Wildflower plantings in commercial agroecosystems: The effects on pollinators, predators, herbivores, and floral communities

A DISSERTATION
SUBMITTED TO THE FACULTY OF
UNIVERSITY OF MINNESOTA
BY

Eric Gordon Middleton

IN PARTIAL FULLFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF
DOCTOR OF PHILOSOPHY

Ian V. MacRae and George E. Heimpel, Advisors

August 2020

Acknowledgements

There are many people who helped in large and small ways during my time in graduate school that deserve recognition. While the road to this dissertation has not always been a smooth one, the support of colleagues, friends, and family have made it not only possible, but thoroughly enjoyable. For that, I am very grateful.

I would first like to thank my advisors Dr. Ian MacRae and Dr. George Heimpel for their mentorship and guidance, and for trusting me with the ownership of my project. Committee members Dr. Dan Cariveau and Dr. Elizabeth Borer provided valuable advice and feedback throughout my graduate career. Outside of my committee, Dr. Sujaya Rao helped me gain experience as a teacher and a leader, and has always been willing to offer counsel and advice. I would also like to thank Dr. Christopher Philips for bringing me on as a student in the first place and setting me on my course of study.

This work would not have been possible without funding and support from numerous sources. I thank NRC-SARE and AREA II Potato Growers Association for providing operational funds, and the University of Minnesota's Doctoral Dissertation Fellowship, the MGK Fellowship, the Bell Museum's Dayton Fellowship, and the MnDRIVE Global Food Ventures program for contributing to my stipend.

Just as important were all of the students and staff who contributed to my project and to my development as a scientist. Thank you Lindsey Christianson, Grace Sward, and Sydney Glass for assistance in the lab and field. Thank you to all of the members of Frenatae for providing a welcoming community. And thank you to the undergraduate workers Noah Linck, Joe Nelson, Gus Fedje-Johnson, Lily Briggs, Erik Lucas, Lexie

Ogdahl, Caroline Hofmeister, Eli Kleinschmidt, Bailey Brandel, and Samantha Meyers for all of your hard work and dedication.

Lastly, I have to thank my parents John and Marge for their constant support, for reading through drafts of papers, and for providing feedback whenever I needed it. I am truly fortunate to have such a supportive family, who exposed me to critically thinking and the wonder of nature from an early age. And finally, thank you to my partner Elissa, who inspires me to be a better scientist and always encourages me to stop and look at the bugs.

Table of Contents

Chapter 1: Introduction

Chapter 2: Floral community and herbivores: Evaluating a commercially available floral seed mixture when established on-farm

2.3 Materials and Methods

2.4 Results

2.5 Discussion

Chapter 3: Floral plantings in large-scale commercial agroecosystems support both pollinators and arthropod predators

3.3 Materials and Methods

3.4 Results

3.5 Discussion

Chapter 4: Wildflower plantings in commercial agroecosystems promote generalist predators of Colorado potato beetle

List of Tables

List of Figures

Voucher specimens from this dissertation are stored at the University of Minnesota Insect Collection, Hodson Hall 1980 Folwell Ave, St Paul, MN 55108

Chapter 1: Introduction

1.1 Declines in Insect Abundance and Ecosystem Services

The loss of insect abundance and biodiversity has become a serious concern, both among scientists and the general public. While few long-term longitudinal studies on insect abundance exist, there is an increasing scientific consensus that insects across many taxa are disappearing (Hallmann et al. 2017, van Klink et al. 2020). This is a major conservation concern: Of all insects with IUCN-documented population trends, 33% are currently declining, with some orders showing even steeper declines (Dirzo et al. 2014).

While there are many factors affecting the decline of insects, the expansion and intensification of agriculture are primary drivers (Sandhu et al. 2008, Foley et al. 2011). Crops cover ~1.53 billion hectares of land, and agriculture overall takes up 38% of all ice-free land on the planet, severely reducing available natural habitat (Foley et al. 2011). Increasing agricultural intensification has led to increased food production (Foley et al. 2011), but has also resulted in reductions of insect abundance and biodiversity. Plants that bumblebees depend on for forage have declined significantly in both range and local frequency in the past century in the UK, with the losses largely attributed to agricultural practices and expansion (Carvell et al. 2006). In the United States between 2008 and 2013, bee populations were predicted to decrease across 23% of the United States, with the decline associated with a loss of natural habitat to row crops (Koh et al. 2016).

Beyond conservation concerns, the loss of insects due to agricultural practices can also reduce important ecosystem services in agroecosystems. Ecosystem services are benefits provided to humans by the environment and the organisms within it, ranging from pollination and pest suppression, to recreational value and aesthetic appeal

(Millennium Ecosystem Assessment 2005, Fiedler et al. 2008). Insects and other arthropods provide enormous value in the form of ecosystem services, with wild insects providing an estimated $57 billion US annually in the US alone (Losey and Vaughn 2006). Worldwide, the value of pollinators was estimated to be 153 billion euros in 2005 (Gallai et al. 2009). However, with the loss of insect species and abundance, there is a strong fear of losing important ecosystem services as well (Dirzo et al. 2014). Across Great Britain, reductions in animal species that provide pollination and pest control services resulted in a corresponding decrease in the resilience and stability of ecosystem services (Oliver, Isaac, et al. 2015). Much of our current, high production agricultural land is not suitable for ecosystem services provided by insects. When modeling the potential for biocontrol services across Europe, large proportions of existing agroecosystems lacked any nearby semi-natural habitat, and had low potential to provide biological control services to growers (Rega et al. 2018). Additionally, there are diminishing returns when it comes to services like pollination. For pollinator-dependent crops, increasing agricultural intensification comes with increasingly marginal benefits and increased yield instability (Deguines et al. 2014). The phylogenetic diversity of bees in agricultural landscapes decreased significantly with increasing agricultural land use, and led to decreased pollination services and crop yield (Grab et al. 2019). Taken together agroecosystems are lacking in insect abundance, yet also most in need of the ecosystem services insects provide.

Short of significant changes in human diet or agricultural production methods it is unlikely that agricultural intensity or land use will decrease in the future (Tilman and Clark 2014, Clark and Tilman 2017), and focusing on creating more sustainable agroecosystems will be beneficial to conservation efforts (Perfecto and Vandermeer 2010). If the quality of the landscape matrix is improved by providing stable sources of habitat and forage for insects, it could help to offset the loss of insects and ecosystem services that come with commercial agricultural practices.

1.2 Methods to Preserve Insects and Services

Preserving biodiversity while simultaneously promoting ecosystem services on agricultural land is therefore becoming increasingly necessary and desirable. However, there are a number of problems: Most agricultural production in the United States focuses on large monocultures and intensive management, leading to highly disturbed and homogeneous landscapes. There is little existing plant biodiversity, and few natural areas that have not been given over to agricultural production. Finally, it is difficult to carve out new areas for establishing habitat because it will reduce the amount of land used for production.

While preserving existing natural areas has been proposed as an effective conservation strategy (Phalan et al. 2011), in the homogeneous landscape of many agricultural settings, it may be more practical to increase landscape heterogeneity on a small scale (Fischer et al. 2008). Therefore, increasing landscape heterogeneity in whatever ways possible on the largest scale feasible could provide the greatest opportunity to make agricultural land more hospitable to beneficial insects. The results from previous studies suggest that more complex agroecosystems can lead to greater ecosystem services and beneficial insect abundance. As landscape complexity increased in agroecosystems, suppression of aphids increased 6-fold, and natural enemy predation on aphids was mostly complementary, with few notable effects of intra-guild predation

(Martin et al. 2015). Pollinators and pollination services respond similarly. Increased natural forest led to increased pollination in nearby coffee crops (Ricketts and Lonsdorf 2016) and a higher proportion of nearby natural habitat improved the stability and predictability of pollination services in watermelon (Kremen et al. 2004).

Increasing diversity on a landscape-scale is not strictly necessary however. Local interventions can be important for increasing natural enemy populations as well. Increased plant and litter cover led to increased abundance of spiders in managed grasslands, and local factors were found to be more impactful than landscape-level effects (Horvath et al. 2015). Small areas of habitat, if they provide the correct resources, can prove to be as beneficial as larger areas. Patches of hill prairie in Iowa were as species rich as larger prairie preserves in the same area, despite having lower floral diversity (Hendrix et al. 2010). Additionally, mobile insects such as bees utilize a variety of different habitats throughout the season, following floral resources as concentrations of available food shift (Mandelik et al. 2016). This suggests that even patchy distributions of high-quality forage can be of great benefit to pollinators in agricultural land.

Increasing plant diversity is key to promoting additional insect abundance or diversity. A global meta-analysis found that increased in-field plant diversity led to increased abundance and richness of arthropods overall, and especially for pollinators and predators (Lichtenberg et al. 2017). More mobile organisms appeared to benefit more, whereas less mobile arthropods like herbivores and detritivores benefitted less. Another meta-analysis found increasing plant diversity in agroecosystems was correlated with enhanced abundance of natural enemies, decreased herbivore numbers, and reduced crop damage, although there was also a small cost to crop yields (Letourneau et al. 2009).

Increasing plant biodiversity in agroecosystems has also been strongly linked to increased bee and other insect abundance and activity (Nicholls and Altieri 2013). There are many methods of increasing plant diversity in agroecosystems that support beneficial insects, including hedgerows (Morandin et al. 2014), beetle banks (Thomas et al. 1991, Collins et al. 2002), and floral plantings.

More so than just increased plant diversity, the presence of floral resources is particularly important to many beneficial insect taxa. The availability of floral resources was found to be the primary factor directly impacting pollinator populations in agroecosystems (Roulston and Goodell 2011) and floral resources were also determined to be the limiting factor for pollinator populations in England (Dicks et al. 2015). Floral resources, such as increased pollen and nectar, appear to enhance natural enemy abundance more than other factors such as alternative prey and overwintering habitat (Ramsden et al. 2014). While there are many different strategies that can be used to support beneficial insects, establishing flower-rich margins is one of the most effective options, even on a small scale (Garibaldi et al. 2014). With all this in mind, the creation of floral resources in agricultural settings can create heterogeneity, increase plant diversity, and increase floral resources within agroecosystems.

1.3 Floral Plantings

Establishing plantings of perennial flowers in the margins of agricultural fields has been suggested as an effective method to both preserve biodiversity, and to provide multiple ecosystem services in a variety of agricultural settings (Korpela et al. 2013, Westphal et al. 2015). The main goal of such floral plantings is to provide food for beneficial insects in the form of pollen and nectar, although they can also provide a stable source of habitat, more favorable microclimates (Barone and Frank 2003), or sources of alternative prey (Hoffmann et al. 2018). Additionally, floral plantings can be created in areas not usually used for agricultural production, and many growers are willing to consider creating these plantings (Arbuckle 2018).

When successful, floral plantings can increase the abundance and diversity of pollinators and arthropod predators, and can provide a measure of ecosystem services in nearby crops (Blaauw and Isaacs 2014a, Tschumi, Albrecht, Bärtschi, et al. 2016). Because of this, floral plantings have been integrated as agri-environmental schemes in the UK (Carvell et al. 2007), and Switzerland (Haaland and Bersier 2011), and are used as part of sustainable agricultural practices. In the United States, various groups provide commercially available floral planting seed mixtures (Operation Pollinator 2020, Xerces Society 2020), and programs such as STRIPS focus on the benefits of prairie and floral plantings when established on-farm (Gill et al. 2014). Floral plantings have been studied in multiple countries, and their impacts on conservation and ecosystem services documented.

However, floral plantings have infrequently been studied in commercial, intensively managed agroecosystems. Many studies examine small floral plantings (although see Kleijn et al. 2018), and take place on experimental plots (Korpela et al. 2013, Balzan et al. 2016), or in agroecosystems without intensive management (Feltham et al. 2015, Tschumi et al. 2015). Less research has been conducted on large-scale floral plantings on commercial agricultural land: areas where insect conservation is most needed and where ecosystem services could provide the most benefit. While some studies on large floral plantings do take place in commercial and conventionally managed agricultural areas (Grass et al. 2016, Kleijn et al. 2018), few address the impacts of floral plantings on multiple beneficial taxa or ecosystem services.

1.4 Scope of Dissertation

To determine how floral plantings affect insect conservation and ecosystem services in intensively managed agroecosystems, I examined large-scale perennial floral plantings established around commercial potato fields. I worked closely with a commercial producer of potatoes in central Minnesota, who planted over 200 hectares of floral plantings in the margins of dozens of conventionally managed potato fields in 2015 and 2016. In this setting, I was able to study large, on-farm floral plantings around intensively managed crops, and more completely assess how floral plantings function when implemented on a commercial scale.

This dissertation focuses on several key aspects of on-farm floral plantings in commercial agroecosystems: the establishment of floral plantings and their effects on deleterious species; conservation of beneficial insects and the potential to provide ecosystem services; and direct measurement of biological control of key pest species. Chapter 2 addresses how well floral plantings establish on-farm, and if they provide potential ecosystem disservices in the form of increased herbivore abundance. Chapter 3 focuses on how floral plantings affect conservation of pollinators and predators, both within field margins and in nearby crops. Chapter 4 investigates biological control of Colorado potato beetle, and how floral plantings impact this major pest of potato crops. Taken together, this work addresses how floral plantings function when established on intensively managed, commercial farms, and determines the impact on floral communities, herbivores, pollinators and predators, and ecosystem services provided.

Chapter 2: Floral community and herbivores: Evaluating a commercially available floral seed mixture when established on-farm

2.1 Overview

Wildflower plantings have been established in the margins of agricultural fields to provide resources and habitat for beneficial arthropods. However, floral plantings do not always lead to desired changes in floral communities and can attract herbivores and crop pest species. Little is known about how well floral plantings fare or if they create ecosystem disservices after being established on farm, especially when they are created on a large scale in commercial agricultural areas. To determine the impact of large-scale floral plantings on herbivores and floral communities in commercial agroecosystems, we compared field margins planted with a commercially available seed mixture to unmanaged field margins. Floral plantings led to significantly higher floral cover and richness from late June-September. Floral plantings also increased the proportion of native and perennial forbs present in margins. However, many species within the seed mixture failed to establish, and floral cover and richness was not increased in early June, when floral plantings can be especially impactful for beneficial insects. Floral plantings did not lead to increased herbivore abundance, either in field margins or within adjacent potato crops, but there were notable differences in herbivore communities between treatments. Floral margins had significantly greater numbers of Coleoptera and Orthoptera while control margins had higher abundance of Hemiptera. Commercially available floral plantings can increase both the number and richness of flowering forbs in agricultural settings and do not increase herbivore abundance. However, they may not fully realize the diversity of the original seed mixture or provide benefits in the early season.

2.2 Introduction

Crop production is becoming increasingly reliant on intensive management practices and large monocultures of crops (Foley et al. 2011). This results in landscapes scarce in natural habitat (Rega et al. 2018), leading to lower plant and arthropod biodiversity within agricultural areas (Carvell et al. 2006, Koh et al. 2016). In addition to conservation concerns, a lack of biodiversity also reduces ecosystem services that much of agriculture relies on, (Dale and Polasky 2007, Oliver, Heard, et al. 2015). In order to mitigate biodiversity losses and to retain important ecosystem services, sources of plant diversity and habitat need to be integrated into commercial agroecosystems.

Increasing plant diversity in agroecosystems shows promise for promoting biodiversity and ecosystem services (Chaplin-Kramer and Kremen 2012, Nicholls and Altieri 2013). Greater in-field plant diversity can lead to increased arthropod abundance and richness, with mobile organisms such as pollinators and predators benefitting from increased plant diversity more (Lichtenberg et al. 2017). Higher plant diversity was also found to decrease herbivore abundance and crop damage while increasing the abundance of natural enemies (Letourneau et al. 2009).

While many options exist for increasing on-farm plant diversity, establishing perennial wildflower plantings in uncultivated field margins has become increasingly popular. This practice does not remove land from crop production, and is appealing to growers for its lack of opportunity costs (Arbuckle 2015). Floral plantings can increase biodiversity and arthropod abundance, helping to conserve organisms within agroecosystems (Jacot et al. 2007, Pywell et al. 2015, Grass et al. 2016). Floral plantings and the organisms they attract can also provide multiple ecosystem services, including pollination (Blaauw and Isaacs 2014a), pest suppression (Tschumi, Albrecht, Bärtschi, et al. 2016), and soil retention (Schulte et al. 2017). Particularly successful floral plantings can reduce the need for pesticide applications (Gurr et al. 2016), and can simultaneously promote pollinators and predators (Balzan et al. 2016, Campbell et al. 2017). Because of these successes, seed mixtures for floral plantings are now commercially available, and some are being established on a large scale by interested growers.

Although floral plantings can provide benefits, there is a great deal of variety in floral plantings, ranging from monoculture of annuals (Balzan 2017, Quinn et al. 2017) to highly diverse perennial seed mixes (Blaauw and Isaacs 2015, Warzecha et al. 2018). While results vary across seed mixtures, several seed mix traits have been identified that better promote beneficial taxa. High floral cover (Scheper et al. 2015, Williams et al. 2015, Kleijn et al. 2018), high species richness (Tonietto et al. 2017, Buchanan et al. 2018), perennial flowers (Frank and Künzle 2006, Buchanan et al. 2018), and native species (Isaacs et al. 2009, Williams et al. 2015) have all been linked with increased attractiveness to pollinators, predators, or increased overall arthropod diversity. Additionally, consistent floral resource availability throughout the growing season is important for promoting pollinators, predators, and the services they provide, especially early and late in the season (Balzan et al. 2014, Gill et al. 2014, Scheper et al. 2015, Williams et al. 2015). Finally, florally diverse seed mixtures are often seen as more attractive to stakeholders and growers, incentivizing their creation for aesthetic appeal (Arbuckle 2018, Hoyle et al. 2018). Many commercially available seed mixtures therefore attempt to incorporate these qualities.

However, there are still unknowns regarding perennial floral plantings, especially for large-scale plantings that have been established on-farm. The full diversity of seed mixtures may not be realized when established (Forehand et al. 2006, Amy et al. 2018), and some seed mixtures do not perform well in the field (Carreck and Williams 1997). This can lead to floral plantings that do not always increase floral cover or richness compared to control areas. Additionally, most studies of floral plantings are conducted on small fields or in research plots and deal with small-scale plantings, sometimes only measuring a few square meters (Barbir et al. 2015, Pellissier and Jabbour 2018). This is particularly important because larger floral plantings can have different impacts on insect communities (Blaauw and Isaacs 2012, 2014b). Taken together, commercially available seed mixtures used by growers and established in large, commercial agroecosystems are understudied.

