a two-year study, we conducted pollinator observations and measured floral resources among six different candidate border crops that provide a range of possible benefits to growers including nitrogen fixation, fodder, and biofuel (Table 1). The border crops tested were alfalfa, sainfoin, cup plant, silflower, Kernza, and a pollinator prairie mix which included three grass species (*Andropogon gerardi* (Vitman, Poales: Poacea); *Schizachyrium scoparium* (Michx., Poales: Poaceae); *Sporobolus aspera* (Hack., Poales: Poaceae), two legume species (*Dalea purpurea* (Vent., Fabales: Fabaceae); *Senna marliandica* (L., Fabales: Fabaceae)) and four forb species (*Salvia azurea* (Michx ex Lam., Lamiales: Lamiaceae); *Helianthus maximiliani* (Schrad., Asterales: Asteraceae); *Artemisia ludoviciana* (Nutt., Asterales: Asteraceae); *Liatris punctate* (Hook., Asterales: Asteraceae); see Supp Table 1 [online only] for more information). While peak flower densities are expected to vary by crop treatment, the presence of flowers generally overlap throughout the season (USA National Phenology Network 2021).

We established four study sites in 2018, with each site 1–2 km apart. Each site contained six 5.5 m × 5.5 m plots, each representing one of the six different crop treatments. This design resulted in a total of 24 sampling plots (four sites × six treatments). Plot placement was randomized to ensure early-blooming treatments and late-blooming treatments would not be planted adjacent to one another to maximize physical separation between plots flowering at the same time. Plots within a site were separated by a minimum 10 m wide border of tall fescue grass (*Festuca arundinacea* Schreber, Poales: Poaceae), which was mowed bi-weekly.

Silflower, cup plant, and prairie species were started from seed in Jiffy peat pellets within a greenhouse for at least eight weeks before transplant. Thirty-six seedlings each of silflower and cup plant were transplanted into each of their respective treatment plots, spaced 91 cm apart from each other, on 15 September 2018. Sixteen seedlings of each prairie species were transplanted into each prairie plot, spaced 46 cm apart from each other on 19 April 2019. The arrangement of prairie species within each plot was prerandomized. Alfalfa, sainfoin, and Kernza were planted as normal row crops on 20 September 2018, with 18 cm between rows within a plot. Seeding rates were 9 kg/ha for alfalfa, 14 kg/ha for sainfoin, and 11 kg/ha for Kernza. No herbicides, pesticides, or fertilizers were applied to the plots for the duration of the study. Weeds were managed by mowing plot perimeters

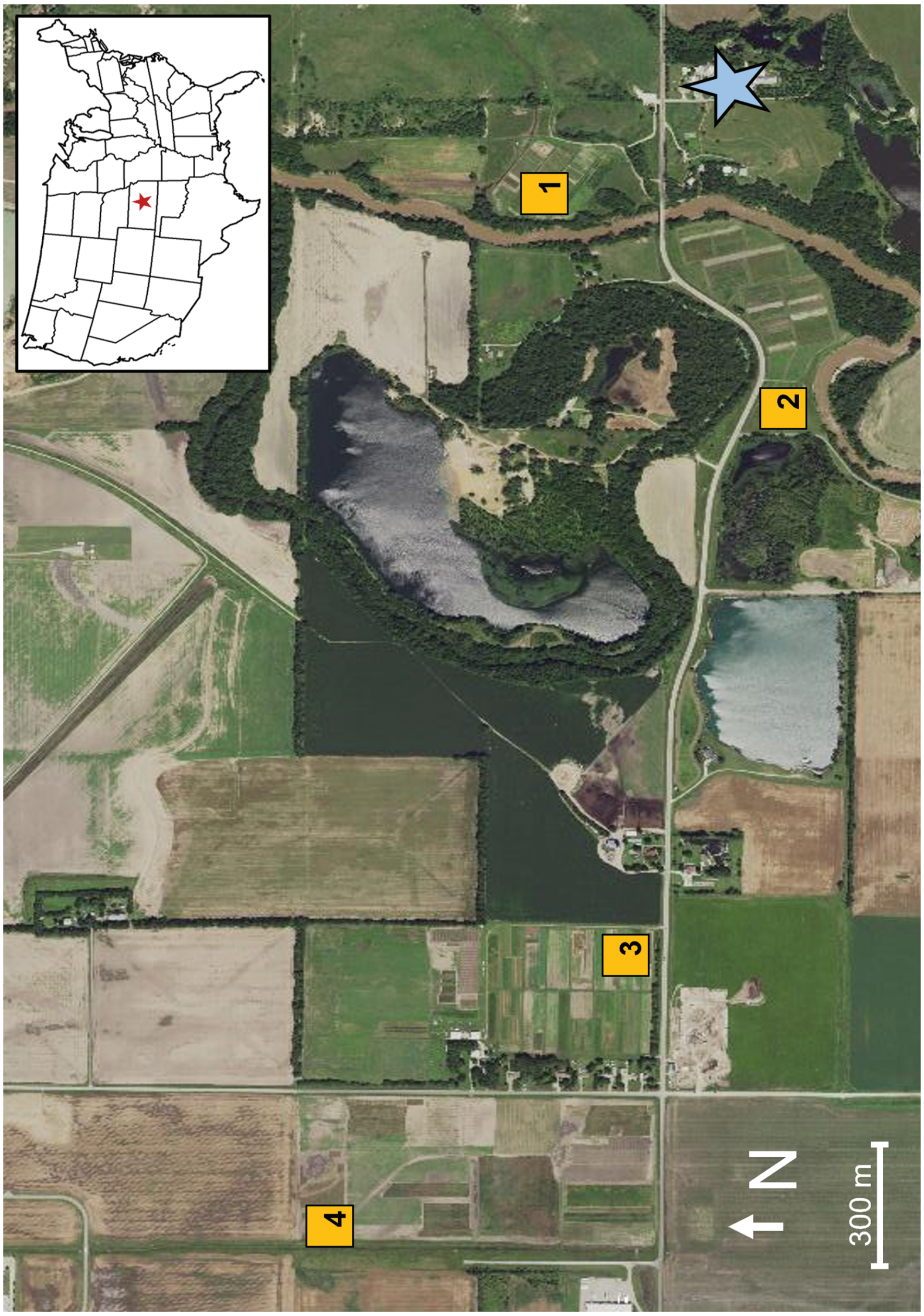

Fig. 1. A satellite image of The Land Institute near Salina, KS. The research facility is indicated by the star. Numbered boxes indicate the four site locations.