Beyond the qualities of floral communities, the possibility that floral plantings could produce ecosystem disservices must also be considered (Zhang et al. 2007). Floral plantings may provide resources for herbivorous insects, and can support increased populations of herbivores (Woodcock et al. 2008, Huusela-Veistola et al. 2016). Additionally, crop pests can move from cropland into nearby natural land or field margins (Blitzer et al. 2012), and floral plantings may provide resources and refuge to crop pests. Floral plantings can also increase herbivore abundance within nearby crops. Native wildflowers increased herbivore abundance in adjacent blueberry crops (Walton and Isaacs 2011), floral plantings increased *Lygus lineolaris* abundance in nearby strawberries (McCabe et al. 2017), and flowers increased the rate of herbivory by lepidopteran pests in adjacent tomato fields (Balzan et al. 2016). However, these results are counterbalanced by other work showing a neutral effect of wildflower plantings on herbivores in crops. A separate study on floral margins around blueberry fields found that floral plantings did not significantly increase herbivore abundance (Blaauw and Isaacs 2015), and wildflower strips next to oilseed rape were less attractive to pest species than the nearby crops, and did not harbor greater herbivore numbers (Hatt et al. 2015). While results are mixed, floral plantings do have the potential to support herbivores within field margins and nearby crops, and increased herbivore abundance needs to be assessed as a possible ecosystem disservice when establishing floral plantings on-farm.

To determine whether large-scale floral plantings established in commercial agroecosystems provide the changes to floral communities that are most beneficial to providing ecosystem services, and if they create potential ecosystem disservices by promoting herbivorous insects, this study addresses the following questions.

1. How does a commercially available seed mixture affect floral cover and floral richness when compared to unmanaged field margins?
2. Do floral plantings favor perennial, native, and intentionally planted flowering forbs compared to control margins?
3. Are floral traits (cover, richness, perennial and native flowers) consistent throughout the season in floral and control margins?
4. Do floral plantings impact herbivore abundance and communities within margins?
5. Do floral plantings impact herbivores within adjacent fields?

2.3 Methods

2.3.1 Experimental Design

Field work was conducted in conjunction with a commercial producer of potatoes in central Minnesota, who established floral plantings in the unmanaged margins of 42 central pivot-irrigated potato fields in 2015 and 2016. Both the size of the floral plantings (2,200-20,000 m^2), and the number of corners planted with the floral seed mixture (1-3 of the 4 available corners) varied depending on the field. Margins without floral plantings were left unmanaged.

Floral plantings consisted of a commercially available seed mixture marketed by Syngenta and Pheasants Forever as part of Operation Pollinator (Operation Pollinator 2020). The seed mixture consisted of two separate seed mixtures: one designed to promote honeybees, and the other to promote Monarch butterflies. Under this program, 50% of the area to be planted with flowers was to be given over to honeybee plantings, and 50% to Monarch plantings. The seed mixture for honeybees consisted of 3 species of grass and 16 species of flowering forbs, and the seed mixture for Monarchs consisted of 7 species of grass and 36 species of flowering forbs (Appendix 1). The honeybee seed mixture was largely a subset of the Monarch seed mixture, with only 4 forb species and 1 grass species not found in the Monarch mixture. In our study system, the grower who was participating in Operation Pollinator was unsure of exactly which fields had been sown with the honeybee mixture, and which had been sown with the Monarch mixture, or if the two seed mixtures had been combined. For this reason, we classified all floral plantings as the same for analysis.

Fields in the study area were on a 3-year rotation of potatoes, corn, and beans (either dry beans or soybeans depending on the field). In order to account for variation in management practices among different crops, only fields that were planted with potatoes were used in our study. Potato crops were conventionally managed, with fungicide applied twice a week, and an in-furrow neonicitinoid treatment at planting. Fields that were both planted with potatoes and had an established floral planting were assessed for suitability for this study. Some margins that had been planted with floral seed mixture had subsequently been destroyed by farm equipment or appeared to have failed to establish. Other areas while labeled as having been planted with flowers, showed no evidence of plantings (likely mislabeled). Thus, 20 fields that were both indicated by growers as having been planted with flowers and that appeared to have been planted with flowers upon on-site visual inspection early in the season (late May) were included in the study. Fields were selected whose margins were at least 400m apart from each other as well as from other floral plantings in the area. Fields with at least one corner planted with flowers and at least one corner left unmanaged were selected and all accessible margins sampled. To account for variation between fields, floral margins were compared to control margins on the same field. Six fields were sampled in 2017, eight fields in 2018, and six fields in 2019. Sampling occurred in early June, late June, late July, late August, and late September, for a total of five sampling dates per year.

2.3.2 Floral Sampling

Sampling consisted of floral transects conducted once a month. Floral transects began in the center of field margins, and extended perpendicular to the edge of the field for 15 meters. A 1x1 meter square of PVC tubing was placed at 5 meter intervals for a total of 4 sampling sites per margin, and all flowering forbs within the square counted and identified to species. All 4 sampling sites were pooled for analysis. Additionally, richness data was supplemented by a visual survey of the entire margin, where any common forb species the transect failed to capture were identified recorded as present. Flowers were identified in the field using the Wildflowers of Minnesota Field Guide (Tekiela 1999) and later verified in the lab using the website Minnesota Wildflowers (Minnesota Wildflowers 2020). Flowers that could not be identified in the field were photographed and cross-checked against Minnesota Wildflowers at a later date.

Floral cover was measured by counting the total number of flowers or inflorescences (depending on the species and flower morphology) and calculating the average flowering area for each species using flower size data available at Minnesota Wildflowers. Flower size measurements were verified with in-field observations. Area was summed for each transect location, and divided by the total area sampled to determine the percentage floral cover. Flowering forbs were identified as perennial/annual, and native/exotic. Finally, flowers were classified as “cultivated” if they were present in one or both of the Operation Pollinator seed mixture, or “unmanaged” if they were not present in either seed mixture.

Results were analyzed using generalized linear mixed effects models (GLMM) with the glmmADMB package (Skaug et al. 2016) in R (R Core Team 2020), (Version 3.3.2). Floral cover of perennial flowers per transect was divided by total floral cover to estimate the percent of the community that was perennial. The same technique was used to determine the percent native and cultivated floral cover. To determine how the presence of floral plantings impacted floral traits overall, separate analyses were run in which floral cover, floral richness, percent perennial cover, percent native cover, and percent cultivated cover were used as response variables. The presence of floral plantings (referred to as Treatment) was used as a fixed effect in all models. Field identity and sampling date (month nested within year) were used as random effects in all models to account for abiotic and landscape variability between fields, and repeated sampling throughout the year respectively. For all models related to floral cover and percent floral cover, variance was high, and negative binomial was selected as the distribution with a log link function. For floral richness data, a Poisson distribution was used.

To determine how floral traits varied by month, floral cover, floral richness, percent perennial cover, percent native cover, and percent cultivated cover were used as response variables in separate analyses, with treatment and month used as fixed effects, and field identity as a random effect. Similar to previous models, negative binomial was used as the distribution for models related to floral cover and percent cover, while Poisson was used for floral richness models.

2.3.3 Herbivore Sampling

Herbivores were sampled in field margins, and inside the crop at the edge, and 10, 30, and 50 meters into the field. Herbivore sampling was conducted via sweep net transects, and pitfall traps placed in pairs. Sweep-net transects consisted of 50 pendulum sweeps with a 38 cm diameter heavy canvas sweep net while walking slowly through the vegetation. Contents were transferred to 3.5 liter plastic storage bags and frozen for later analysis. Pitfall traps were created by burying 180 ml red solo cups up to their brim in the ground, and filling them 1/4 full of water with dish soap mixed in. Two pitfall traps were placed ~2 meters apart at each sampling location (Margin, edge, 10m, 30m, 50m), and were pooled for analysis. Pitfall traps were left in place for 18-24hrs, and then collected. The contents were filtered through squares of half-millimeter mesh and frozen.

Individuals were identified to family, and occasionally down to genus and species depending on the taxa and relevance of crop pest status.

Herbivore data from sweep net transects and pitfall traps were pooled together for analysis. The total number of herbivores per sampling location per field were summed to estimate overall herbivore abundance, and the same process was applied to individual taxa. Results were analyzed using GLMM in a similar manner to analyses for floral traits. To determine the impact of floral plantings on herbivore abundance, separate analyses were run for overall herbivore abundance within field margins, overall herbivore abundance within potato crops, and for individual taxa within field margins and within potato crops. Treatment was used as a fixed effect in all models, and sampling location in the crop was added as a fixed effect for analyses of arthropods within potato crops. Field identity and sampling date (month nested within year) were used as random effects, and negative binomial selected as the distribution, with a log link function. For herbivore taxa where fewer than 10 individuals were collected, no analyses were conducted.

2.4 Results

2.4.1 Floral Communities

Across all sampling dates, a total of 60 flowering forb species were identified. Of those, 23 were part of the seed mixtures (Table 2.1), while the remaining 37 were not part of either seed mixture (Appendix 2). Within floral planting margins, a total of 43 flowering forb species were found, compared to 39 flowering forb species in control margins. Floral plantings resulted in significantly higher floral cover when compared to control margins overall (z=6.81, p=9.9e-12), and margins with floral plantings had significantly higher floral richness than control margins (z=8.94, p=2e-16) (Fig. 2.1).

Separated by month, floral cover was highest in both floral and control margins in late June, July and August (Fig. 2.1). Floral richness was highest in late June and July in floral and control margins. Across the season, floral cover and richness were predominately increased by floral plantings. In early June, floral cover was very low in both floral and control margins, and plantings had no significant effect on floral cover (z=1.5, p=0.13), or floral richness (z=1.41, p=0.157). In late June, floral cover (z=4.56, p=5.10e-06) and richness (z=4.93, p=8e-07) were higher in floral margins. July had similar effects for cover (z=3.63, p=2.8e-04) and richness (z=6.36, p=2.1e-10), as did August cover (z=2.99, p=0.0028) and richness (z=2.07, p=0.039) and September cover (z=2.36, p=1.83e-02) and richness (z=3.31, p=0.00095) (Fig. 2.1).

The proportion of perennial floral cover was marginally significantly higher in floral plantings overall (z=1.7, p=0.088) (Fig. 2.2). However, this effect was not consistent throughout the season, with only August showing a marginal increase in the proportion of perennial floral cover in floral plantings (z=1.66, p=0.097) (Fig. 2.3). The proportion of native cover was significantly higher in floral margins overall (z=3.18, p=0.0015) (Fig. 2.2), although was also not consistent throughout the season (Fig. 2.3). Floral margins had a higher overall proportion of cultivated floral cover compared to unmanaged cover (z=5.28, p=1.3e-07) (Fig. 2.2). Other than early June (z=1.53, p=0.126), floral margins had a significantly greater proportion of cultivated cover throughout the season (Fig. 2.3).

2.4.2 Herbivores

Between 2017 and 2019, a total of 63,026 herbivores were collected. The presence of floral plantings did not impact the overall abundance of herbivores in margins (z=0.13, p=0.9) (Fig. 2.4). Floral plantings affected the abundance of herbivores throughout the season differently, with significantly fewer herbivores in floral margins in early June (z=-2.16, p=0.031). All other months had no significant effect of treatment. At the level of order, floral plantings contained significantly more herbivorous Coleoptera and Orthoptera (Table 2.1). Control margins had significantly more Hemiptera (Table 2.1), largely driven by the two most abundant taxa, Aphidae and Cicadellidae (Fig. 2.5).

Within potato crops, 4,629 herbivores were collected in crops adjacent to floral margins and 6,392 in crops adjacent to control margins. There was no overall effect of floral plantings in margins on herbivore abundance in potato crops (z=0.11, p=0.92) (Fig. 2.4). There was a significant effect of distance from field margins, with decreasing herbivore abundance further into the crop (z=-3.19, p=0.0014). Within potato fields, few herbivorous taxa were affected by the presence of floral margins, except for Orthoptera. Significantly more Orthoptera overall were found in fields adjacent to flowers as well as greater numbers of Gryllidae and Tettigoniidae, and marginally more Acrididae (Table 2.2). Throughout the year, the effect of flowers on in-crop herbivore abundance varied: In late June, flowers led to significantly more herbivores (z=2.12, p=0.034), while there was no effect in July (z=0.13, p=0.9), or August (z=-1.59, p=0.11).

2.5 Discussion

2.5.1 Floral Establishment

Floral plantings led to greater overall floral cover and floral richness when established in commercial agroecosystems. However, there was high variation between fields, and several cases where margins planted with flowers did not lead to greater cover compared to control margins. In a few cases, control margins actually had greater floral cover or diversity. This variation could be due to several factors. Many of the floral margins that had low cover or diversity were primarily grass. Preventing the spread and establishment of persistent grassy species is necessary for productive floral plantings (Pywell et al. 2005, Carvell et al. 2007), and in the cases of poor cover and richness, grass may have taken over after floral plantings were established. Differences in soil type or microclimate between fields also may have played a role in successful establishment (Amy et al. 2018), and differential success in floral plantings within studies is common (Scheper et al. 2015, Ouvrard and Jacquemart 2018).

Floral plantings did not result in all species in the seed mixture establishing, even when plantings increased cover, richness, and other desirable floral traits. Floral plantings in our study contained on average 3-4 flowering forb species at any given time, and even during peak richness in late June and July, had only 6 flowering forb species on average. These results indicate that the majority of forb species in the seed mixture did not bloom consistently or at all, especially considering many of the species are expected to bloom throughout multiple months. Other studies on floral plantings have had similar results, where diverse seed mixtures can either fail to create diverse plantings, or not all species present establish and bloom (Carreck and Williams 1997, Balzan and Moonen 2014, Williams et al. 2015). In some cases, this can lead floral plantings to be ineffective. Farms with floral plantings can have lower bee and flower diversity if floral plantings are species poor or rely too heavily on specific species to increase floral cover (Wood et al. 2015).

While many seed mixtures include numerous species, plantings where all species do not bloom still provide benefits, and the presence of specific forbs can be more impactful than increased richness. In a comparative study of different seed mixtures, of 94 different flowering forbs present, only 14 were considered crucial to maintaining the pollinator community, and 4 species supported 80% of flower visitors (Warzecha et al. 2018). Additionally, bee diversity was highest in the least speciose mixture tested (Warzecha et al. 2018). In another study, out of the 22 forb species found in floral plantings, 4 accounted for 85% of pollinator visits (Feltham et al. 2015). In flower-rich hay meadows, the majority of floral visits were to *Trifolium repens*, which was not included in the seed mix and grew out of the seed bank (Ouvrard et al. 2018). In large part, the benefits of increased floral richness seem to be most impactful at a low number of species. Seed mixtures containing 7-8 species can significantly improve attractiveness to pollinators and natural enemies compared to monoculture plantings (Gill et al. 2014). While increased floral richness is important, and monocultures of flowers do not appear to provide equivalent benefits to polycultures (Buchanan et al. 2018), the full diversity of a seed mixture does not necessarily need to be expressed in the field in order to see benefits (Williams et al. 2015), and more species-rich mixtures do not necessarily yield better results.

Creating floral plantings that provide floral resources throughout the year is a critical component of successful pollinator plantings in multiple growing regions (Williams et al. 2015). The presence of floral resources early and late in the growing season has been identified as particularly important (Scheper et al. 2015, Timberlake et al. 2019). In our study, floral plantings significantly increased floral cover and richness late in the season in September. However, floral plantings did not impact cover or richness in early June. This lack of increased cover and richness in the early season can be problematic for the function of floral plantings. Similar results in other studies led to decreased abundance of beneficial species and biocontrol services (Balzan and Moonen 2014, Balzan et al. 2014). The absence of floral resources can be detrimental to bumblebees as well, as they are dependent on early-season forage (Scheper et al. 2015). While flowering period alone is not a good predictor of overall attractiveness of floral plantings to insects (Carrié et al. 2012), it is important to the efficacy of floral plantings in agorecosystems.

The majority of the flowering forbs found in our study were perennial, and the majority of floral cover came from perennial flowers. While floral plantings resulted in a marginally greater proportion of perennial cover, the overall amount of perennial cover was greatly increased in floral plantings compared to control margins. A greater absolute amount of perennial cover could be more impactful than a greater proportion of perennial cover. The addition of select native perennials has been suggested as a way to improve seed mixtures (Gill et al. 2014), indicating that an increase in specific, targeted perennial species may make seed mixtures more attractive to beneficial insects. Additionally, increased perennial richness may be an important factor. Greater Heteroptera abundance and richness was associated with increased perennial richness in floral plantings (Frank and Künzle 2006).

Early June floral communities varied from other months significantly in numerous ways other than just cover and richness. The percent of perennial cover was low in both floral and control margins in early June, as was the percent native cover and percent cultivated cover. Most of the flowers that were found in both floral and control margins in early June were annual and biennial non-native plants that were not a part of the seed mixtures. Augmenting plantings with new species that are known to flower early could be beneficial to achieve the greatest success from floral plantings throughout the duration of the growing season.

2.5.2 Herbivores

Floral plantings did not increase the abundance of herbivores within floral margins compared to control margins. This is similar to the results of several previous studies, where floral plantings had no significant effect on herbivore abundance (Blaauw and Isaacs 2015, Hatt et al. 2015), and could result from a variety of causes. The floral plantings within our study system significantly increased the abundance of predatory taxa present within field margins (Middleton et. al, unpublished), likely leading to increased predation on many herbivorous taxa we observed. Additionally, herbivore abundance in floral plantings was spread more evenly across multiple taxa, (Fig. 2.5), and potentially prevented any one taxa from becoming highly abundant. The herbivore community in control margins was dominated by Hemiptera, with Cicadellidae and Aphidae in particular accounting for the majority of all individuals collected. Herbivores in floral plantings were notable more diverse, with Orthoptera, Coleoptera, and Miridae and representing a greater part of overall abundance (Fig. 2.5). Floral plantings can provide improved habitat for orthopterans (Jacot et al. 2007), and this was particularly apparent in our study. Additionally, floral plantings increased the abundance of Miridae, many of which were *Lygus lineolaris*. Floral strips led to increased *L. lineolaris* abundance in a previous study, and may provide improved forage for generalist pests (McCabe et al. 2017). Flowers have also been linked to increased abundance of phytophagous beetles in field margin plantings (Woodcock et al. 2008), similar to the results of our study. In another study, Auchenorrhycha abundance was lower in floral strips compared to control strips (Huusela-Veistola et al. 2016). The authors speculate this is because many Auchenorrhycha species feed on grass, while many heteropterans feed on forbs. These previous findings are consistent with our results that control margins, which normally had more grass, also had significantly greater numbers of Cicadellidae. Overall, floral plantings increased herbivore diversity, but did not increase abundance, similar to other studies (Blaauw and Isaacs 2012).