Table 1. Ecological characteristics of the six candidate border crops. References for crop benefits are listed below table

Border Crop	Scientific Name	Functional Group	Benefits	Planting Practice	Bloom Period
Alfalfa	*Medicago sativa*	Legume	• Nitrogen-fixing[a] • Fodder[a]	Monoculture	May–July[i]
Sainfoin	*Onobrychis viciifolia*	Legume	• Nitrogen-fixing • Anti-bloat fodder[b] • Harvested after flowering[c]	Monoculture	May–July[j]
Cup Plant	*Silphium perfoliatum*	Native aster	• Flood and freeze resistant[d] • Fodder[d] • Biofuel[e] • Oilseed	Monoculture	July–Sept.[k]
Silflower	*Silphium integrifolium*	Native aster	• Drought tolerant[f] • Fodder • Biofuel • Oilseed Crop[g]	Monoculture	July–Sept.[k]
Kernza	*Thinopyrum intermedium*	Grain	• Perennial grain crop	Monoculture	June–July[l]
Prairie mix	*Andropogon gerardi* *Schizachyrium scoparium* *Sporobolus aspera* *Dalea purpurea* *Senna marliandica* *Salvia azurea* *Helianthus maximiliani* *Artemisia ludoviciana* *Liatris punctata*	Native grasses, legumes, asters, mints	• Grain crop[h] • Perennial Fodder	Polyculture	June–Oct.

[a]Carlsson and Huss-Danell (2003).
[b]Howarth et al. (1978).
[c]Borreani et al. (2003).
[d]Weaver et al. (1935).
[e]Vilela et al. (2018).
[f]NC State (2021b).
[g]Gansberger et al. (2015).
[h]Schlautman et al. (2018)
[i]Chen et al. (2018).
[j]Ogle et al. (2007).
[k]USDA (2018).
[l]Duchene et al. (2021).

and hand-weeding. Within the plots, all weeds were removed biweekly during 2019. In 2020 only field bindweed (*Convolvulus arvensis* L., Solanales: Convolvulaceae) and Johnsongrass (*Sorghum halepense* L., Poales: Poaceae) were removed biweekly.

Alfalfa plots were mowed twice per growing season (June and August) after each bloom period and sainfoin plots were mowed once per season, also after its blooming period (June), to simulate forage cuttings that would typically be collected from these crops. All plots were flail mowed to 23 cm in October of each growing season.

Pollinator Collection

We conducted pollinator observations for two growing seasons (2019–2020). During the blooming period of each crop treatment, we conducted 10-min timed collections in each plot (two observations for each plot), with random walks within and around the treatment plot during the 10-min timeframe. The time was paused during insect handling. We sampled each crop treatment about once a month during its bloom period, which resulted in sampling about 2–3 times per year per crop, giving a total of 32–48 observation hours over the course of two years. Pollinator observations were only conducted on days without rain, and at temperatures above 18 degrees Celsius. The crop treatments varied in sampling efforts due to differences in the length of their bloom periods throughout the year. Kernza was observed for a total of 4 hr throughout the study period, alfalfa was observed for a total of 5.3 hr, sainfoin for a total of 4 hr, cup plant for 4 hr, silflower for 5.3 hr, and prairie had a total of 8 hr.

Pollinators (bees, syrphids, bee flies, moths, skippers, and butterflies) that landed on inflorescences within the plot were hand-collected using aerial nets (38 cm in diameter) or hand-held insect vacuums (Heavy Duty 18-volt Hand-Held DC Vac/Aspirator built on Skil hand-held vac platform from BioQuip, catalogue number: 2820GA). If we failed to capture an individual pollinator, it was counted only in the abundance data. If the species identity of the specimen was apparent, it was also included in species richness data. Monarch butterflies (*Danaus plexippus* L., Lepidoptera: Nymphalidae) were not collected due to their recent declines in population sizes, but were identified in the moment and included in the abundance and species richness data. All captured specimens were placed in twist-cap sample vials on ice until they were transported to a 0°C freezer. They were then pinned and identified to the species level, except for hover and bee flies, which were identified to the family level.

The keys utilized to identify bee species were: *Bees of the tallgrass prairie region and greater Midwest* (unpublished, Arduser 2019), *Key to the Agapostemon of eastern North America* (Portman and Arduser 2019), and *Bumble bees of North America: An Identification Guide* (Williams et al. 2014). Lepidopteran species were identified by Jan

Metlevski, at Kansas State University. Bee species were identified by the author (JB) and Dr. Michael Arduser at Saint Louis University, St. Louis, MO. *Agapostemon* (Guérin-Méneville, 1884, Hymenoptera: Halictidae) specimens identified by the author (JB) were verified using specimens from the Museum of Entomological and Prairie Arthropod Research, at Kansas State University in Manhattan, KS. Specimens are currently stored within the lab of Dr. Tania Kim, with some specimens to be donated to the Museum of Entomological and Prairie Arthropod Research.

Floral Resources

For each crop treatment, we measured floral resource availability (i.e., flower density, floral resource amount, and bloom duration). Flower density was measured by counting the number of inflorescences within a 0.25 m^2 quadrat randomly placed within each treatment plot (N = 3 quadrats per plot). In 2019, flower density was measured twice in each plot during the crop's bloom period. In 2020, flower density was measured more frequently (biweekly from May to September) rather than just during specific treatment bloom periods. We standardized floral resource amount by multiplying floral densities by the average area of each flower species (League 2004, Michigan State 2021, Native Plant Trust 2021, NC State 2021a). Finally, because the duration of floral resource availability would influence pollinator visitation rates, we calculated the number of weeks that flowers were in bloom for each crop within each year.

Statistical Analyses

For each sampling year, pollinator abundance (the total number of individual pollinators observed) and species richness (number of species observed) were recorded per treatment. Because of the unequal sampling effort between treatments, pollinator abundance and richness were standardized for statistical comparisons. Pollinator abundance was standardized by totaling the pollinator abundance within each treatment per year and then dividing by the number of times that treatment was sampled per year. Species richness counts were standardized by totaling the species richness per treatment observed in each sampling round, and then averaging this total richness across the number of sampling rounds each treatment received per year. Because dipterans were not identified down to species, they were not included in the species richness analysis.