Within adjacent crops, herbivore abundance was also unaffected by the presence of floral margins. The edge of the crop had significantly higher herbivore abundance compared to locations further into potato crops. This result suggests that some herbivores were spilling over form margins to inhabit the adjacent potatoes. It is also important to note that fields in our study system were conventionally managed, with fungicide applied twice a week, and an in-furrow neonicitinoid treatment at planting. This may have had a homogenizing effect on the insect community within potato fields. However, even with the potential effects of conventional management, there were some observable differences between herbivores in crops adjacent to floral and control margins. Crops adjacent to floral margins had significantly greater numbers of Orthoptera, and on average had fewer Aphidae compared to crops adjacent to control margins. The increased similarity of in-crop communities is perhaps to be expected, considering crop monocultures are likely to support similar groups of herbivores. Large numbers of Chrysomelidae were also found in both floral and control fields in the form of Colorado potato beetle (CPB), the primary pest of concern for potato growers in this region. Floral plantings in our study had no significant effect on CPB abundance (Middleton and MacRae, unpublished).

2.6 Conclusions

Floral plantings in field margins have the potential to provide resources for beneficial insects and increase plant diversity in agroecosystems. When established on commercial, conventionally managed farms, floral plantings increased floral cover and floral richness across most of the growing season, and increased the percentage of perennial and native cover compared to control margins. Herbivore abundance within field margins and adjacent potato crops was unaffected, although herbivore communities had significant differences between floral and control areas. Floral plantings did not result in greater cover, richness, or proportion of native flowers in early June when floral resources are most needed to support beneficial insect populations. While many species in the seed mixture did not establish, large-scale floral plantings resulted in increased floral abundance and diversity, and more perennial and native species. Such plantings provide floral resources to promote pollinators and predators within agroecosystems, while not supporting increased herbivore populations.

2.7 Acknowledgements

We thank RD Offutt Farms for allowing the use of their fields for this study and for their collaboration on this project. We acknowledge the support and funding from the Northern Plains Potato Growers Association, the Sustainable Agriculture Research and Education Program, the Doctoral Dissertation Fellowship at the University of Minnesota, the Dayton Bell Museum Fund, and the MnDRIVE Global Food Ventures program. Additionally, we are grateful to George Heimpel, Daniel Cariveau, Elizabeth Borer, Lindsey Christianson, and Christopher Philips, and undergraduate technicians Noah Linck, Joe Nelson, Gus Fedje-Johnson, Lily Briggs, Erik Lucas, Lexie Ogdahl, Caroline Hofmeister, Eli Kleinschmidt, Bailey Brandel, and Samantha Meyers for their help in the field and laboratory.

2.8 Figures and Tables

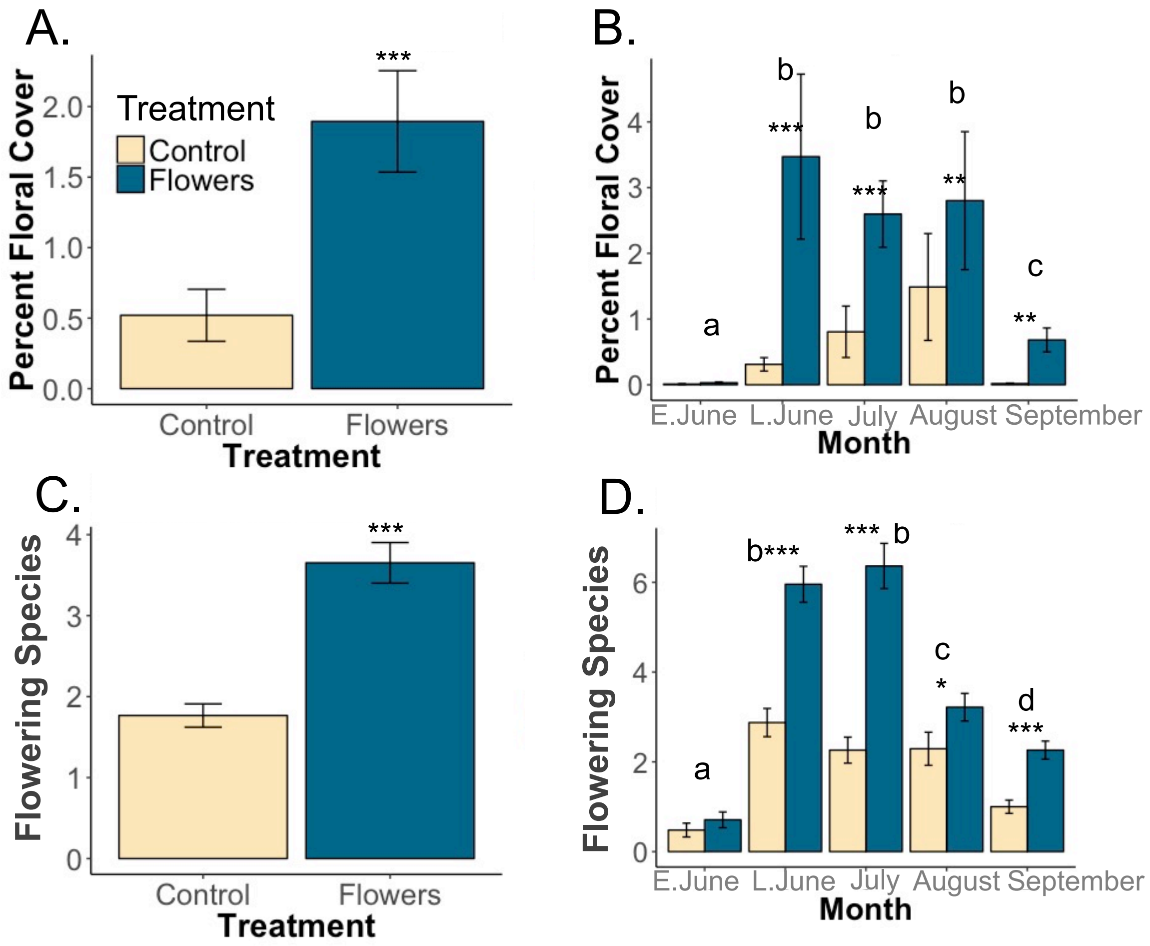

Figure 2.1. Floral cover A) overall and B) by month, and floral richness C) overall and D) by month in field margins. Bars represent mean cover and richness ,+/- 1 SE. Asterisks denote significant difference between treatments. * $p<0.05$, ** $p<0.01$, *** $p<0.001$. Letters denote significant differences in overall cover or richness between months.

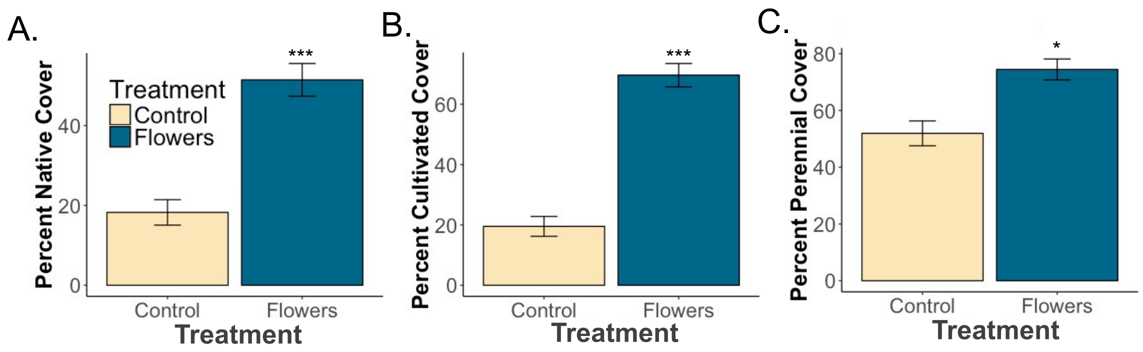

Figure 2.2. Percent of total floral cover that is A) Native, B) Cultivated (part of the floral plantings seed mixture), and C) Perennial, averaged across all months and years of study. Bars represent mean percentage +/- 1 SE. Asterisks denote significant difference between treatments. * p<0.05, ** p<0.01, *** p<0.001.

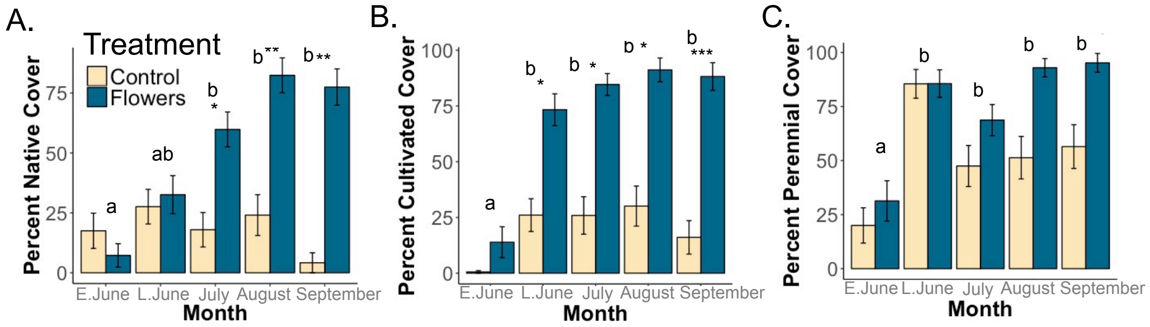

Figure 2.3. Percent of total floral cover that is A) Native, B) Cultivated (part of the floral plantings seed mixture), and C) Perennial by month. Bars represent mean percentage +/- 1 SE. Asterisks denote significant difference between treatments. * $p<0.05$, ** $p<0.01$, *** $p<0.001$. Letters denote significant differences in overall cover or richness between months.

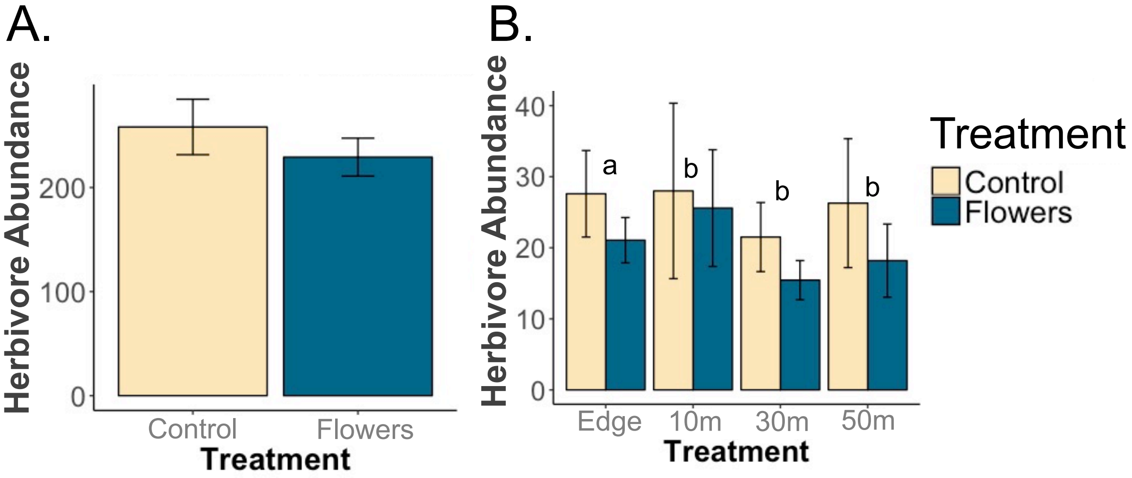

Figure 2.4. Overall herbivore abundance in A) Field margins and B) Adjacent potato crops separated by sampling location. Bars represent mean herbivore abundance +/- 1 SE. Asterisks denote significant difference between treatments. * p<0.05, ** p<0.01, *** p<0.001. Letters denote significant differences in abundance between locations.

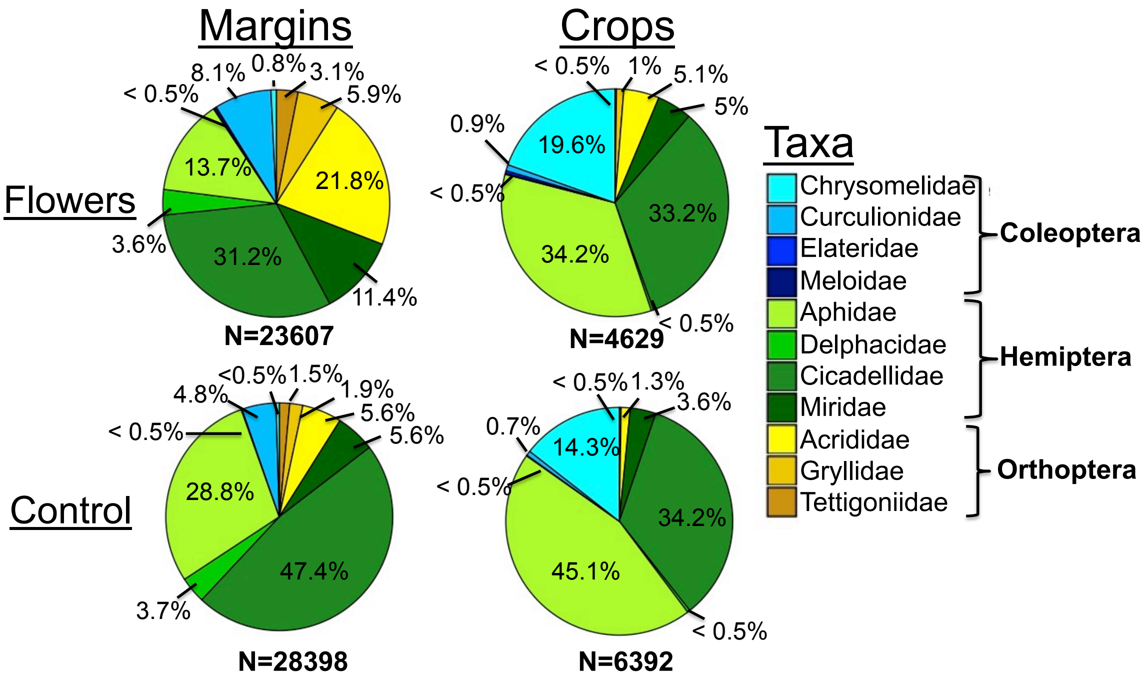

Figure 2.5. Herbivore community within floral and control margins and potato fields. Data summed across all years of study, and summed across all sampling locations within potato crops

Table 2.1. Flower species present in seed mixtures used in this study, and found in floral and control margins. "X" indicates species was present in a seed mixture, or observed in a field margin.

Common Name	**Scientific Name**	**Honeybee Mixture**	**Monarch Mixture**	**Found in Floral Margins**	**Found in Control Margins**
Alfalfa SD Common	*Medicago sativa*	X	X	X	X
Alsike Clover	*Trifolium hybridum*	X	X	X	X
Birdsfoot Trefoil	*Lotus corniculatus*	X	X	X	X
Crimson Clover	*Trifolium incarnatum*	X	X		
Sainfoin	*Onobrychis viciifolia*	X	X	X	
Hoary Vervain	*Vergena stricta*	X	X		
Maximillian Sunflower	*Helianthus maxmilliani*	X	X	X	
Partridge Pea	*Chamaecrista fasciculata*	X	X		
Phacelia	*Phacelia angelia*	X	X		
Showy Goldenrod	*Solidago speciosa*	X	X	X	X
Sky Blue Aster	*Aster azureus*	X	X	X	X
Smooth Blue Aster	*Aster laevis*	X	X		
Ladino White Clover	*Trifolium repens*	X		X	
Medium Red Clover	*Trifolium pratense*	X		X	X
White Blossom Sweet Clover	*Melilotus officinalis*	X		X	X
Yellow Blossom Sweet Clover	*Melilotus officinalis*	X		X	X
Black-Eyed Susan	*Rudbeckia hirta*		X	X	
Canada Milkvetch	*Astragalus canadensis*		X		
Common Milkweed	*Asclepias syriaca*		X	X	X
Evening Primrose	*Oenothera biennis*		X	X	
Ox-Eye Sunflower	*Heliopsis helianthoides*		X	X	
Foxglove Beardtongue	*Penstemon digitalis*		X		
Ironweed	*Veronia fasciculata*		X		
New England Aster	*Aster novae-angliae*		X		
Pale Purple Coneflower	*Echinacea pallida*		X		
Blue Sage	*Salvia azurea*		X		
Prairie Cinquefoil	*Potentilla arguta*		X		
Prairie Coneflower	*Ratibida columnifera*		X	X	
Purple Coneflower	*Echinacea purpurea*		X	X	
Purple Prairie Clover	*Dalea purpurea*		X	X	
Rough Blazingstar	*Liatris aspera*		X	X	
Sawtooth Sunflower	*Liatris aspera*		X		
Shell Leaf Penstemon	*Penstemon grandiflorus*		X	X	
Showy Tick Trefoil	*Desmodium canadense*		X		
Stiff Goldenrod	*Solidago rigida*		X	X	X
Stiff Sunflower	*Helianthus pauciflorus*		X		
Tall Boneset	*Eupatorium altissimum*		X		
White Prairie Clover	*Dalea candidum*		X		
White Yarrow	*Achillea millefolium*		X	X	X
Wild Bergamont	*Monarda fistulosa*		X	X	

Table 2.2. Herbivorous taxa sampled in field margins and potato crops. Count data are summed across all years of study. Within potato crops, data are summed across all sampling locations.

	Herbivore		**Margins**				**Potato Crop**			
Order	**Family**	**Genus/Species**	**Floral Margin**	**Control Margin**	**z value**	**p value**	**Floral Crop**	**Control Crop**	**z value**	**p value**
Coleoptera			2203	1546	4	6.40E-05	971	967	0.77	0.43853
	Chrysomelidae		179	134	1.54	0.12	906	917	0.23	0.819
		Alticini	79	32	0.87	0.38568	17	26	-1.36	0.17
		Diabrotica barberi	10	10	0.72	0.4709	0	3	-	-
		Leptinotarsa decemlineata	6	4	0.46	0.647	886	884	0.34	0.733
		Other spp	84	88	0.35	0.726	3	4	-	-
	Curculionidae		1914	1376	3.63	0.00028	40	43	0.45	0.65
	Elateridae		10	10	0.14	0.89	18	2	2.65	0.008
	Meloidae		100	26	1.88	0.0602	7	5	0.81	0.4182
Hemiptera			14124	24303	-2.52	0.012	3366	5325	-0.89	0.38
	Aphidae		3229	8183	-2.41	0.016	1583	2881	-0.5	0.62
	Delphacidae		856	1064	-0.82	0.41	16	25	-1	0.32
	Cicadellidae		7359	13461	-2.77	0.0056	1537	2186	-0.67	0.51
	Miridae		2680	1595	3.66	0.00025	230	233	-0.35	0.7291
		Lygus lineolaris	835	513	2.32	0.02	153	146	0.66	0.51
		Other spp	1845	1082	3.35	0.00082	77	87	-0.35	0.7291
Orthoptera			7280	2549	7.83	4.7E-15	292	100	3.65	0.00026
	Acrididae		5151	1600	6.52	7E-11	234	83	1.96	0.0503
	Gryllidae		1399	529	6.1	1.00E-09	48	15	2.65	0.008
	Tettigoniidae		730	420	3.67	0.00024	10	2	2.15	0.032

Chapter 3: Floral plantings in large-scale commercial agroecosystems support both pollinators and arthropod predators

3.1 Overview

1. Beneficial insect populations and the services they provide are in decline, largely due to agricultural land use and practices.

2. Establishing perennial floral plantings in the unused margins of crop fields can help conserve beneficial pollinators and predators in commercial agroecosystems. We assessed the impacts of floral plantings on both pollinators and arthropod predators when established adjacent to conventionally managed commercial potato fields.

3. Floral plantings significantly increased the abundance of pollinators within floral margins compared with unmanaged margins, and the effect increased with increasing floral cover within margins. The overall abundance of arthropod predators was also significantly increased in floral plantings, although it was unrelated to the amount of floral cover.

4. Within adjacent potato crops, the presence of floral plantings in field margins had no effect on the abundance of pollinators or predators, although higher floral cover in margins did increase in-crop pollinator abundance.

5. *Synthesis and Applications*: Our results show floral plantings increase the abundance of beneficial insects in field margins, but do not necessarily increase abundance in nearby crops. Establishing floral plantings on a large scale in commercial agroecosystems can help conserve both pollinators and predators, but may not increase ecosystem services. For the provision of ecosystem services, commercial growers should ensure plantings provide increased floral cover to promote in-field pollinator abundance.

Key Words: Agroecosystems, pollinators, predators, habitat management, floral plantings, floral resources

3.2 Introduction

Insect abundance and diversity is decreasing across many taxa worldwide (Potts et al. 2010, Dirzo et al. 2014, Hallmann et al. 2017). While there are many factors affecting this loss, the expansion and intensification of agriculture is a primary driver (Sandhu et al. 2008, Foley et al. 2011). In particular, commercial, conventionally managed agriculture has been highly disruptive to habitat on which insects rely (Kotze and O'Hara 2003, Tscharntke et al. 2005, Carvell et al. 2006, Koh et al. 2016). Beyond being a conservation concern, insects provide important ecosystem services. Within agriculture, biological control and pollination services provided by insect natural enemies and wild bees were estimated to be worth over $7.5 billion in the US (Losey and Vaughn 2006), and 35% of total crop production worldwide depends on pollinators (Klein et al. 2007). As human populations have grown, our reliance on these ecosystem services has also grown (Aizen et al. 2009, Calderone 2012). Additionally, many agricultural practices that are growing in popularity, such as organic farms, rely more heavily on biodiversity and benefit significantly more from ecosystem services when compared to conventionally managed agriculture (Sandhu et al. 2010).

Despite this reliance on insect-provided ecosystem services, the loss of insect abundance and biodiversity from agricultural practices leads to a loss of ecosystem function (Oliver et al. 2015). Reductions in insect numbers due to commercial agriculture can severely impact the benefits that humans receive from ecosystems, especially within agricultural settings themselves (Grab et al. 2019). Short of significant changes in diet or production methods, it is unlikely that agricultural intensity or overall land use will decrease in the future (Tilman and Clark 2014). Focusing on creating more sustainable existing agroecosystems will be beneficial to conservation efforts (Perfecto and Vandermeer 2010) and may help curb the loss of ecosystem services that benefit agricultural production.

Establishing plantings of perennial flowers in the unused margins of agricultural fields has been proposed as an effective method to both preserve biodiversity, and provide ecosystem services in agricultural settings (Korpela et al. 2013, Westphal et al. 2015). Floral plantings provide important forage such as nectar and pollen, as well as sources of prey, overwintering habitat, and improved microclimate for various insect taxa (Barone and Frank 2003, Haaland et al. 2011, Ramsden et al. 2014, Hoffmann et al. 2018, Ganser et al. 2019). Additionally, plantings in field margins are preferred by growers compared to in-field alternatives (Arbuckle 2015), and many growers are willing to consider creating plant and flower-rich plantings (Jacot et al. 2007, Arbuckle 2018).

Floral plantings have become increasingly popular in recent years, and have been most frequently investigated for their potential to promote pollinators and pollination services. The overall abundance of pollinators and of specific taxa can increase with the presence of wildflower plantings (Scheper et al. 2015, Kleijn et al. 2018), with bumblebees in particular responding positively to the addition of floral resources (Carvell et al. 2007, Williams et al. 2015). Floral plantings can also promote pollinators within nearby agricultural areas, and have both increased the abundance of wild bees and hoverflies in adjacent blueberry fields (Blaauw and Isaacs 2014a), and have been linked to greater numbers of wild bees in the surrounding landscape (Kleijn et al. 2018).

Pollinators that spill over from floral plantings into fields can provide valuable pollination services to a wide variety of crops (Blaauw and Isaacs 2014a, Feltham et al. 2015, Sutter et al. 2018).

Although much attention has been given to how floral plantings impact pollinators, plantings can also promote insect predators. Floral plantings can attract multiple predatory taxa and increase their abundance compared to control areas (Balzan et al. 2016, Tschumi, Albrecht, Collatz, et al. 2016). These predators can also spill over into adjacent crops and provide biological control services (Ramsden et al. 2014, Blaauw and Isaacs 2015, Woodcock et al. 2016). In some circumstances, the presence of natural enemies precludes the need for pesticide applications to control crop pests (Tschumi, Albrecht, Collatz, et al. 2016). Since floral plantings in agroecosystems can provide for pollinators and predators, several studies have examined if plantings can promote both at once. Wildflower plantings simultaneously increased pollinator and predator abundance (Pywell et al. 2015, Balzan et al. 2016, Campbell et al. 2017), and provided both increased biological control services and pollination services to nearby crops (Blaauw and Isaacs 2014a, 2015).

However, the efficacy of floral plantings can vary across agroecosystems due to crop type or the surrounding landscape (Tscharntke et al. 2005), and beneficial taxa can respond differently to plantings (Quinn et al. 2017, Sutter et al. 2018). Little research has been conducted on the impacts of floral plantings when implemented on-farm in commercial, conventionally managed agricultural landscapes, where the losses of insect abundance and diversity are most pronounced. Furthermore, the plantings that have been studied are often small, measuring only a few hundred square meters at most (although see Grass et al. 2016). This is particularly important because floral plantings of larger size can have different impacts on the number and type of insects that are attracted compared to smaller plantings (Blaauw and Isaacs 2014b, Quinn et al. 2017). To date, few studies have examined the impact of floral plantings on both pollinators and predators in commercial settings, especially for large plantings.

To determine how large, perennial floral plantings impact pollinators and predators in commercial agroecosystems, this study addresses four principal questions:

1. What impact do floral plantings have on pollinators in the margins of commercial agricultural fields?
2. How do floral plantings affect pollinators within agricultural fields?
3. What impact do floral plantings have on predators in the margins of commercial agricultural fields?
4. How do floral plantings affect predators within agricultural fields?

3.3 Materials and Methods

3.3.1 Experimental Design

Field work was conducted in central Minnesota, where a commercial potato grower established ~2 km^2 of floral plantings around 42 conventionally managed, center-pivot irrigated potato fields in 2015 and 2016. Floral plantings were created using a commercially available seed mixture marketed by Syngenta and Pheasants Forever (Operation Pollinator 2020) consisting of two varieties: a “Honeybee” mixture and a “Monarch” mixture (Appendix 1). Floral plantings were seeded in the unmanaged margins of the fields, in sections ranging from 2,200-20,000 m^2 depending on the available space. Plantings were established in 1-3 of the 4 available corners around the potato fields, while the remaining corners were left as unmanaged vegetation (Fig. 3.1).

Fields in the study area were on a 3-year rotation of potatoes, corn, and soybeans or dry beans. To minimize variability due to different crop types, only potato fields were sampled. Potato fields were conventionally managed, with biweekly aerial fungicide applications and an in-furrow neonicotinoid treatment at planting. Potato fields that had at least one corner planted with flowers and at least one corner left unmanaged, and had margins at least 400m apart were selected for this study. To minimize among-field climatic, soil, and surrounding landscape variability, floral margins were compared to control margins for the same field. Six fields were sampled in 2017, eight fields in 2018, and six fields in 2019. Sampling occurred approximately once a month from late May until late September for a total of five sampling dates per year. In 2018, sampling only took place May-August due to consistent cold temperatures and rain in September.

3.3.2 Floral Sampling

In our study system, the grower who established the floral plantings was unsure exactly which fields had been sown with which of the two seed mixtures, or if the mixtures had been combined. For this reason, we classified all floral plantings as the same for analysis, and measured floral cover to determine how well floral plantings established.

Floral cover was assessed for both floral and control margins via transects. A 1x1 meter square made of PVC tubing was placed at five meter intervals along a 15 meter transect, for a total four sampling sites per margin, and all flowers within the square were counted and identified to species. Flowering forbs were identified using the Wildflowers of Minnesota Field Guide (Tekiela 1999) and verified in the lab using the website Minnesota Wildflowers (Minnesota Wildflowers 2020). Floral cover was measured by counting the total number of inflorescences and calculating the average flowering area for each species using flower size data available at Minnesota Wildflowers, verified with in-field observation. Area was summed across all species and sampling sites for each field margin, and converted to average percent floral cover per square meter for final analysis.

3.3.3 Pollinator Sampling

Pollinators were sampled in field margins and inside the crop at four locations: the edge (0 meters), and 10, 30, and 50 meters into the field. Pollinator sampling was conducted via pollinator transects, sweep net transects, and pitfall traps placed in pairs. Pollinator transects consisted of timed walks with an aerial net, capturing all observed bees and hoverflies within 3 meters to either side. Transects in the margins of fields consisted of 5 minutes of active sampling time, and transects at all locations within the potato crop lasted 3 minutes each. Captured pollinators were transferred to a kill jar and frozen for later identification. Sweep-net transects consisted of 50 pendulum sweeps with a heavy canvas sweep net while walking slowly through the vegetation. Pitfall traps were created by burying 180 ml red solo cups up to their brim in the ground, and filling them 1/4 full of water with dish soap mixed in. Two pitfall traps were placed ~2 meters apart at each sampling location (Margin, edge, 10m, 30m, 50m), and were pooled for analysis. Pitfall traps were left in place for 18-24hrs, and then collected. All collected insects were frozen for later identification. Syrphidae were identified to family, and bees were identified to genus using taxonomic keys on the website Discover Life (Discover Life 2020). Pollinator data from pollinator transects, sweep nets, and pitfall traps were pooled together, and the total number of pollinators per sampling location per field were summed to estimate overall pollinator abundance both in field margins and within potato crops. The same process was applied to individual taxa.

3.3.4 Predator Sampling

Predators were sampled in field margins and inside the crop at the edge, and 10, 30, and 50 meters into the crop. Predator sampling was conducted via sweep net transects and pitfall traps, in the same manner as described for pollinators. Insect predators were identified to the family level, and non-insect arthropod predators identified to order, with the exception of the members of the spider families Salticidae and Thomisidae. Predator data were pooled together, and the total number of predators per sampling location per field summed to estimate overall predator abundance. Predators were further broken down into categories of Epigeal and Foliar for analysis. Epigeal predators were those in the insect families Carabidae, Staphylinidae, and the non-insect arthropod orders Opiliones and Chilopoda. Spiders found in the pitfall traps that were not Salticidae or Thomisidae were also classified as Epigeal. Foliar predators consisted of all other groups, as well as spiders that were captured in sweep net transects. Individual taxa were also assessed to determine how floral plantings impacted specific groups. This was done both within margins, and within the adjacent potato crops.

3.3.5 Data Analysis

Results were analyzed using generalized linear mixed effects models (GLMM) with the glmmADMB package (Skaug et al. 2016) in R (R Core Team 2020), (Version 3.3.2). To determine how floral plantings impact pollinator abundance, separate models were created with overall pollinator abundance in margins, overall pollinator abundance in crops, and bee abundance in margins and in crops as response variables. Abundances of individual pollinator taxa were also used as response variables in separate analyses. Treatment, percent floral cover, and their interaction were used as fixed effects in all models, where “Treatment” referred to whether field margins were planted with flowers (Flowers), or left unmanaged (Control). Models were created with all possible combinations of fixed effects, and compared via delta AIC values. Models with the lowest delta AIC were selected as the model of best fit. For analyses of in-crop pollinators, sampling location was also added as a fixed effect, alternatively as a continuous variable, and as a factor in separate analyses to determine overall effect of distance into the crop and differences between specific sampling locations respectively. Field identity and date (month nested within year) were included as random effects in all models to account for abiotic and landscape variability between fields, and repeated sampling throughout the year respectively. Count data were overdispersed, and negative binomial was selected as the distribution, with a log link function. For pollinator taxa where fewer than 10 individuals were collected, no analyses were conducted.

Models were constructed for predators in a similar manner. To determine how floral plantings impact predator abundance, separate models were created with overall predator abundance in margins, overall predator abundance in crops, and foliar and epigeal predator abundances in margins and in crops as response variables. Treatment, percent floral cover, and their interaction were used as fixed effects in all models, and location within crop added as a fixed effect for in-crop analyses. Field identity and date were used as random effects, with a negative binomial distribution. Models of best fit were selected via comparison of delta AIC values, and for predator taxa with fewer than

10 individuals, no analyses were conducted (All models and AIC values for pollinator and predators listed in Appendix 3).

3.4 Results

3.4.1 Pollinators

A total of 1,819 pollinators were collected from 2017-2019. Within field margins, floral plantings resulted in significantly greater pollinator abundance (Fig. 3.2), and higher floral cover corresponded to higher pollinator numbers (Table 3.1). Individual taxa responded differently to the presence of flowers in field margins. In all cases, floral plantings either significantly increased pollinator abundance, or there was no significant effect of treatment (Table 3.2). Bee abundance was significantly increased by floral plantings and by higher floral cover (Table 3.1). At the family level, higher numbers of Andrenidae were correlated with higher floral cover, while treatment did not have an effect. Apidae abundance increased with higher floral cover, and treatment. Floral plantings led to significantly higher numbers of Syrphidae, and Megachillidae, while floral cover did not have an effect (Table 3.2).

Within potato crops, the model of best fit for pollinators included treatment, floral cover, and the interaction between the two (Table 3.1). The presence of floral plantings in adjacent margins on their own had no effect on the total number of pollinators present in potato fields. However, increasing floral cover within field margins led to a significantly higher number of pollinators in adjacent potato crops, and higher floral cover in control margins had a significantly greater impact on pollinator abundance in adjacent crops compared to higher floral cover in floral margins (Fig 3.3). In-crop bee abundance was also positively related to higher floral cover, and this effect was significantly greater in crops adjacent to control margins (Table 3.1). Most individual pollinator taxa had too few individuals for in-crop analyses, although there were significantly more Halictidae in crops adjacent to control margins (z=-2.52, p=0.012). Increasing distance into potato crops resulted in marginally fewer pollinators (z=-1.77, p=0.076) and bees (z=-1.67, p=0.094) (Fig. 3.2).

3.4.2 Predators

A total of 17,139 predators were collected during this study. In field margins, treatment was the only fixed effect in models of best fit for overall predator and foliar predator abundance (Table 3.1). Floral plantings in field margins significantly increased overall predator abundance (Fig 3.4) and foliar predator abundance within margins. When analyzed separately, the amount of floral cover in field margins did not have a significant impact on the abundance of predators overall (z=0.83, p=0.4), or on foliar predators (z=1.11, p=0.27). For epigeal predators, treatment, floral cover, and their interaction were all part of the model of best fit (Table 3.1). Epigeal abundance was significantly increased by floral plantings, although greater floral cover led to significantly lower abundance. Increased cover in floral margins had a marginally less negative effect on epigeal predator abundance compared to increased cover in control margins (Fig 3.5).

The majority of measured taxa either had significantly higher abundance in floral margins, or were unaffected by treatment. At the level of order, Hemiptera and Opiliones had significantly higher abundances in floral margins. Control margins had significantly higher abundances of the family Coccinellidae (Table 3.3). Individual taxa had different responses to floral cover. At the level of order, increased floral cover in the margins led to increased abundance of predatory Coleoptera and Hemiptera. Araneae abundance declined with increasing floral cover. The abundance of several families of predators increased with increasing floral cover, such as Cantharidae, Anthocoridae, and Chysopidae adults. Staphylinidae also increased with higher floral cover, although the effect was only marginally significant. The abundance of spiders other then Salticidae and Thomisidae declined with increasing floral cover (Table 3.3).