To test the effect of crop treatment on overall pollinator abundance and species richness, we conducted a two-way ANOVA with crop treatment (6 levels), site (4 levels), year (2 levels), and 2-way interactions as fixed factors in the model, and standardized pollinator abundance or species richness as the response variables. Preliminary results showed no difference in the response variables among sites, so we removed 'site' as an independent variable from the statistical model to improve model fit (ΔAIC =18.42). To determine the relative treatment performance in attracting pollinator abundance or species richness, we ran a Tukey HSD (honest significant difference) multiple comparison test to test for significant differences between treatments, averaged across years. To determine how bee and lepidopteran abundance and richness were differentially affected by crop treatment, we conducted ANOVAs as mentioned above separately for bees and lepidopterans. To measure the treatment effect on overall pollinator community composition, we conducted a permutational MANOVA (PERMANOVA, Bray Curtis dissimilarity) for pollinators all together, bee communities only, and lepidopteran communities only. Because dipterans were not identified down to species, they were not included in the PERMANOVA analysis.

To measure the effect of treatment floral resource availability, we utilized separate one-way ANOVAs for floral densities (number of flowers per plot), floral resource amount (area of floral resource = floral density × average of flower species in plot), and weeks in bloom (number of weeks flowers were observed). A Tukey HSD comparison test was used to test for significant differences between treatments. We then ran a multiple regression to test the relationship between floral density, floral resource amount, and bloom duration on the abundance of pollinators collected per year. To meet model assumptions, floral resource amount and flower density were log transformed, pollinator abundance was square root transformed, bee abundance was log transformed, and lepidopteran abundance was square root transformed. All analyses were conducted in R v4.0.0, utilizing the *vegan* package v2.5-6 (Oksanen et al. 2019).

Table 2. Results from two-way ANOVAs measuring the impact of treatment, year, and their interaction on the abundance and species richness of all pollinators combined, bees only, and lepidopterans only. Lepidopteran abundance and richness were not significantly impacted by treatment, year, or their interaction. The * indicates a significant p-value (p < 0.05)

Response variables	Predictor variables	Test statistic (df)	p-value
Pollinator abundance	Treatment	$F(4, 39) = 4.12$	0.009*
	Year	$F(1, 39) = 12.14$	0.002*
	Treatment × Year	$F(4, 39) = 1.89$	0.138
Pollinator richness	Treatment	$F(4, 39) = 3.89$	0.012*
	Year	$F(1, 39) = 1.06$	0.311
	Treatment × Year	$F(4, 39) = 0.30$	0.873
Bee abundance	Treatment	$F(5, 47) = 23.50$	>0.001*
	Year	$F(1, 47) = 9.19$	0.005*
	Treatment × Year	$F(5, 47) = 2.04$	0.097
Bee richness	Treatment	$F(4, 39) = 9.68$	>0.001*
	Year	$F(1, 39) = 0.21$	0.648
	Treatment × Year	$F(4, 39) = 9.05$	>0.001*
Lepidopteran abundance	Treatment	$F(4, 39) = 2.26$	0.086
	Year	$F(1, 39) = 0.61$	0.442
	Treatment × Year	$F(4, 39) = 0.25$	0.250
Lepidopteran richness	Treatment	$X^2(4, 39) = 15.24$	0.004*
	Year	$X^2(1, 39) = 2.54$	0.111
	Treatment × Year	$X^2(4, 39) = 2.07$	0.277

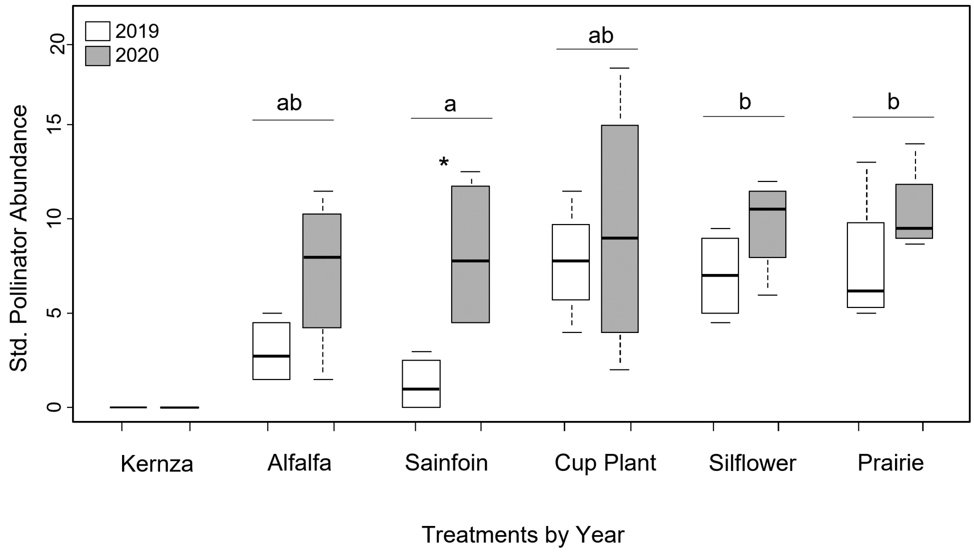

Fig. 2. Crop treatment effects on total pollinator abundance, standardized by sampling effort. Pollinators were sampled from each of the six crop treatments in 2019 (white) and 2020 (gray). Lowercase letters denote significant differences between crop treatments, while the asterisk represents a significant difference between years within one crop treatment. Kernza was not included in this statistical analysis because <5 pollinators were observed over the two years.

Table 3. PERMANOVA results measuring the effect of crop treatment on pollinator community composition. We measured the overall pollinator community, bee community only, and lepidopteran community only. All communities were significantly impacted by crop treatment and year. All communities except lepidopterans were significantly impacted by the interaction of treatment and year

Community	Predictor variable	Test statistic (df)	*p*-value
All Pollinators	Treatment	$F(4, 36) = 2.11$	0.001
	Year	$F(1, 36) = 2.79$	0.001
	Treatment × Year	$F(4, 36) = 1.30$	0.028
Bees	Treatment	$F(5, 31) = 1.78$	0.001
	Year	$F(1, 31) = 2.67$	0.002
	Treatment × Year	$F(3, 31) = 1.39$	0.042
Lepidopterans	Treatment	$F(4, 26) = 1.43$	0.039
	Year	$F(4, 26) = 1.90$	0.043
	Treatment × Year	$F(4, 26) = 0.65$	0.949

Results

All Pollinators

During this experiment, we observed a total of 596 individual pollinators, and captured 377 pollinators consisting of 74 different species of bees and lepidopterans, and 36 total individuals belonging to the family Syrphidae. Of this total, 293 bees were captured, with 50 species identified; and 84 lepidopterans were captured, out of which 23 species were identified. A complete species list for each crop treatment is listed in Supp Table 2 (online only).

To calculate crop treatment effects on the overall pollinator abundance, species richness, and community composition, Kernza was removed from these specific analyses because only five specimens were caught across all plots. The combined abundances of all pollinators (bees, lepidopterans, and syrphids) varied with treatment ($F_{4,39} = 4.12, p = 0.009$) and year ($F_{1,39} = 12.14, p = 0.002$ [see Table 2]). The interaction between treatment and year was not significant ($F_{4,39} = 1.89$, $p = 0.138$). Prairie and silflower attracted significantly higher overall pollinator abundance than sainfoin ($p = 0.024$ and 0.045, respectively; Fig. 2, Supplemental Table S3). Pollinator species richness was also affected by treatment ($F_{4,39} = 3.89$, $p = 0.012$) but was not affected by year ($F_{4,39} = 0.30$, $p = 0.873$ [see Table 2]). Pollinator species richness followed the same trend as pollinator abundance, with prairie and silflower attracting significantly higher species richness compared to sainfoin ($p = 0.011$ and 0.011, respectfully; Supp Table 3 [online only]).

Community composition was significantly impacted by crop treatment (PERMANOVA $F_{4,36} = 2.11$, $p = 0.001$), year ($F_{1,36} = 2.79$, $p = 0.001$), and the interaction of treatment and year ($F_{4,36} = 1.30$, $p = 0.028$ [see Table 3, Fig. 3]). Alfalfa treatments were dominated by lepidopterans, with only two bee specimens caught over the two-year study (Supp Table 2 [online only]), while sainfoin was dominated by bees, with only two lepidopteran specimens caught. Cup plant also had more bees compared to lepidopterans, with only three lepidoptera species caught. Silflower composition was similar to cup plant, but supported more lepidopteran species, six of which were different species than seen in cup plant. Prairie supported both pollinator taxa well. It had the highest number of bee species and the second highest number of lepidopteran species, with 34 bee species and 13 lepidopteran species captured.

Bees

Bee abundance and richness were significantly impacted by crop treatment ($F_{5,47} = 23.50$, $p < 0.001$ and $F_{4,39} = 9.68$, $p < 0.001$, respectively [see Table 2]). Bee abundance and richness were significantly higher in sainfoin, cup plant, prairie, and silflower compared to alfalfa and Kernza (Fig. 4). Prairie and silflower also attracted significantly higher bee abundance and richness than sainfoin and Kernza (Supp Table 3 [online only]). Bee abundance significantly increased with year ($F_{4,30} = 9.05, p < 0.001$), while there was significant interaction with year and treatment for bee richness ($F_{1,47} = 9.19$, $p < 0.01$ [see Table 2]). Sainfoin attracted higher bee abundance in 2020 compared to its bee abundance in 2019 (Tukey HSD $p = 0.039$) and outperformed alfalfa and Kernza in 2020, but not 2019 (Tukey HSD $p = 0.003$ and 0.039, respectively).

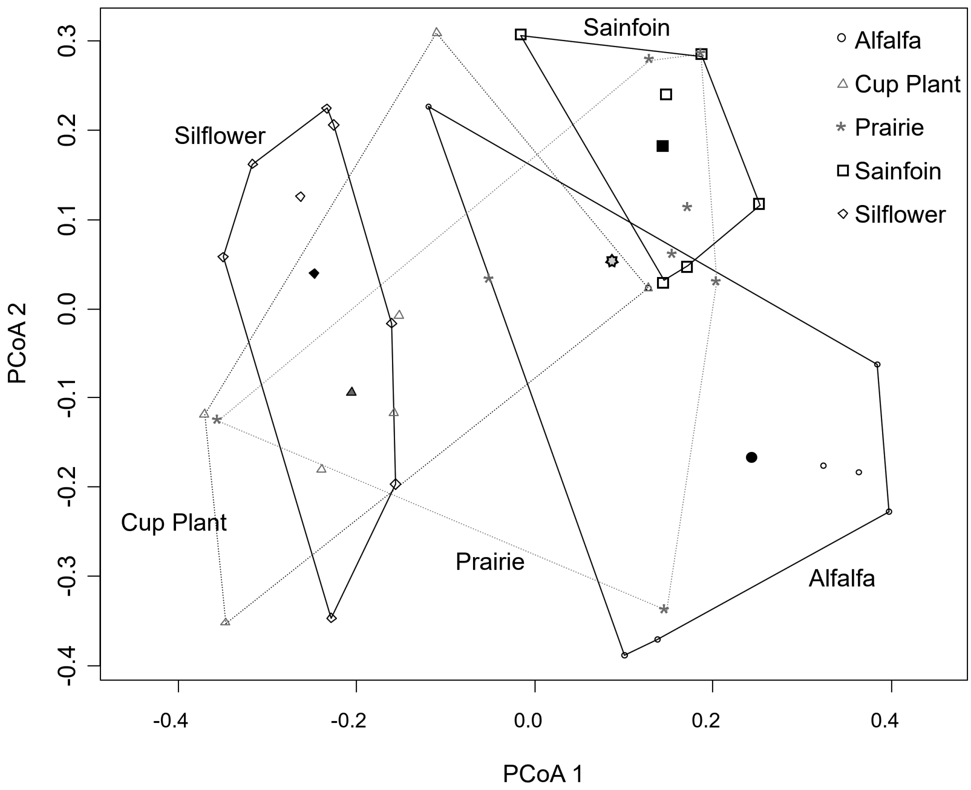

Fig. 3. Ordination of pollinator community composition for all pollinators among crop treatments by plot. Kernza was excluded from analysis because less than five specimens were observed over the course of two years. Pollinators were combined over the two sampling years.