Models of best fit for predators within fields had only floral cover as a fixed effect, with no significant effect of floral cover (Table 3.1). Analyzed separately, there was no significant effect of treatment on the overall abundance of predators within fields (z=0.18, p=0.86) (Fig. 3.4), or on the abundance of foliar (z=-0.16, p=0.87) and epigeal predators (z=0.61 p=0.54) (Fig. 3.6). Individual taxa were predominantly unaffected by treatment, with only Opiliones abundance significantly increased by floral margins (Table 3.4). Salticidae, Cantharidae, and Staphylinidae abundance increased with increasing floral cover in margins, while Thomisidae abundance declined (Table 3.4).

3.5 Discussion

3.5.1 Pollinators and Predators in Margins

We found both pollinator and predator abundance in field margins were increased by the presence of floral plantings. Our results are similar to numerous previous studies (Ramsden et al. 2014, Blaauw and Isaacs 2015, Venturini et al. 2017), and may be due to several factors. The seed mixture in this study has a high proportion of native plants and high species richness, which are linked to increased arthropod abundance and diversity in other studies (Jacot et al. 2007, Isaacs et al. 2009, Tonietto et al. 2017). This could explain in part why floral plantings here were successful in increasing predator abundance, when they have not always been in other studies (Haaland et al. 2011, Cox et al. 2014). Additionally, floral resources such as pollen and nectar are frequently a limiting resource for pollinators in agroecosystems (Roulston and Goodell 2011, Dicks et al. 2015), and establishing floral plantings can provide the sources of food pollinators require and increase their abundance.

The effects of floral cover on beneficial arthropod abundance in field margins are more complicated. While increased floral cover resulted in increased pollinator abundance, there was no effect of floral cover on overall predator abundance or foliar predator abundance, and a significant negative effect on epigeal predator abundance. From our results, it appears that pollinator abundance increases both with the presence of floral plantings, and increased floral cover, while predator abundance increases with the presence of floral plantings, and is unaffected or decreases with increased floral cover. In previous studies on pollinators, floral plantings that increased floral cover compared to control margins were more attractive to pollinators (Scheper et al. 2015), and floral density can be a stronger predictor of bee abundance than the presence or absence of plantings (Kleijn et al. 2018). From these studies, it appears that a greater number of flowers providing nectar and pollen results in greater bee abundance. For predators, improved microclimate (Barone and Frank 2003), alternative prey (Hoffmann et al. 2018), or other factors provided by floral plantings may be more important than a greater number of flowers overall (although see Ramsden et al. 2014). Studies on beetle banks have shown that increased habitat and shelter provided by plantings without flowers can have a positive impact on predators in agricultural settings (Thomas et al. 1991, Prasad and Snyder 2006). While not directly measured, the floral margins in our study system were composed of observably more dense, tall, and leafy foliage than control margins in most cases. This increased shelter and physical structure may provide the correct conditions to favor predators more so than increased floral cover.

The abundances of many individual pollinator taxa were positively correlated with floral margins. For pollinators, the genus *Bombus* responded most positively to the presence of flowers, similar to the results of many other studies (Pywell et al. 2005, Carvell et al. 2007, Korpela et al. 2013). Other genera more common in floral margins, such as *Apis*, *Melissodes*, and *Megachile,* are predominantly larger-bodied bees. In general, larger bees are capable of longer flights and greater foraging distances (Greenleaf et al. 2007), and therefore may be able to seek out patches of resources in the landscape to a greater degree than smaller and less mobile bees can. Floral plantings established in commercial agroecosystems similar to our study system may be more likely to support larger bees that are capable of traveling longer distances to reach floral plantings.

Many predatory taxa responded positively to floral plantings as well. Notably, the subfamily Phymatinae showed the greatest increase in relative abundance in floral margins. Phymatinae are ambush predators, and specifically wait on flowers for their prey (Balduf 1939). Similarly, Anthocoridae has been positively associated both with flowers and greater plant diversity (Lundgren et al. 2009, Atakan 2010), and was increased by floral margins and greater floral cover in our study. Two other taxa, Thomisidae and Cantharidae, were also increased in floral margins, and can be linked to a preference for flowers (Chittka 2001, Williams 2006). However, both Phymatinae and Thomisidae did not benefit from increasing floral cover as would be expected. Specific flower species found within floral margins may be more favorable towards these taxa, and influence their abundance more than overall floral cover.

Other predators were more abundant in floral margins that do not have a clear biological relationship to flowers, including several epigeal taxa and epigeal predators overall. For some taxa like Carabidae, increased vegetation cover in wildflower plantings has led to increased abundance and richness in previous studies (Frank and Reichhart 2004). The observed increase in epigeal abundance provides additional evidence that factors other than the presence of flowers per se have a stronger influence on predator abundance within floral plantings.

Although most predator groups were increased by the presence of floral plantings, Coccinellidae was significantly more abundant in control margins. This is particularly surprising seeing as coccinellid abundance often increases with the addition of floral plantings (Tschumi, Albrecht, Bärtschi, et al. 2016, Quinn et al. 2017), and ladybeetles are often used as example organisms that could benefit from increased floral diversity, as many species consume pollen and nectar (Bertolaccini et al. 2008, Lundgren 2009). Prey species favoring coccinellids may have been more prevalent in control margins, or microclimatic conditions within grassy areas could have been preferable over conditions within floral plantings.

3.5.2 Pollinators and Predators in Crops

Floral margins did not lead to greater numbers of pollinators or predators in adjacent crops, unlike the results of previous studies (Blaauw and Isaacs 2014a, Blaauw and Isaacs 2015, Kleijn et al. 2018). For pollinators, this may be at least partially due to the crop type: Potato flowers offer no nectar and require sonication to extract pollen, possibly limiting this resource to specific taxa such as bumblebees (Batra 1993). Potatoes next to control margins did attract a marginally significantly greater number of *Bombus*, and since control margins were more frequently lacking in floral resources, it follows that bumblebees may forage within adjacent potato fields to a greater extent. For most pollinators however, there may be little incentive to move into adjacent potato fields.

Our results showing more bees in floral margins, but fewer bees within potato crops near floral margins (Fig. 3.7), could also indicate that floral plantings are acting to concentrate bees more than being a source (Morandin et al. 2014). If floral plantings provide all the necessary resources for bees, and nearby crop fields offer little, it is unlikely bees will spill over into surrounding crops. Considering many bees will favor and return to resource rich patches (Osborne et al. 1999), floral plantings may serve to draw bees away from crops. While not necessarily a concern for conservation purposes, floral margins concentrating bees within margins could be problematic if floral plantings are expected to promote pollination services.

For predators, floral margins had little effect on abundance in potato fields, and almost no taxa measured within crops were significantly affected by this treatment. The one exception was Opiliones, possibly because some are highly mobile predators and spilled over from floral margins (Pinto da Rocha et al. 2007). Our results suggest that few predators are moving from crop margins into adjacent fields, contrary to the findings of other studies (Macfadyen, Davies, et al. 2015). Similar to pollinators, this may be due to a lack of resources within potato fields compared to field margins. Additionally, the predator communities within crops and within margins were very different from one another (Fig. 3.8). These differences further suggest that predators are not simply spilling over from margins. Instead, our results indicate that different predator communities inhabit crop fields compared to margins, and that while some spillover likely happens (as evidenced by higher abundances of predators in at the edge of the crop), the overall communities appear distinct.

3.6 Conclusions

Floral plantings provide a method to promote pollinators and predators within commercial agroecosystems, while limiting disruption to growers. Our results show that when floral plantings are established on a large scale on commercial farms, they increase the overall abundance of both pollinators and predators. In particular, pollinators respond positively to increased floral cover, whereas predators appear to benefit from other factors associated with the floral plantings. The numbers of beneficial insects did not increase in nearby potato fields however, indicating that floral plantings may act to concentrate pollinators and predators rather than export them to surrounding areas. These results can help policy-makers and growers determine how best to manage land in order to provide both for the conservation of beneficial insects, and for the ecosystem services they provide in commercial agroecosystems.

3.7 Acknowledgements

We thank RD Offutt Farms for allowing the use of their fields for this study and for their collaboration on this project. We acknowledge the support and funding from the Northern Plains Potato Growers Association, the Sustainable Agriculture Research and Education Program, the Doctoral Dissertation Fellowship at the University of Minnesota, the Dayton Bell Museum Fund, and the MnDRIVE Global Food Ventures program. Additionally, we are grateful to George Heimpel, Daniel Cariveau, Elizabeth Borer, and

Lindsey Christianson, and undergraduate technicians Noah Linck, Joe Nelson, Gus Fedje-Johnson, Lily Briggs, Erik Lucas, Lexie Ogdahl, Caroline Hofmeister, Eli Kleinschmidt, Bailey Brandel, and Samantha Meyers for their help in the field and laboratory.

3.8 Figures and Tables

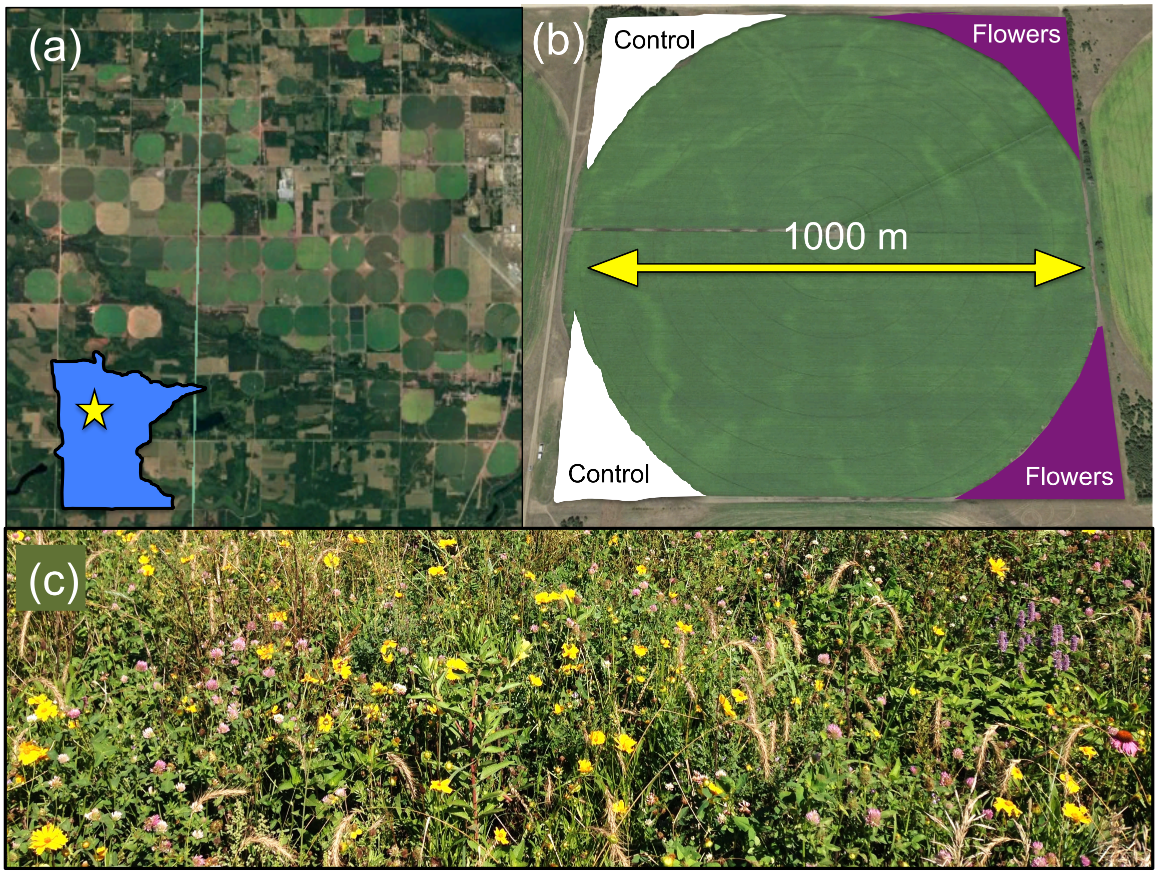

Figure 3.1. (a) Aerial image of representative section of study agroecosystem, and location within Minnesota designated by star. (b) Typical configuration of floral (purple) and control margins (white) around fields. (c) Typical floral margin mid-season

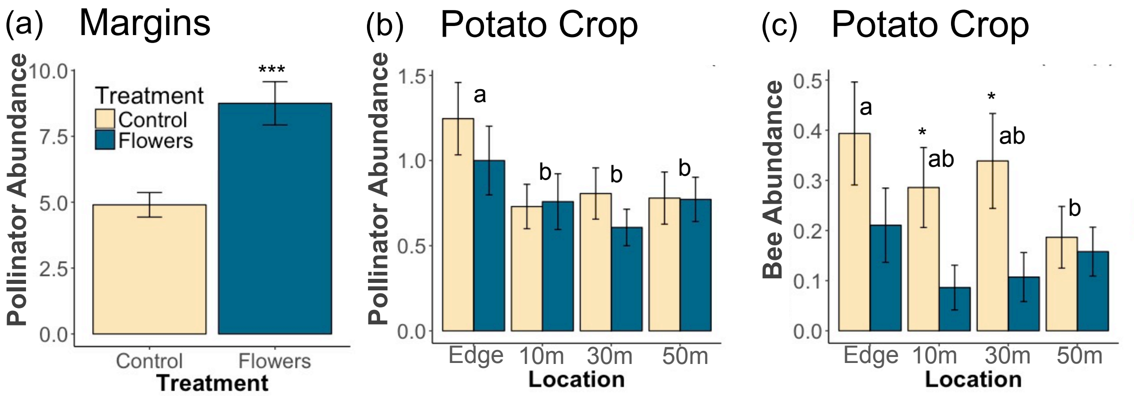

Figure 3.2. Mean (+/- 1 SE) abundance of (a) pollinators in field margins, (b) pollinators within potato crops, and (c) bees within potato crops. Asterisks denote significance between treatments (* p<0.05, ** p<0.01, *** p<0.001). Letters denote significant differences in overall abundance between locations.

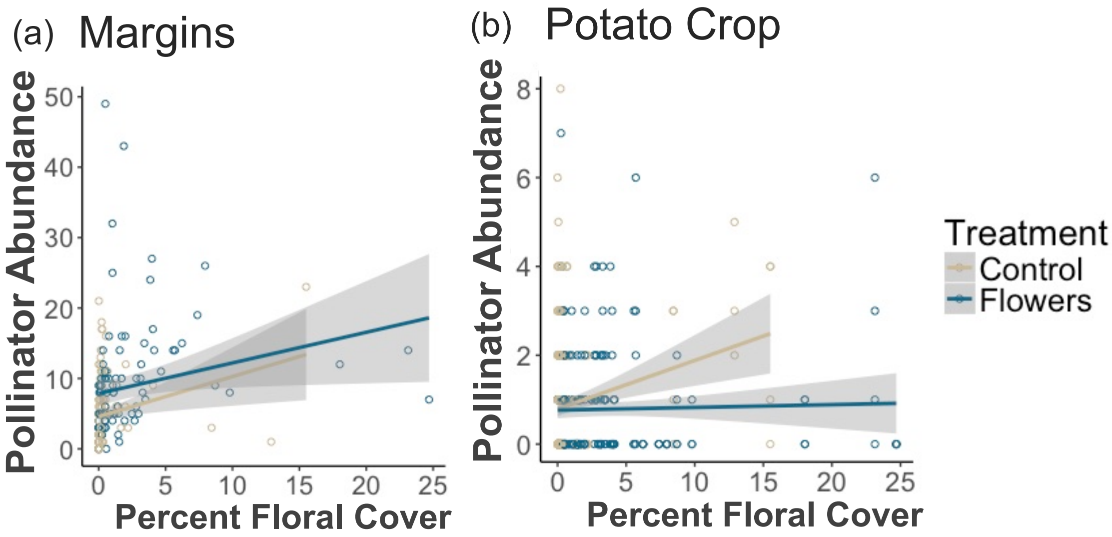

Figure 3.3. Effect of floral cover on pollinator abundance in (a) field margins and (b) potato crops. Shaded area represents 95% confidence interval. The effect of floral cover was significantly greater in crops adjacent to control margin compared to floral margins (z=-3.29, p=0.001).

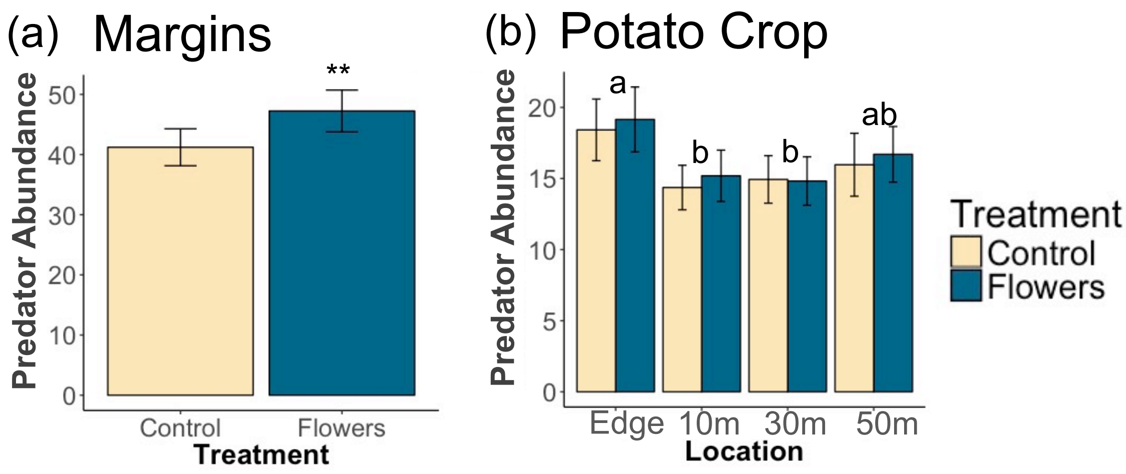

Figure 3.4. Mean (+/- 1 SE) abundance of (a) predators in field margins, (b) predators within potato crops. Asterisks denote significance between treatments (* $p<0.05$, ** $p<0.01$, *** $p<0.001$). Letters denote significant differences in overall abundance between locations.