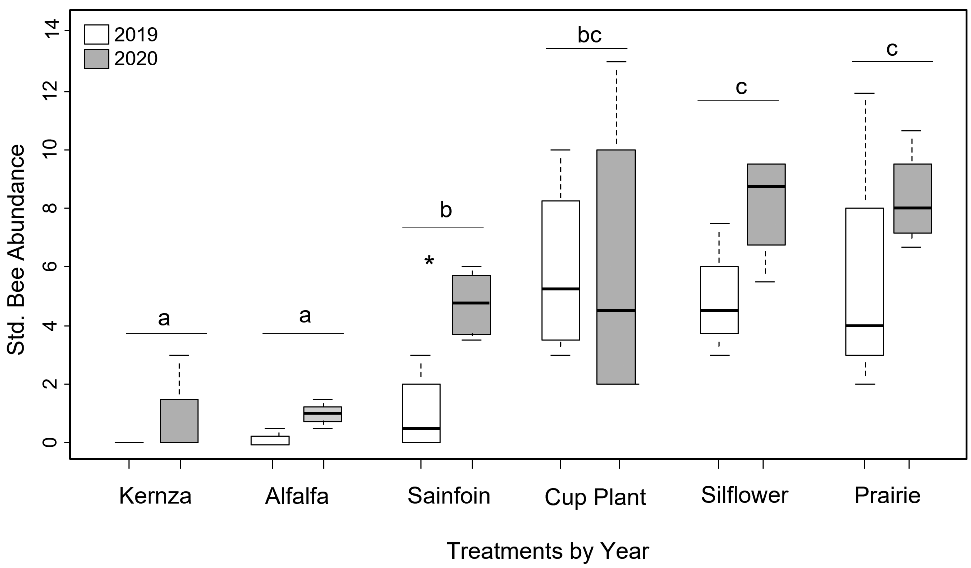

Fig. 4. Average bee abundance in each crop treatment, standardized by sampling effort from 2019 (white) and 2020 (gray). Lowercase letters denote differences between crop treatments, while the asterisk represents a significant difference between years within one crop treatment.

Bee community composition was affected by the interaction between treatment and year ($F_{3,31} = 1.39$, $p = 0.042$), crop treatment alone ($F_{5,31} = 1.78$, $p = 0.001$), and year ($F_{1,31} = 2.67$, $p = 0.002$ [Table 3, Fig. 5]). Alfalfa treatments supported two bee species total: *Halictus ligatus* (Cressson, Hymenoptera: Halictidae) and *Lasioglossum tegulare* (Robertson, Hymenoptera: Halictidae) (Supp Table 2 [online only]), and sainfoin was dominated by *Apis mellifera* (L., Hymenoptera: Apidae) and *Megachile brevis* (Say, Hymenoptera: Megachilidae). Cup plant attracted *Agapostemon texanus* (Cresson, Hymenoptera: Halictidae) and *Agapostemon virescens* (F., Hymenoptera: Apidae) and species belonging to the genus *Melissodes* (L., Hymenoptera: Apidae), which overlaps with the species attracted by silflower (*A. virescens* and *H. ligatus*) and prairie (*A. virescens* and other members of the

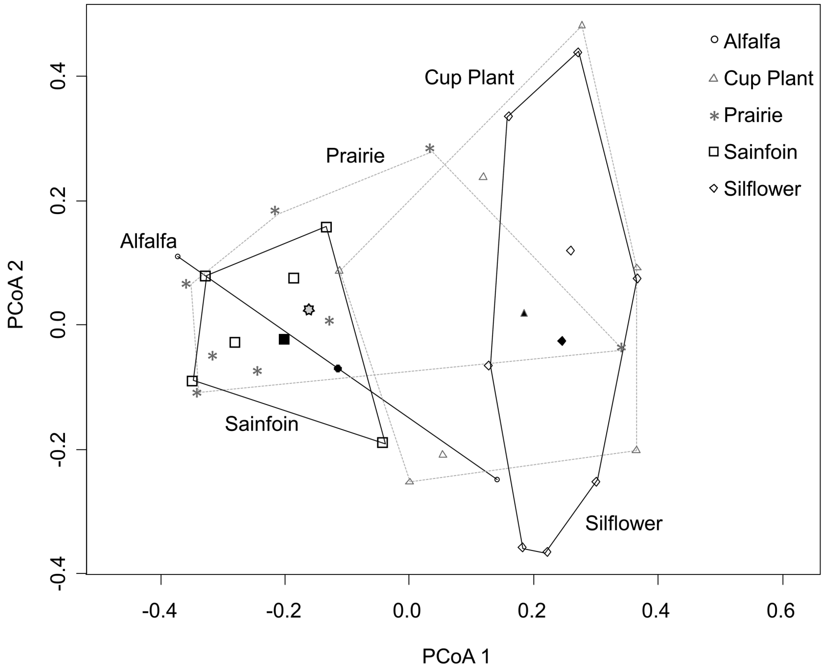

Fig. 5. Ordination of bee community composition among crop treatments by plot. Pollinators combined over the two sampling years.

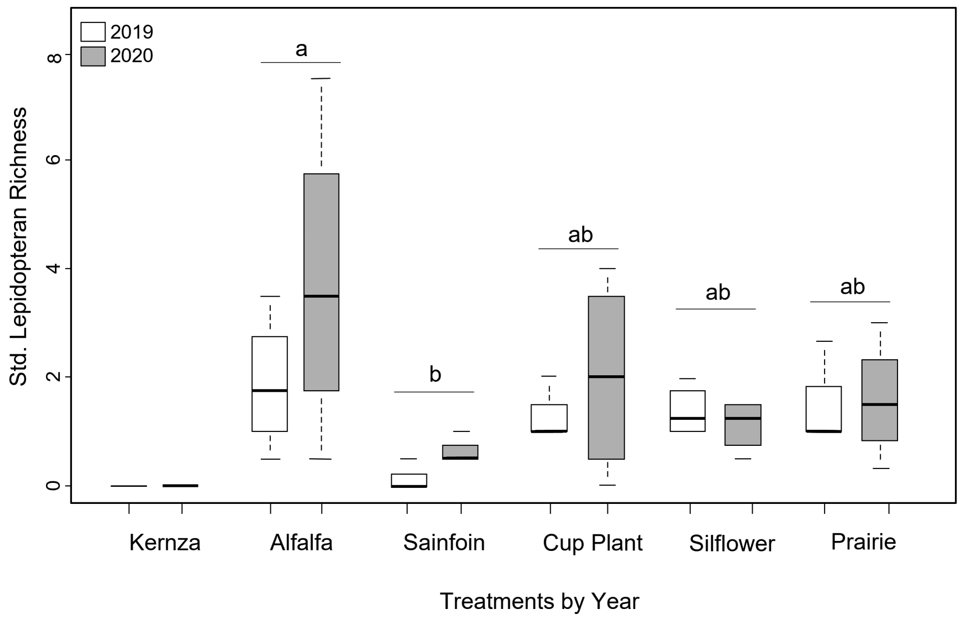

Fig. 6. Average lepidopteran species richness in each crop treatment in 2019 (white) and 2020 (gray). Lowercase letters denote differences between crop treatments.

Augochlorini tribe), and *Melissodes communis* (Cresson) (Supp Table 2 [online only]).

Lepidopterans

Because no lepidopteran specimens were caught in the Kernza treatments, this crop was removed from all lepidopteran data analyses. Treatment did not have an overall significant effect on lepidopteran abundance ($F_{4,30}$ = 2.26, p = 0.086), nor did year or the interaction between year and treatment ($F_{1,30}$ = 0.61, p = 0.442 and $F_{4,30}$ = 1.42, p = 0.250, respectively [see Table 2]). Lepidopteran species richness followed a similar trend, with alfalfa attracting significantly more species than sainfoin (Fig. 6, Supp Table 3 [online only]).

Significant overall differences in community composition between crop treatments ($F_{4,26}$ = 1.43, p = 0.039) and year ($F_{1,26}$ = 1.90, p = 0.043) were found for the lepidopterans (see Table 3, Fig. 7). The interaction between treatment and year was insignificant ($F_{3,26}$ = 0.65, p = 0.949). Alfalfa was dominated by *Cupido comyntas* (Godart, Lepidoptera: Lycaenidae) and *Epargyreus clarus* (Cramer, Lepidoptera: Hesperiidae), while sainfoin was only observed attracting two total lepidopteran individuals: *Echinargus*

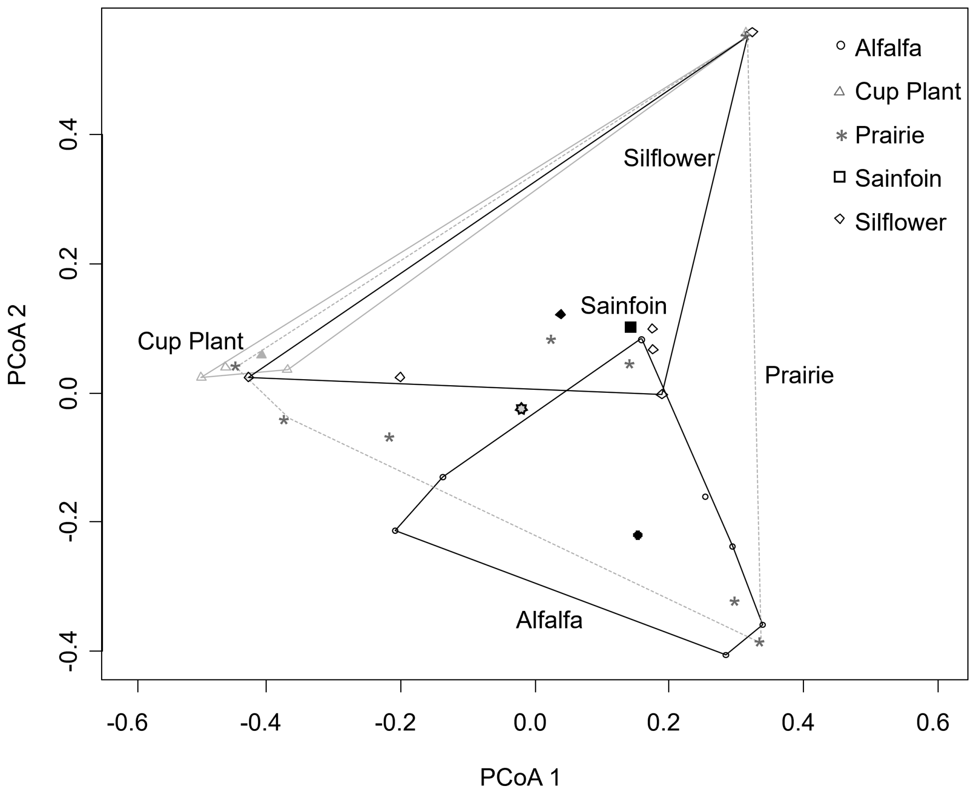

Fig. 7. Ordination of Lepidopteran community composition among crop treatments, with pollinators combined over the two sampling years.

isola (Reakirt, Lepidoptera: Lycaenidae) and *E. clarus* (Supp Table 2 [online only]). The cup plant lepidopteran community differed from the other treatments, as it only attracted four total species over the two-year study: *Atalopedes campestris* (Boisduval, Lepidoptera: Hesperiidae), *Poanes zabulon* (Boisduval and Le Conte, Lepidoptera: Hesperiidae), *E. clarus*, and *Vanessa cardui* (L., Lepidoptera: Nymphalidae) or *V. virginiensis* (Drury, Lepidoptera: Nymphalidae). Silflower attracted a similar set of species, attracting mostly *A. campestris* and *V. cardui* or *V. virginiensis*, overlapping some with the cup plant community. Prairie attracted a high diversity of lepidopterans and overlapped with most other crop treatment communities, attracting mostly *E. clarus*, *Helicoverpa zea* (Boddie, Lepidoptera: Noctuidae), and *A. campestris*.

Floral Resources

Crop treatments significantly differed in floral resource area ($F_{5,42}$ = 21.43, p < 0.001), number of flowers ($F_{5,42}$ = 13.94, p < 0.001), and weeks in bloom ($F_{5,42}$ = 3.88, p = 0.005). Prairie plots had the highest floral density (Fig. 8a) and floral area (Fig. 8b) but they were not statistically different from alfalfa, cup plant or silflower. Weeks in bloom were also similar across treatments with the exception of Kernza (Fig. 8c, Supp Fig. 1 [online only]). Pollinator abundances were positively influenced by the number of weeks in bloom ($F_{1,44}$=25.63, p < 0.001) and floral resource area ($F_{1,44}$=5.35, p = 0.025), but not the densities of flowers ($F_{1,44}$=2.60, p = 0.113, Fig. 9).

Discussion

Overall, we found that cup plant, silflower, and prairie border crops, which are perennial and native to Kansas, received the highest overall pollinator abundance and species richness compared to Kernza, alfalfa, and sainfoin border crops. Alfalfa supported the highest abundance and richness of lepidopteran species, but performed poorly for all other pollinator groups. We also found that the differences in pollinator attraction between years were significant, suggesting that the age of border crops could be a factor influencing pollinator communities. We found that differences in floral resource area, density, and duration of bloom varied significantly between certain border crops, which may explain how some crops attracted more pollinators than others. Studying crop attractiveness to pollinators during their first growing season may provide valuable insight into the potential costs and benefits growers may experience during initial establishment of their border crops.