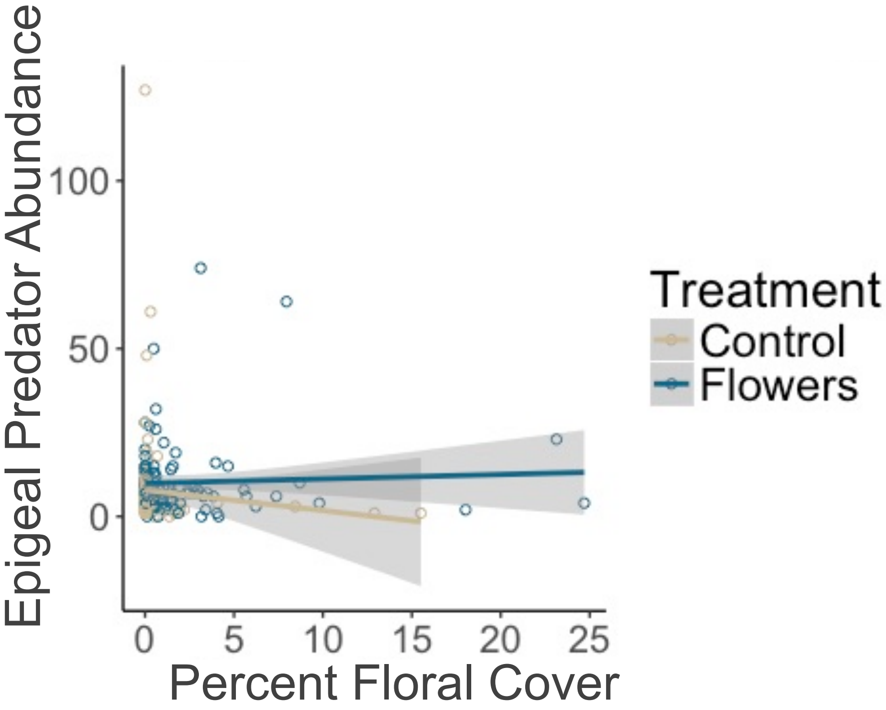

Figure 3.5. Effect of floral cover on epigeal predator abundance in field margins. Shaded area represents 95% confidence interval. The effect of floral cover was marginally less negative in floral margins compared to control margins (z=1.79, p=0.073).

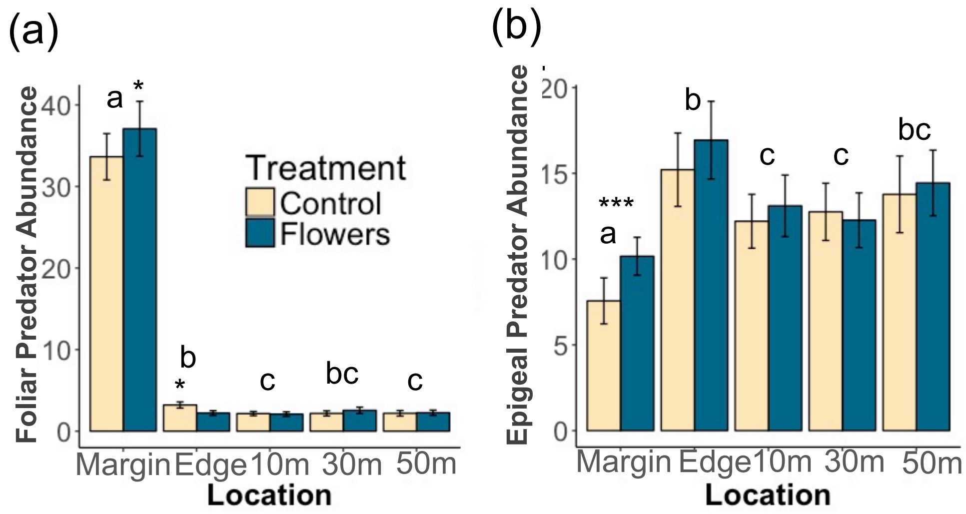

Figure 3.6. Mean (+/- 1 SE) (a) epigeal predator abundance, and (b) foliar predator abundance. Asterisks denote significance between treatments (* p<0.05, ** p<0.01, *** p<0.001). Letters denote significant differences in overall abundance between locations.

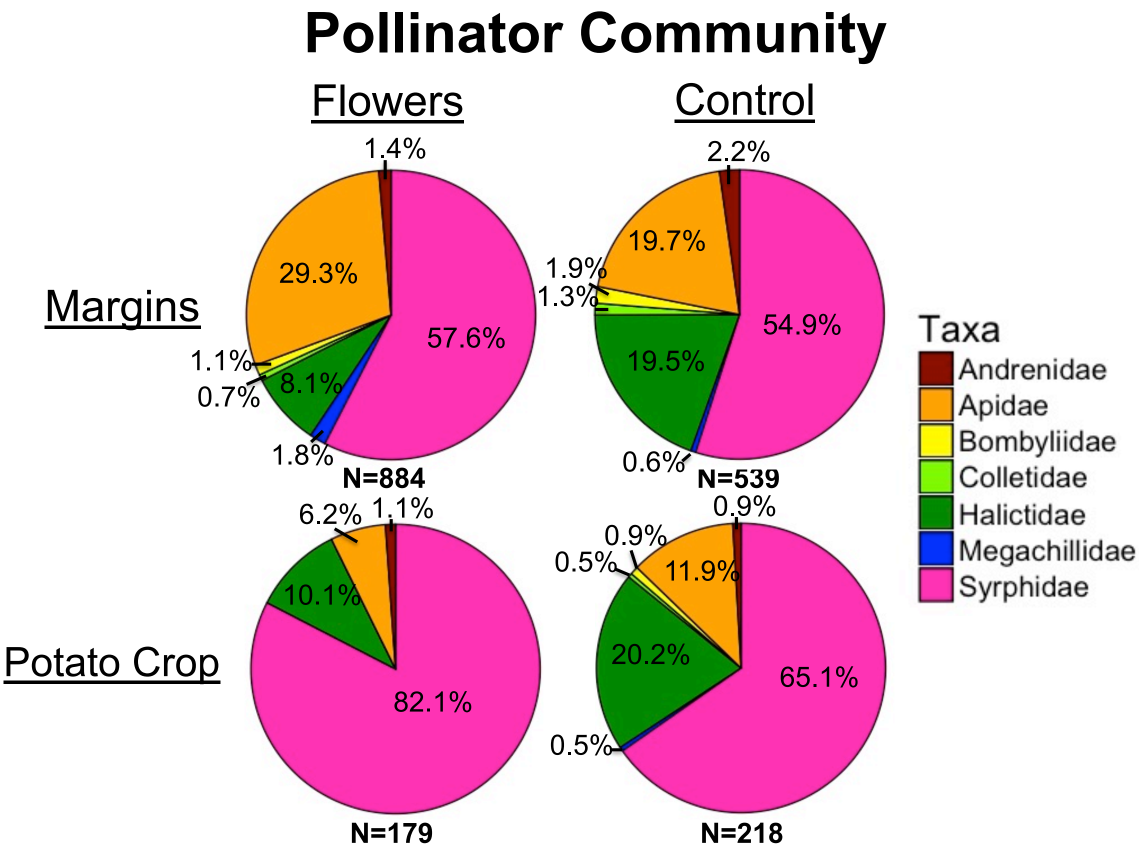

Figure 3.7. Pollinator community in margins and potato crops, with and without floral plantings.

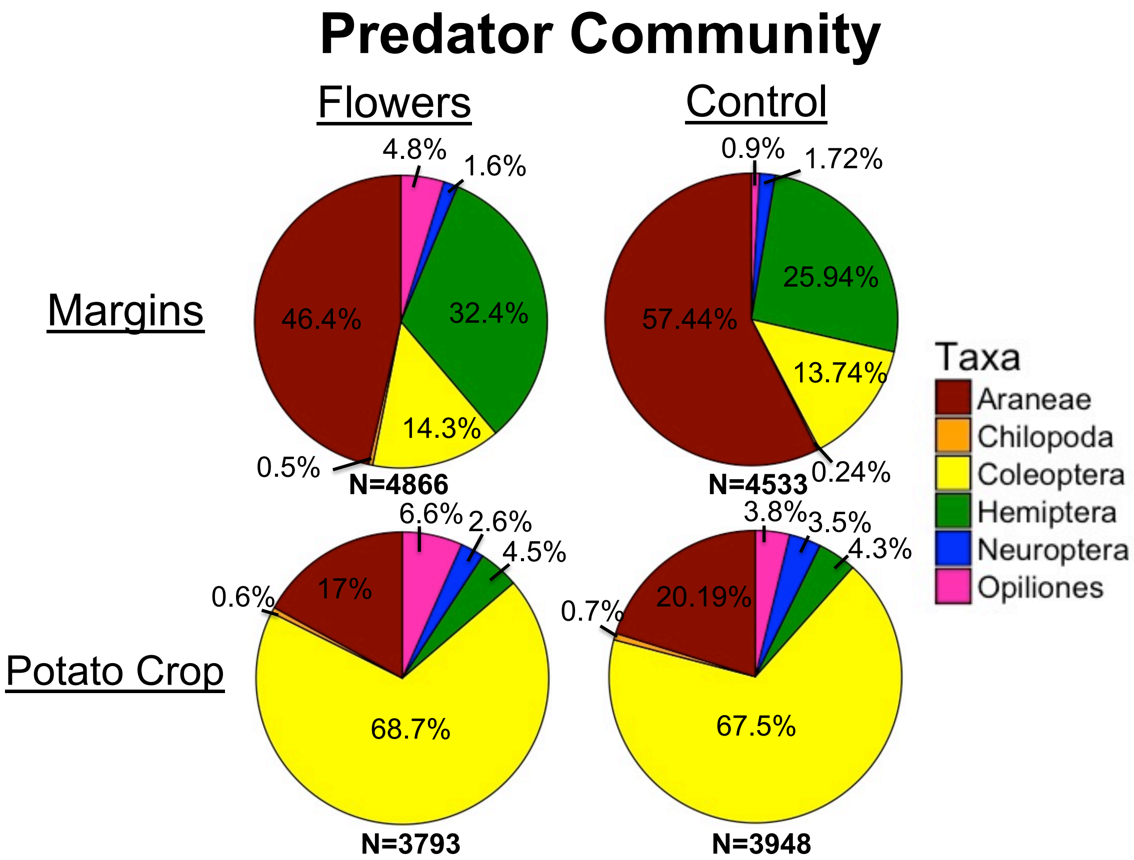

Figure 3.8. Predator community in margins and potato crops, with and without floral plantings.

Table 3.1. Models of best fit for pollinator and predator abundance within field margins and in potato fields. Models were selected via backwards elimination and comparison of AIC values.

			Model	Treatment			PercentCover			Interaction		
				Est. Std	z	p	Est. Std	z	p	Est. Std	z	p
Margin	Pollinators	Total	Treatment+Cover	0.4954	4.46	8.4e-06	0.0430	3.15	0.0016			
		Bees	Treatment+Cover	0.454	2.76	0.0057	0.110	4.08	4.5e-05			
	Predators	Total	Treatment	0.1917	2.65	0.008						
		Foliar	Treatment	0.171	2.09	0.036						
		Epigeal	Treatment*Cover	0.4001	3.28	0.001	-0.1232	-2.13	0.033	0.1107	1.79	0.073
Crop	Pollinators	Total	Treatment*Cover	0.0514	0.33	0.741	0.1351	3.92	8.9e-05	-0.1391	-3.29	0.001
		Bees	Treatment*Cover	-0.3176	-1.06	0.290	0.1170	2.48	0.013	-0.1833	-2.23	0.026
	Predators	Total	Cover				-0.00980	-1.1	0.27			
		Foliar	Cover				-0.00448	-0.36	0.72			
		Epigeal	Cover				-0.00897	-0.87	0.38			

Table 3.2. Pollinator abundance, z values, and significance by treatment and floral cover within field margins. Bolded values are significant ($p<0.05$). Taxa with fewer than 10 individuals were not analyzed.

				Margins			
Pollinator		Number of Individuals		Treatment		Floral Cover	
Family	Genus	Flowers	Control	z value	Significance	z value	Significance
Bombyliidae		10	10	0.67	0.5	-0.16	0.88
Syrphidae		509	296	4.06	**4.90E-05**	1.38	0.16897
Andrenidae		12	12	-0.22	0.82	3.53	**0.00041**
	Andrena	12	10	0.13	0.9	2.73	**0.0063**
	Calliopsis	0	1	---	---	---	---
	Perdita	0	1	---	---	---	---
Apidae		259	106	5.15	**2.60E-07**	4	**6.40E-05**
	Anthophora	0	1	---	---	---	---
	Apis	88	33	2.43	**0.015**	3.28	**0.001**
	Bombus	128	49	4.17	**3.10E-05**	3.78	**0.00015**
	Ceratina	5	12	-0.99	0.32261	-0.93	0.3535
	Epeolus	1	0	---	---	---	---
	Melissodes	36	10	2.86	**0.0042**	2.69	**0.0071**
	Nomada	1	1	---	---	---	---
Colletidae		6	7	-0.22	0.82	0.82	0.41
	Colletes	0	1	---	---	---	---
	Hylaeus	6	6	0.02	0.98	-1.24	0.22
Halictidae		72	105	-0.5	0.62	0.01	0.988
	Agapostemon	6	4	0.71	0.47	-1.06	0.29
	Augochlora	1	0	---	---	---	---
	Augochlorella	7	11	-0.29	0.77138	-1.14	0.25394
	Halictus	4	7	-0.44	0.66	0.25	0.81
	Lasioglossum	52	79	-1.03	0.303	-0.47	0.6349
	Sphecodes	2	4	---	---	---	---
Megachilidae		16	3	2.69	**0.0071**	1	0.32
	Ashmeadiella	1	0	---	---	---	---
	Heriades	0	1	---	---	---	---
	Hoplitis	2	0	---	---	---	---
	Megachile	10	1	2.39	**0.017**	1	0.3164
	Osmia	3	1	---	---	---	---

Table 3.3. Predator abundance, z values, and significance by treatment and floral cover within field margins. Bolded values are significant ($p<0.05$). Taxa with fewer than 10 individuals were not analyzed.

			Margins					
	Predator		Number of Individuals		Treatment		Cover	
Order	Family	Genus/Species	Flowers	Control	z value	Significance	z value	Significance
Araneae			2260	2604	-0.39	0.7	-2.69	**0.0072**
	Salticidae		156	212	-0.11	0.91	0.65	0.52
	Thomisidae		271	180	3.22	**0.0013**	0.39	0.696
	Other spp		1833	2212	-0.91	0.36	-3.34	**0.00085**
Chilopoda			22	11	1.76	0.079	0.68	0.5
Coleoptera			697	623	1.6	0.11	2.85	**0.0043**
	Cantharidae		209	100	1.96	0.0501	2.39	**0.017**
	Carabidae		218	132	3.68	**0.00023**	-0.08	0.94
	Coccinellidae		96	289	-3.39	**0.00069**	1.29	0.2
		Adults	79	169	-2.68	**0.0074**	1.58	0.11
		Larvae	17	120	-2.39	**0.017**	-0.12	0.903
	Staphylinidae		174	102	2.51	**0.012**	1.72	0.085
Hemiptera			1579	1176	3.62	**3.00E-04**	2.97	**0.003**
	Anthocoridae		759	680	2.1	**0.036**	3.83	**0.00013**
	Lygaeidae	*Geocoris* spp	77	80	0.88	0.377	-0.9	0.366
	Nabidae		255	232	1.29	0.2	-0.28	0.78
	Pentatomidae	*Podisus maculiventris*	1	0	---	---	---	---
	Phymatinae		245	97	4.88	**1.00E-06**	1.05	0.29
	Reduviidae		242	87	5.5	**3.70E-08**	0.58	0.56
Neuroptera			76	78	0.26	0.798	1.4	0.1617
	Chrysopidae		73	77	0.09	0.926	1.38	0.1668
		Chrysopa spp Adult	25	27	-0.24	0.81	2.11	**0.035**
		Chrysopa spp Larvae	48	50	0.24	0.8137	0.7	0.48242
	Hemerobiidae		3	1	---	---	---	---
Opiliones			232	41	4.71	**2.50E-06**	0.47	0.642

Table 3.4. Predator abundance, z values, and significance by treatment and floral cover within potato crops. Bolded values are significant ($p<0.05$). Taxa with fewer than 10 individuals were not analyzed.

			Potato Crop					
	Predator		Number of Individuals		Treatment		Cover	
Order	Family	Genus/Species	Flowers	Control	z value	Significance	z value	Significance
Araneae			644	797	-0.19	0.84577	-1.11	0.26908
	Salticidae		25	24	0.09	0.93	2	**0.045**
	Thomisidae		54	62	0.09	0.93	-2.2	**0.028**
	Other spp		565	711	-0.26	0.7913	-0.75	0.454
Chilopoda			23	29	-0.17	0.86	0.74	0.46
Coleoptera			2606	2664	0.04	0.97	-0.68	0.5
	Cantharidae		7	9	0.12	0.902	2.01	**0.045**
	Carabidae		1493	1590	-0.03	0.97	0.35	0.72
	Coccinellidae		26	30	-0.06	0.95	-0.06	0.96
		Adults	25	24	0.53	0.6	0.21	0.83
		Larvae	1	6	---	---	---	---
	Staphylinidae		1080	1035	0.85	0.3972	-2.01	**0.04473**
Hemiptera			169	169	-0.14	0.892	-1	0.315
	Anthocoridae		153	147	0.36	0.716	-1.14	0.2528
	Lygaeidae	*Geocoris* spp	3	3	---	---	---	---
	Nabidae		9	14	-0.7	0.49	0.12	0.9
	Pentatomidae	*Podisus maculiventris*	0	0	---	---	---	---
	Phymatinae		0	3	---	---	---	---
	Reduviidae		4	2	---	---	---	---
Neuroptera			99	139	-0.82	0.4145	0.64	0.5223
	Chrysopidae		96	135	-0.85	0.398	0.57	0.5694
		Chrysopa spp Adult	33	42	-0.46	0.65	0.41	0.68
		Chrysopa spp Larvae	63	93	-1.12	0.2635	0.08	0.9331
	Hemerobiidae		3	4	---	---	---	---
Opiliones			252	149	4.05	**5.20E-05**	0.8	0.423

Chapter 4: Wildflower plantings in commercial agroecosystems promote generalist predators of Colorado potato beetle

4.1 Overview

Wildflower plantings in agroecosystems can support arthropod predators, and may have the potential to increase conservation biological control of pest species in nearby crops. Colorado potato beetle (CPB) is a significant defoliator of potato that is resistant to many forms of management. Promoting natural enemies of CPB by establishing perennial wildflower plantings in field margins may provide a measure of control for this pest. We examined the impacts of floral plantings on the abundance of known CPB predators, predation of CPB egg masses, and CPB populations in a commercial agroecosystem. Floral plantings increased the abundance of CPB predators, but did not significantly increase the rate of predation of sentinel CPB egg masses within field margins. Within nearby potato fields, predator abundance and predation rates on CPB eggs were unaffected by the presence of flowers. Colorado potato beetle abundance in potato fields was also not impacted by floral plantings. However, floral margins may provide improved overwintering opportunities for CPB, and further investigation is needed. Perennial wildflower plantings show potential for attracting predators that prey on Colorado potato beetle, but these benefits do not extend into nearby potato crops.