The composition of the overall pollinator community was significantly different among treatments and year, and the interaction between treatment and year was also significant. These findings suggest that age of border crops may impact the ability of the crop to attract a number of pollinators and may also impact the identity of the pollinator species (Krimmer et al. 2019). It is also possible that this was the result of random yearly fluctuations in the pollinator community, therefore longer-term studies are needed to disentangle the effects of plot establishment from inter-annual variation in insect abundances. Cup plant and silflower pollinator communities usually had few overlapping species with sainfoin and alfalfa, and they attracted far more bee species. Prairie treatments overlapped with both the sunflower and legume groups, showing that prairies as border crops may be able to attract a broader pollinator community compared to other crops. Kernza attracted a very low number of pollinators, as expected considering it is a wind-pollinated species and therefore has small flowers that are generally unattractive to most pollinators compared to flowering forbs. Alfalfa attracted low bee richness as well, but attracted a high abundance of lepidopterans. Its

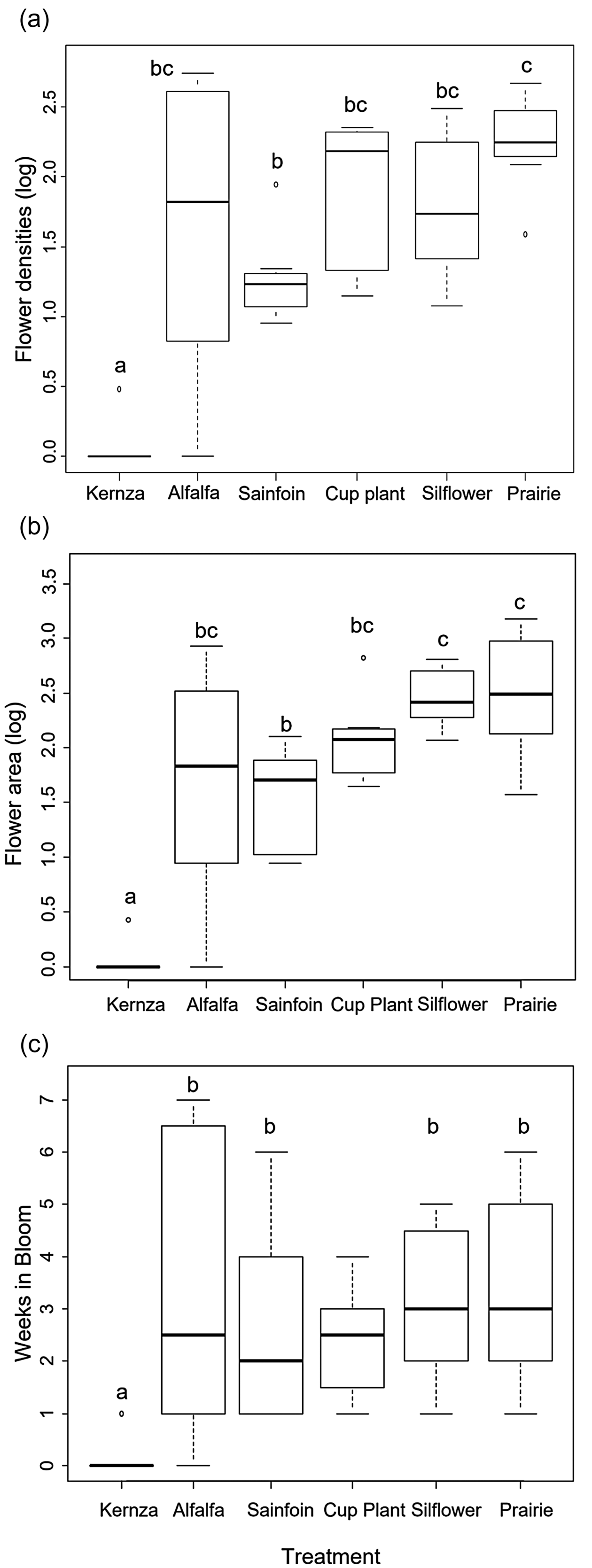

Fig. 8. Floral resource availability among crop treatments. (a) number of flowers in plot, (b) floral resource area, and (c) weeks in bloom. Lowercase letters denote differences between crop treatments.

pollinator community overlapped with other treatments and was not statistically different from prairie, silflower, or cup plant.

Alfalfa may have attracted a lower level of bee abundance and species richness due to its floral morphology. Alfalfa flowers have a tripping mechanism that can strike pollinator visitors in the head (Larkin and Graumann 1954). When a pollinator visits an alfalfa flower, it generally lands on the keel (two fused petals) and extends its mouthparts into the flower for nectar, which in turn trips the pollen-laden sexual column within the alfalfa flower and ultimately strikes the pollinator in the head, covering it with pollen (Bohart 1957). This may deter some pollinators such as honey bees, who have been observed to learn the tripping mechanism and change their visitation methods to avoid being struck (Reinhardt 1952). It is possible that other species of bees visiting our study sites may have been deterred by the tripping mechanism as well, and therefore may have chosen to visit other plots containing flowering plants that do not have mechanical triggers. However, we did not directly observe or measure this in our study.

Because we observed differences in pollinator community composition among the different border crops, growers may be able to utilize specific border crops to support specific pollinator groups. We were able to identify border crops that were more attractive to certain pollinators than other border crops, which provides more detailed information to growers that are considering different hedgerows to implement near their fields. If a grower's main goal is to support the most diverse set of pollinators over the course of the growing season, we suggest the addition of a prairie mix border crop, such as the one designed for this study, rather than utilizing alfalfa as a border crop. The prairie border crop treatment attracted the highest overall pollinator abundance and richness compared to the other border crops. Its long bloom period, high diversity of native prairie plants, and high floral resource amount may enable it to attract a wide variety and an abundance of both bees and lepidopterans throughout the growing season (Kremen and Miles 2012). While we cannot disentangle the relative importance of bloom duration and floral diversity in this study, previous studies have found that both are important for attracting pollinators year-round (Ghazoul 2006, Rollings and Goulson 2019).

If a grower is interested in supporting a high abundance of pollinators, but is not interested in utilizing a border crop grown in a polyculture, then silflower or cup plant could be implemented interchangeably based on their statistically similar bloom periods and pollinator attraction abilities. The perennial sunflower crop treatments are also statistically comparable to prairie mixes in terms of the floral resource amount they provide. These perennial sunflower border crops are not only comparably attractive to pollinators as some native prairie plants, but they also have the potential to provide some agronomic benefits to the grower, such as serving as a fodder or a biofuel crop if harvested after their bloom periods (Weaver et al. 1935, Vilela et al. 2018; see Table 1). Silflower and cup plant also attracted fewer adult lepidopterans than alfalfa and prairie mix, which could lower some concerns of these specific border crops attracting lepidopteran pests. Because these crops can be grown in monocultures, they may align more with mechanized farming practices compared to border crops like the prairie mix.

The spillover of native pollinators from border crops or hedgerows into the adjacent crop may benefit growers through increased yields and seed sets if the growers rely on pollination services for crop production. Permanent, natural hedgerows (containing native wildflower species) of at least three years old have been observed to significantly increase pollination services of native pollinators within a

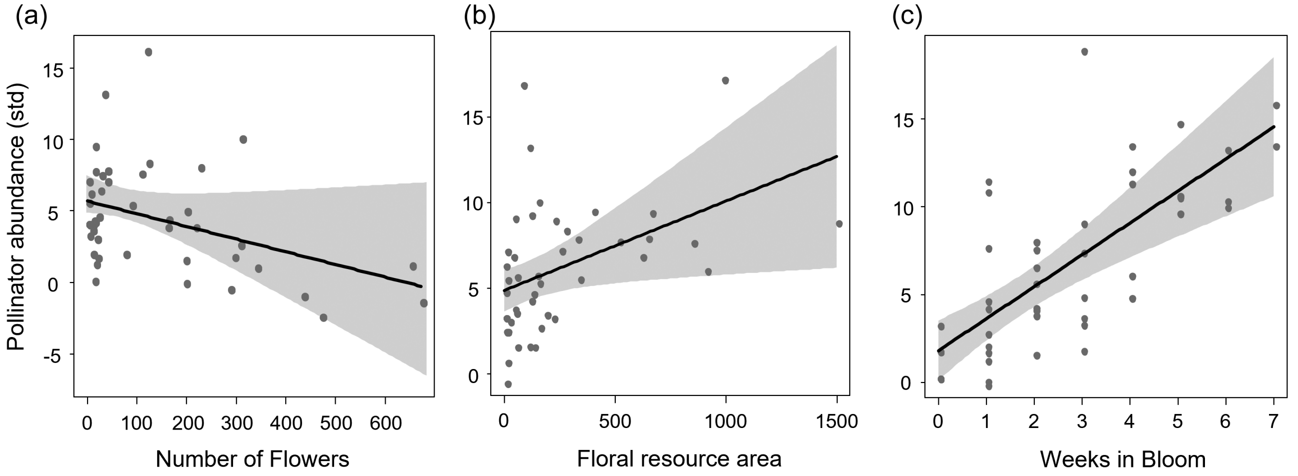

Fig. 9. Relationships between standardized pollinator abundance and (a) number of flowers in plot, (b) floral resource area, and (c) weeks in bloom.

main crop field in contrast to crop fields without hedgerows (Blaauw and Isaacs 2014). Natural hedgerows that are at least 10 yr old can significantly facilitate pollinator visitation up to 100 m into the main crop from the field edge (Morandin and Kremen 2013). While we did not measure spillover in our study, our results suggest that silflower and cup plant border crops that were two years old were similar in attractiveness to pollinators compared to the natural (prairie mix) border crop. Thus, silflower and cup plant may have great potential as a long-term border crop option for growers in terms of attracting pollinators to their field edges. However, the long-term effects of these crops on the pollinator community and their ability to facilitate spillover are still unknown and require further study.

While row crops such as corn and wheat do not specifically rely on invertebrate pollination, other crops with the ability to self-pollinate such as soybeans may benefit significantly from insect pollination. The spillover of pollination services from natural areas, such as forests, to soybean fields can significantly increase with proximity to the natural area and increase pollinator movement between the crop and natural areas (Monasterolo et al. 2015, González et al. 2016), and may therefore increase soybean yields up to 21% on average (USDA 2020, Garibaldi et al. 2021). This could mean that even growers cultivating crops not dependent on insect pollination can increase yields if they find effective ways to increase the amount of natural habitat near their fields.

Year significantly impacted overall pollinator abundance, while the interaction between treatment and year also significantly impacted bee species richness. We only conducted this study across two years and therefore we cannot disentangle yearly fluctuations in pollinator densities from establishment effects. However, the increase in pollinator densities was only observed in one cropping treatment (sainfoin) and not others, suggesting that environmental conditions associated with establishment in sainfoin in the first year was affecting visitation. This increase in pollinator abundances in sainfoin in the second year may be due to less weed invasion in its second year of the study (Hybner 2013) which could have increased visitation by pollinators. This result suggests that different border crops may incur delays in attracting pollinators and should be considered by growers during crop selection.

When it comes to border crop implementation, growers may perceive a potential economic loss due to concerns of pest control, as the ability of border crops to attract or actually aid in controlling crop pests is still debated (Bianchi et al. 2006, Morandin and Kremen 2013). While pest attraction was not the main point of our study, to address this concern we did note any adult lepidopteran agricultural pests found within our 2019 and 2020 pollinator collections and conducted a preliminary sweep sampling for insect herbivores and the larval stages of lepidopteran pest species in 2020. We found only one major and one minor adult lepidopteran pest species caught throughout the two-year study (*Helicoverpa zea*, or 'corn earworm' and *Colias eurytheme,* or 'alfalfa caterpillar butterfly'), of which there were five and seven specimens caught in total, respectively, throughout the entire experiment. Our sweep samples from 2020 indicated that herbivore densities vary substantially across treatments (Supp Fig. 1 [online only], unpublished data), and that alfalfa attracted a large density of thrips compared to prairie and silfower. Long-term sampling is needed to determine whether native perennial border crops harbor insect pests and whether they spill over into the adjacent crop habitat. Care must be taken in treating the main crop for pests, as spraying insecticides could drift into the hedgerows and potentially harm pollinators and other beneficial insects (Bernauer et al. 2015, Sgolastra et al. 2019).

Conclusion

We found that native flowering border crops, such as prairie mixes and native sunflower species, can support high levels of pollinator abundance and species richness compared to other nonnative border crops such as Kernza and alfalfa. Growers have the option to support high numbers of pollinators by utilizing prairie mixes or implementing monocultures of perennial sunflowers, such as silflower and cup plant. The different crop treatments tested offer flexibility to farmers and their goals, and therefore may be more readily implemented by growers interested in supporting abundant and diverse sets of pollinators on their land.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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