Keywords: Colorado potato beetle, floral resources, predators, conservation biological control, natural enemies, wildflowers

4.2 Introduction

Arthropod predators can provide valuable pest suppression services in agricultural landscapes. In the US alone, pest control by wild insects has been estimated to be worth

~$4.5 billion each year (Losey and Vaughn 2006), and insect predators provide important services in a wide variety of cropping systems (Letourneau et al. 2009, Perdikis et al. 2011). However, many crops are grown in commercial, homogeneous agroecosystems, which are often low in plant diversity and scarce in resources for predatory arthropods (Foley et al. 2011, Gonthier et al. 2014). Commercial agroecosystems such as these make it difficult for beneficial predators to persist, and limit the services they can provide (Tscharntke et al. 2005, Oliver, Isaac, et al. 2015).

Increasing plant diversity in agroecosystems by establishing plantings of perennial flowers and grasses in the unused margins of fields can help reverse this trend and increase predator abundance and pest control (Letourneau et al. 2009, Haaland et al. 2011). Floral plantings such as these can provide alternative prey (Hoffmann et al. 2018), nectar (Ramsden et al. 2014), overwintering habitat (Ganser et al. 2019), and improved microclimate (Barone and Frank 2003) that sustain predator populations. Floral plantings have been shown to attract greater numbers of multiple predatory taxa compared to control areas (Balzan et al. 2016, Tschumi, Albrecht, Collatz, et al. 2016), and increase their abundance in nearby crops (Walton and Isaacs 2011). Floral plantings have also been linked to increased biological control services and reduced pest abundance in a variety of crops. For example, flowers in field margins significantly decreased pest pressure and insecticide applications in rice (Gurr et al. 2016), increased biological control services in blueberry (Blaauw and Isaacs 2015) and strawberry (Grab et al. 2018), and reduced pest numbers and feeding damage in wheat (Tschumi et al. 2015, Tschumi, Albrecht, Bärtschi, et al. 2016, Woodcock et al. 2016). Predators attracted and supported by flowers can help suppress a variety of pest species, and could help to manage pests that have proved difficult to control via conventional means.

Colorado potato beetle, *Leptinotarsa decemlineata* Say (Coleoptera: Chrysomelidae) (CPB) is a prolific pest of potato, capable of causing significant yield losses (Hare 1990, Weber 2003, Liu et al. 2012), and is widely considered to be the primary insect pest of concern for many potato growing regions (Alyokhin et al. 2008, Giordanengo et al. 2013). Colorado potato beetle has historically been difficult to manage, stemming in large part from its ability to evolve resistance to a variety of different insecticides (Casagrande 1987, Whalon et. al 2019). Despite this, insecticide applications remain the primary control method for beetle infestations (Giordanengo et al. 2013, Huseth et al. 2014), even though the long term viability of this approach is in question (Alyokhin et al. 2015).

Conservation biological control of CPB shows some promise. A number of specialist insect predators and parasitoids have been found to significantly reduce CPB numbers, including *Perillus bioculatus* Fabricius (Hemiptera: Pentatomidae) and *Lebia grandis* Say (Coleoptera: Carabidae) (Biever and Chauvin 1992, Cloutier and Bauduin 1995, Weber et al. 2006). Generalist predators in the families Chrysopidae, Carabidae, Nabidae, Salticidae, Opiliones, and some coccinelids such as *Coleomegilla maculata* De Geer (Coleoptera: Coccinellidae) and *Hippodamia convergens* Guérin-Méneville (Coleoptera: Coccinellidae) can also reduce CPB numbers (Drummond et al. 1990, Heimpel and Hough-Goldstein 1992, Hilbeck and Kennedy 1996, Hilbeck et al. 1997). Many of the main predators of CPB prey upon early instar larvae or eggs (Groden et al. 1990, Cappaert et al. 1991), including all of the above listed natural enemies (Hough-Goldstein et al. 1993). Predation of CPB eggs by generalist predators has been observed to be density-independent, allowing it to be compatible with control methods that reduce colonizing CPB populations (Hilbeck et al. 1997). Furthermore, abundant and well synchronized predators can effectively control CPB numbers on their own (Cappaert et al. 1991).

Promoting predators through the use of floral plantings could help control CPB populations and prevent outbreaks from occurring. Predators attracted by floral plantings often include known natural enemies of CPB (Walton and Isaacs 2011, Balzan and Moonen 2014), and when floral plantings were established adjacent to potato fields in a previous study, they drew in predators and reduced aphid abundance in the crop (Tschumi, Albrecht, Collatz, et al. 2016). Additionally, while potatoes are often intensively managed with pesticides (Giordanengo et al. 2013), floral plantings have still been shown to provide benefits in conventionally managed crops treated with insecticides (Gurr et al. 2016). However, the efficacy of floral plantings vary, and depend largely on the surrounding landscape, crops, and pests in question (Tscharntke et al. 2005, 2016). Additionally, little research has been conducted on the impact of floral plantings on natural enemies or biological control of crop pests when implemented in a commercial agricultural landscape. To date, no studies have examined the impact of floral plantings on conservation biological control of CPB.

Although floral plantings can provide benefits, there are also potential negative outcomes associated with them. Floral plantings can increase the number of herbivorous insects in and around crops, and pests could move from crops into adjacent floral plantings (Walton and Isaacs 2011, Blitzer et al. 2012). Colorado potato beetle adults often overwinter in field margins, and may prefer areas with greater cover or vegetational structure (Weber and Ferro 1993). It is therefore critical to evaluate not just the potential benefits that floral plantings may provide in controlling CPB, but also whether plantings provide improved refuge or overwintering habitat to CPB.

In order to determine how floral plantings impact Colorado potato beetle and its natural enemies, this study addresses the following questions:

1) Do floral plantings affect the abundance of known predators of CPB?

2) Do floral plantings increase predation of CPB egg masses?

3) How do floral plantings influence the abundance of CPB within adjacent potato fields?

4) Do floral plantings provide improved overwintering habitat or refuge for CPB?

4.3 Materials and Methods

4.3.1 Experimental Design

Field work was conducted in central Minnesota, where a large commercial producer of potatoes established approximately 2 km^2 of floral plantings distributed around 42 of their center-pivot irrigated potato fields in 2015 and 2016. Floral plantings were created using a commercially available seed mixture marketed by Syngenta and Pheasant Forever (Operation Pollinator 2020) (Table 4.1). Floral plantings were seeded in the unmanaged margins of the fields, in sections ranging from 2,200-20,000 square meters. Depending on the location, between 1-3 of the four available corners around the potato fields were planted with floral seed mixture, while the remaining corners were left unmanaged (Fig. 4.1).

Fields in the study area were part of a 3-year rotation of potatoes, corn, and soybeans or dry beans. Potato fields were conventionally managed, with aerial applications of fungicide on a biweekly basis, and an in-furrow neonicotinoid treatment at planting. Fields that were planted with potatoes in a given year and had at least one margin with a floral planting and at least one margin left unmanaged were selected and all accessible margins sampled. All sampled field margins were at least 400 meters apart from one another and from any floral plantings on nearby fields. To account for variability between fields, floral margins were compared to control margins on the same field. Six fields were sampled in 2017, eight fields in 2018, and six fields in 2019. Sampling occurred approximately once a month from early June-September for a total of five sampling dates per year. In 2018, sampling only took place early June-August (i.e. four sampling dates) due to consistent rain and cold temperatures in September.

4.3.2 Insect Sampling

Predators and Colorado potato beetle were sampled both in field margins and within the crop itself. Sampling in field margins took place in the center of margins, ~20 meters from the edge of the crop. Sampling was conducted at four locations within potato crops: at the edge, and at 10, 30, and 50 meters into the field. Arthropods were sampled via sweep net transects, and pitfall traps placed in pairs at each location. Sweep-net transects consisted of 50 pendulum sweeps with a 38 cm diameter heavy canvas net while walking slowly through the vegetation. Contents were transferred to 3.5 liter plastic storage bags and frozen. Pitfall traps were created by burying 180 ml red Solo cups (Dart Container Corp. Mason MI) up to their brim in the ground, and filling them 1/4 full of water mixed with dish soap. Pitfall traps were left in place for 18-24 hrs, collected, and had contents strained through ½ millimeter mesh. Collected samples were frozen for later identification.

Insects and other arthropods were identified to family, and occasionally species for specialist predators and for CPB adults and larvae. Predators were identified as known CPB predators according to results of previous studies cataloging generalist predators that were found to prey upon CPB (Heimpel and Hough-Goldstein 1992, Hough-Goldstein et al. 1993, Hilbeck and Kennedy 1996, Hilbeck et al. 1997).

Results were analyzed using generalized linear mixed effects models (GLMM) with the glmmADMB package (Skaug et al. 2016) in R (R Core Team 2020), (Version 3.3.2). The total number of predators per sampling location per field per year were summed together to estimate overall predator abundance, and the same process was applied to individual taxa and CPB to assess how floral plantings impacted specific groups. This was done both for arthropods found within margins, and for those within adjacent potato crops. To test how floral plantings impacted arthropod abundance, separate analyses were run for predators within field margins, predators within potato crops, and CPB within potato crops. The presence of floral plantings (referred to as Treatment) was used as a fixed effect in all models, and sampling location in the crop was added as a fixed effect for analyses of arthropods within potato crops. Field identity and sampling date (month nested within year) were used as random effects in all models to account for abiotic and landscape variability between fields, and repeated sampling throughout the year respectively. For all models, data were overdispersed with high variance, and negative binomial was selected as the distribution with a log link function. For taxa where fewer than 10 total individuals were collected, analyses were not conducted.

4.3.3 Measuring Predation

Predation on Colorado potato beetle was assessed by deploying sentinel prey egg masses in the margins of fields, and at the edge of potato crops. Masses of CPB eggs were collected from un-sampled fields, and frozen for use later in the season. Egg masses were affixed to 5x3 cm white cardstock strips using double-sided tape, paper-clipped to the pole of marker flags ~0.5 meters above the ground, and placed in the margins of fields. Egg mass cards placed at the edge of the potato crop were attached to the underside of potato plant leaves ~0.5m above the ground with a paper clip. At each sampling location, two separate egg mass cards were placed approximately two meters apart. Egg masses contained an average of 35 eggs (range:17-96), and were distributed so an average of 71 (range: 48-117) eggs were present per sampling location. Egg mass cards were left in place for 18-24hrs and collected. Egg mass cards were placed in the margins of fields in August and September 2017, July and August 2018, and June-September 2019. Egg mass cards were placed at the edge of the potato crops in August 2017, July and August 2018, and late June through September 2019. The availability of egg masses to use as sentinel prey dictated how frequently they could be used.

After collection, the number of missing eggs was recorded, as was the number of damaged eggs. These were summed, and then divided by the original number of eggs on the card to estimate the proportion of missing and damaged eggs. The proportion of missing and damaged eggs in margins and at the edge of fields were compared between floral and control margins using GLMM in a similar method as used for arthropod abundance, with Treatment as a fixed effect. In a separate analysis, the abundance of known CPB predators was used as a fixed effect to determine if the proportion of eggs lost varied by predator abundance. Additionally, after observing predator feeding damage on egg mass cards, the abundance of two orthopteran taxa measured in chapter 2 (Tettigoniidae and Acrididae) were used as fixed effects to determine their impact on the proportion of eggs lost. All models used a negative binomial distribution, and had field identity and sampling date used as random effects.

4.3.4 Overwintering Colorado potato beetle

Floral plantings adjacent to potato fields in 2018 were measured for overwintering Colorado potato beetle in early summer 2019. Sentinel plants in the form of Yukon Gold potato plants were placed in the margins of fields to attract newly emerged CPB. Potato plants were grown in greenhouses starting in early May 2019, and then transplanted into the margins of all eight fields previously sampled in 2018. Six potato plants were placed along the edge of each margin in early June 2019, and were spaced 10 meters apart. Plants were monitored once a week from planting until the first week of July for adult CPB and egg masses. When adult CPB were found, they were removed and destroyed to avoid doubly counting individuals. Multiple sentinel potato plants were eaten by vertebrates or died during the course of sampling. To account for margins with fewer potato plants, adult CPB numbers and egg masses were averaged per plant per field margin. Both CPB adult abundance and egg mass abundance were compared between floral and control margins using GLMMs. Treatment was used a fixed effect, with field identity and week as random effects, and a negative binomial distribution.

4.4 Results

4.4.1 Colorado potato beetle predators

A total of 6,504 individuals of known Colorado potato beetle predators were collected in and around commercial potato fields across three years. No specialist predators of CPB, such as *Lebia grandis* or *Perillus bioculatus*, were collected during the course of this study. Within field margins, areas with floral plantings had a significantly greater overall abundance of CPB predators compared to control margins (z=5.47, p=4.4e-08) (Fig. 4.2). Some taxa responded positively to the presence of floral plantings, with significantly higher abundances of Thomisdae, Carabidae, Reduviidae, Opiliones, and the overall abundance of predatory Hemiptera in floral margins (Table 4.2). The abundances of all other measured taxa were not significantly affected by treatment.

Within the potato crop, there was no significant effect of floral plantings on the overall abundance of CPB predators (z=0.42, p=0.67). There was no overall effect of distance into the crop on the abundance of predators (z=-0.74, p=0.46), although the edge of the crop had a significantly greater number of predators than 10m (z=-2.26 p=0.024), and marginally more than 30m (z=-1.81, p=0.07). Predator abundance was not significantly different among sampling locations at 10m, 30m, and 50m (Fig. 4.2). When analyzing all locations within the field together, several predatory taxa were affected by the presence of floral plantings in the margins. *Coleomegilla maculata* and Opiliones abundance was significantly higher in fields adjacent to floral plantings, while Coccinellidae abundance was marginally significantly increased (Table 4.2).

4.4.2 Effects on Sentinel Prey

There was no effect of floral plantings on egg removal within field margins (z=1.01, p=0.31), or at the edge of the crop (z=0.07, p=0.95) (Fig. 4.3). Additionally, there was no significant relationship between the abundance of known CPB predators and the number of sentinel eggs removed or damaged in field margins (z=1.17, p=0.24), or at the edge of the crop (z=0.34, p=0.73). Colorado potato beetle egg masses placed in field margins had a significantly greater proportion of eggs removed or damaged than those placed at the edge of the crop (z=2.25, p=0.025).

Two individual insects were observed eating sentinel egg masses during the study: 1 reduviid, and 1 tettigoniid, both in a single floral margin in 2017. A number of egg mass cards were found with chewing damage and bite marks on the card stock itself, or with the entire egg mass and leaf to which it was affixed missing. These characteristics have previously been found to be indicative of orthopteran feeding (Morrison et al. 2016). The number of missing and damaged eggs in margins was significantly correlated with the abundance of both Tettigoniidae (z=2.23, p=0.026) and Acrididae (z=1.98, p=0.048) in field margins. Too few Tettigoniidae were found at the edge of crops to conduct an analysis, but there was no effect of Acrididae abundance on the proportion of missing and damaged eggs at the edge of the crop (z=-0.31, p=0.76).

4.4.3 Colorado potato beetle abundance

A total of 606 Colorado potato beetle adults and 1,174 larvae were collected during our study. All but 10 CPB adults were found within potato fields, and of those 10, six were found in floral margins and four were found in control margins. A total of 314 CPB adults and 572 larvae were collected in potato fields adjacent to floral plantings, and

282 CPB adults and 602 larvae were found adjacent to control margins. There was no significant effect of floral plantings on the number of CPB adults (z=1.56, p=0.12), larvae (z=-0.7, p=0.49), or the total number of CPB found in the potato crop (z=0.39, p=0.695) (Fig. 4.4). There was a marginally significant effect of location within the field on CPB numbers (p=0.055), with increasing distance into the field leading to fewer CPB (Fig. 4.4). Colorado potato beetle numbers peaked mid-season, with significantly more CPB present in fields in July compared to late June (z=4.50, p=6.8e-06), or August (z=3.78, p=0.00016). There was no significant effect of treatment on CPB numbers for different sampling periods.

4.4.4 Sentinel potato plants

Sentinel potato plants placed in field margins attracted a total of 309 CPB adults and contained 67 CPB egg masses across five weeks of monitoring. Potato plants in floral margins attracted a greater number of CPB adults than control margins (z=3.39, p=7e-04), with a total of 233 adults found in floral margins and 76 in control margins. This effect was largely due to a single floral margin, where almost half of the total number of CPB adults were found (150 adults). Sentinel potato plants in floral margins did not have significantly greater numbers of CPB egg masses (z=1.01, p=0.31), with a total of 46 egg masses found in floral margins, and 21 found in control margins.

4.5 Discussion

4.5.1 Do floral plantings affect the abundance of known predators of CPB?

Margins planted with flowers attracted a greater abundance of generalist predators. These results are similar to previous studies of floral plantings, where a variety of insect predators were enhanced by the addition of flowers (Cox et al. 2014, Tschumi, Albrecht, Collatz, et al. 2016). Increased access to nectar and alternative prey in floral margins likely played a role in increased predator numbers (Ramsden et al. 2014, Hoffmann et al. 2018). While not directly measured, floral plantings also had noticeably denser foliage, which has been previously linked to increased predator abundance (Thomas et al. 1991).

Different predatory taxa responded differently to the addition of flowers. Abundances of Carabidae, Reduviidae, Thomisidae, and Opiliones were higher in floral margins than in control margins, while other taxa were unaffected. Across most previous studies where flowers increased natural enemy numbers, certain predatory taxa responded positively, while others were unaffected or decreased in abundance in floral plantings (Balzan and Moonen 2014, Cox et al. 2014, Blaauw and Isaacs 2015). This differential response could be due to increased foliage cover, or microclimatic conditions that are beneficial to certain predators, but not others (Clark et al. 1997, Barone and Frank 2003). Several of the taxa that were more abundant in floral margins in our study have precedence in the literature, or have clear relationships to flowers. Epigeal predators such as Carabidae have been shown to benefit from wildflower plantings (Frank and Reichhart 2004, Frank et al. 2007), and ambush predators like Thomisidae favor wildflowers while waiting for prey (Chittka 2001). For all taxa promoted by floral plantings, the presence of alternative prey within floral plantings may have been beneficial.

There was no apparent effect of floral margins on known CPB predators in potato crops, with little difference in predator abundance between crops adjacent to floral plantings or control margins. Additionally, the relative abundance of predators within margins was notably different than what was found in adjacent potato fields, with the majority of the in-field predator community consisting of Carabidae. Floral margins and control margins had multiple significant differences between predatory taxa found within them, but there was little difference between fields adjacent to floral plantings and fields adjacent to control margins (Table 4.2). Only Opiliones were significantly more abundant in both the floral margins and in fields adjacent to floral margins. From these results, it appears that the predator community in margins does not correspond directly to the predator community within adjacent crops, and suggests that there may not be much spillover of predators from margins into nearby fields, contrary to what other studies have found (Macfadyen, Hopkinson, et al. 2015). In our study system, floral plantings appear to be acting more to concentrate CPB predators than act as a source. While floral plantings may provide additional food sources and habitat for predators of CPB, there may be no incentive for them to move into nearby potato fields.

Another potential explanation for the discrepancy between predators in the margins and predators in the field is the application of pesticides. Intensive management is common in potatoes (Giordanengo et al. 2013), and may have a disruptive effect on the natural enemies that were sampled within potato fields. However, none of the fields we sampled were treated with a foliar application of insecticide during the season, and in-furrow neonicotinoid applications that were used tend to have lower non-target impacts than foliar insecticides (Huseth and Groves 2014). Additionally, natural enemies of CPB can recolonize fields relatively quickly after being extirpated with insecticide applications (Hilbeck and Kennedy 1996), and large numbers of predators were found within potato fields throughout our study. While the application of pesticides may have had an impact on in-field predator populations, the high numbers of predators observed indicates overall abundance of predators in the crop was unlikely to have been severely affected.

4.5.2 Do floral plantings increase predation of CPB eggs masses?

While floral plantings attracted a more abundant community of predators to field margins, they did not lead to significantly higher rates of removal of CPB eggs. Additionally, there was no significant relationship between overall predator abundance and egg removal or damage. In previous studies of floral plantings, biological control services can remain constant even when predator abundance increases, similar to the results of our study (Cox et al. 2014, Campbell et al. 2017). This could be for a variety of reasons, ranging from a lack of effective natural enemies, to the surrounding landscape composition (Tscharntke et al. 2005, 2016). Although not directly quantified, the surrounding agricultural landscape in our study was fairly heterogenous, including patches of forest, water, and unmanaged land. This agroecosystem may fall outside of the intermediately complex landscape range described by Tscharntke et al. 2005, where habitat management is most likely to provide services. Although floral plantings attracted a greater number of predators, the difference may not have been great enough to have a significant impact on CPB predation, or the natural enemies that were attracted were not effective predators of CPB (Tscharntke et al. 2016). No specialist natural enemies, including those that can strongly impact CPB populations, were found in our study (Biever and Chauvin 1992). Additionally, while many generalist predators will consume CPB eggs, doing so can have adverse effects on predator fitness and survivability, and CPB eggs may not be a preferred food source (Snyder and Clevenger 2004). However, in multiple cases, entire masses of CPB eggs inside floral plantings were removed after being left out for only a day, suggesting that at least some generalist predators found within floral plantings do readily consume CPB eggs.

Both a reduviid and a tettigoniid were observed actively feeding on sentinel prey egg masses during sampling. While reduviids have been previously described as predators of CPB (Cappaert et al. 1991), tettigoniids have not been listed as natural enemies of CPB. Orthopterans have been observed to prey on other crop pest species (Poley et al. 2018), and may prove to be an unexamined natural enemy of CPB. Many sentinel prey egg cards had damage consistent with orthopteran feeding, and the correlation between orthopteran abundance and egg removal in our study provides additional evidence that orthopterans may play a role in consuming CPB eggs. From this, we suspect that orthopteran taxa were likely a primary predator of eggs in our study.

Colorado potato beetles emerging in the spring often colonize the edge of potato fields, and the edge of crops is an important area to focus control efforts (French II et al. 1993, Weisz et al. 1996). However, predation rates at the edge of crops in our study were low overall, and in many cases sentinel egg masses were not damaged at all during a 24 hr. period. These results are in line with our findings regarding the CPB predator community, indicating that CPB predators attracted to floral plantings do not move far into adjacent fields or prey upon CPB to as high a degree as they do in the margins.

4.5.3 How do floral plantings influence the abundance of CPB within adjacent potato fields?

Colorado potato beetle abundance inside potato crops was unaffected by the presence or absence of floral plantings, both for adults and larvae. The lack of difference in CPB numbers between treatments provides further evidence that predators attracted by flowers did not have a strong impact on CPB populations within large-scale, commercial potato crops. However, floral plantings in field margins also did not increase the number of CPB present in potato crops. While floral plantings may not reduce in-field CPB numbers, they do not act to directly support them either. Additionally, we found the greatest abundance of CPB at the edge of crops, with decreasing numbers further into the field. These results are similar to previous studies (French II et al. 1993, Weisz et al. 1996), and suggest that biological control could be useful if predators moved into nearby crops from floral margins.

4.5.4 Do floral plantings provide improved overwintering habitat or refuge for CPB?

Sentinel potato plants in floral plantings attracted more CPB compared to control margins. However, this was largely due to a single field with a very high abundance of beetles: Of the 309 adult CPB collected from sentinel plants, 150 of them were found on potato plants in a single floral margin. A previous study found Colorado potato beetle favored overwintering near tree lines, with an average of 193 adults per square meter in wooded areas compared to 1 adult per square meter in grassy margins near potato fields (Weber and Ferro 1993). The floral margin with high numbers of CPB was located within 50 meters of a tree line, and CPB that overwintered in the tree line may have made their way to the margin. Our method of collecting adults on sentinel potato plants did not control for the possibility that CPB emigrate from tree lines or other nearby areas to the potato plants in field margin. However, many of the other margins that were sampled were similarly close to tree lines, and had low CPB abundance. The floral margin also had notably dense vegetation, which may provide better cover for overwintering beetles, although other floral margins that did not have elevated numbers of CPB also had similarly dense vegetation. Further study is needed to determine if our results are an anomaly, or indicative of floral plantings being a favorable overwintering location for CPB.

Several CPB adults were found during late August sampling within both floral and control margins. These beetles were likely moving beyond the field margins towards more wooded areas, rather than finding host plants or resources within margins (Noronha and Cloutier 1999). Potato fields supply everything CPB need to survive other than preferred overwintering space, and the lack of alternative hosts in floral plantings indicates they would not be attractive to CPB as a food source.

4.6. Conclusions

Floral plantings established in the margins of potato fields can attract communities of generalist predators that prey on CPB. However, floral plantings did not increase predation of CPB egg masses in field margins or in adjacent potato crops, and many of the predators found within adjacent potato fields were not the same as those found within floral plantings. Many of the egg masses that were removed showed signs of orthopteran feeding, and orthopterans may be an unexamined predator of CPB. While the overall abundance of CPB in nearby fields was unaffected by the presence of floral plantings, floral plantings may provide CPB with improved overwintering habitat, and further, more directed study is needed to verify this. Our results demonstrate floral plantings support predators of CPB, but additional study is needed on how best to extend these benefits beyond field margins and into nearby crops.

4.7 Acknowledgements

We thank RD Offutt Farms for allowing the use of their fields and for their collaboration on this project. We acknowledge the support and funding from the Northern Plains Potato Growers Association [grant number 00070053], the Sustainable Agriculture Research and Education Program [grant number 2015-38640-23781], the Doctoral Dissertation Fellowship at the University of Minnesota, the Dayton Bell Museum Fund, and the MnDRIVE Global Food Ventures program. Additionally, we are grateful to George Heimpel, Dan Cariveau, Elizabeth Borer, Lindsey Christianson, and Christopher Philips, and the undergraduate technicians Noah Linck, Joe Nelson, Gus Fedje-Johnson, Lily Briggs, Erik Lucas, Lexie Ogdahl, Caroline Hofmeister, Eli Kleinschmidt, Bailey Brandel, and Samantha Meyers for their field and laboratory assistance.

4.8 Figures and Tables

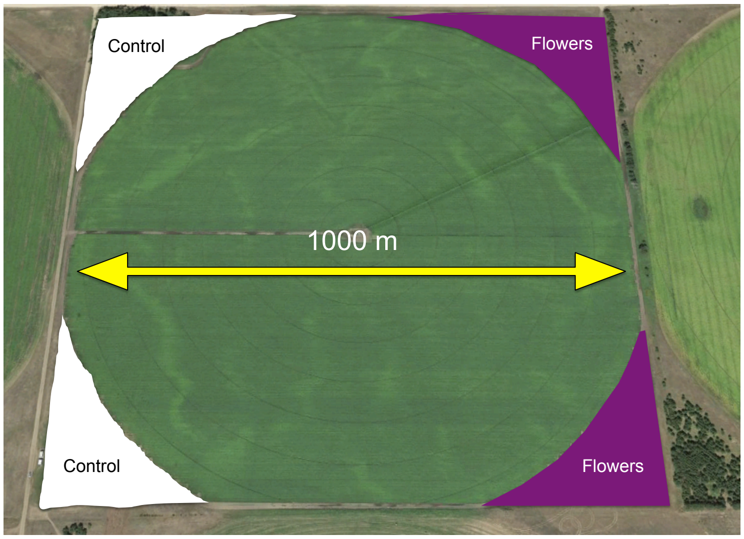

Figure 4.1. Example of a typical potato field in this study, with floral plantings established in two of the margins (purple), and the remaining 2 margins left unmanaged (white). Size of margins and floral plantings varied between fields. Floral margins were compared to control margins on the same field. Base image from Google Earth.

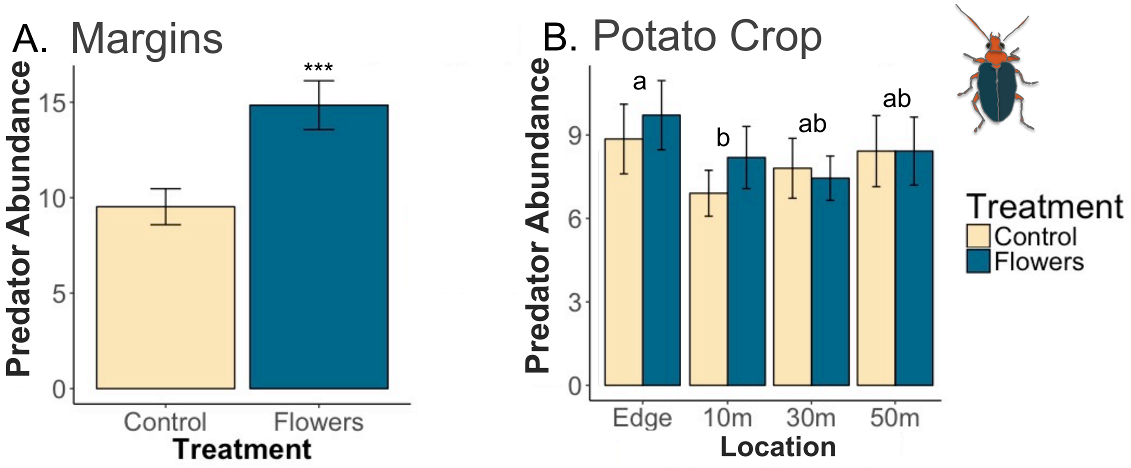

Figure 4.2. Overall abundance of CPB predators (A), in field margins and (B), within the potato field, separated by sampling location. Bars represent average CPB predator abundance summed across all sampling dates (Margin n=14, Potato Crop n=9), and fields (n=20), +/- standard error. Asterisks denote significant difference between treatments (* p<0.05, ** p<0.01, *** p<0.001). Letters denote significant differences in overall abundance between locations.

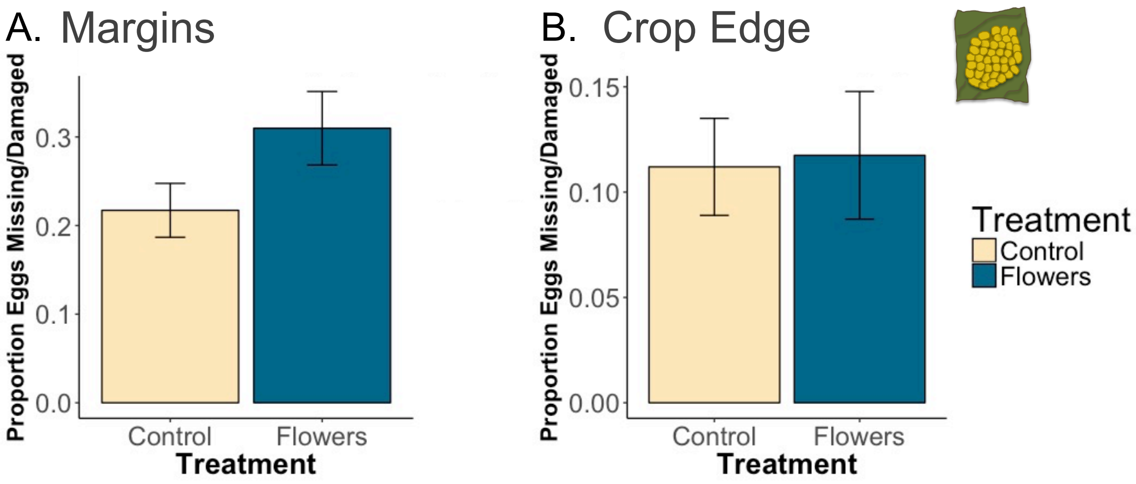

Figure 4.3. Proportion of Colorado potato beetle eggs removed or damaged in (A) margins, and (B) at the edge of the potato crop. Bars represent the average number of eggs missing or damaged summed across all sampling dates (Margins n=9, Edge n=6), and fields (n=20), +/- one standard error. Asterisks denote significant difference between treatments (* $p<0.05$, ** $p<0.01$, *** $p<0.001$).

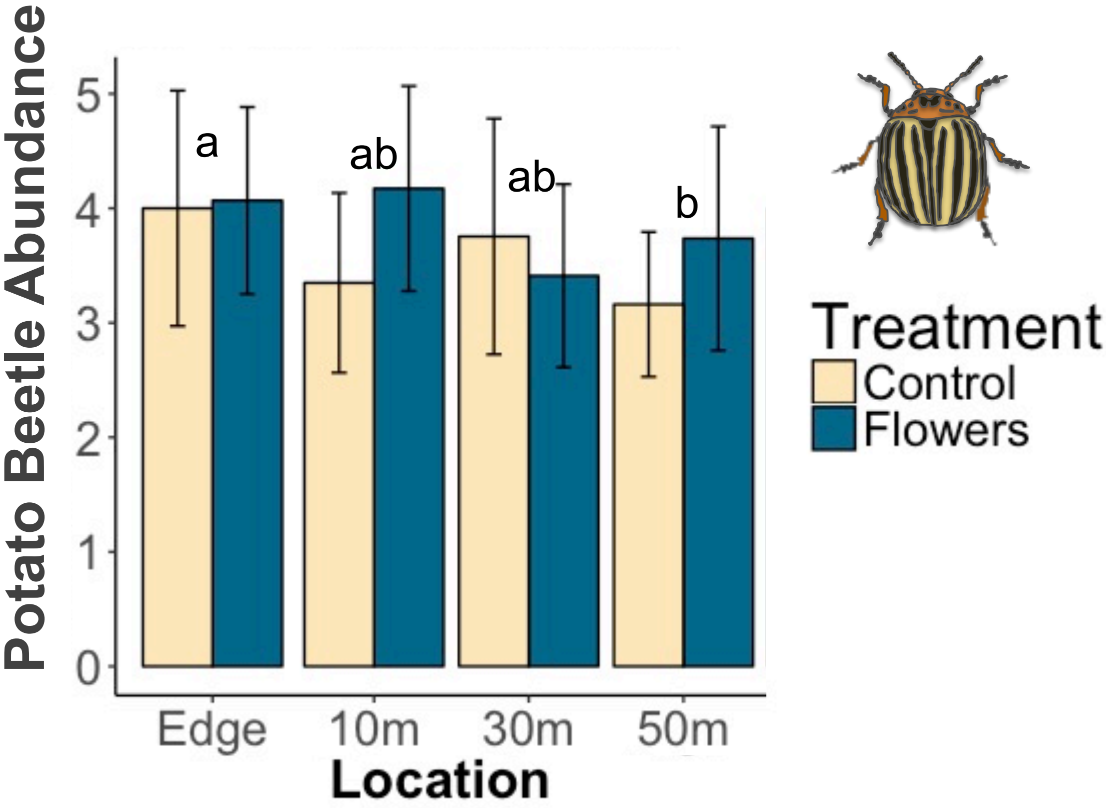

Figure 4.4. Colorado potato beetle abundance within potato crops by sampling location. Bars represent average CPB abundance (adults and larvae) summed across all sampling dates (n=9), and fields (n=20) +/- one standard error. Asterisks denote significant difference between treatments (* $p<0.05$, ** $p<0.01$, *** $p<0.001$). Letters denote significant differences in overall abundance between locations.

Table 4.1. Seed mixtures used to establish floral plantings. “Honeybee” mixture is largely a subset of the “Monarch” mixture.

Monarch Seed Mixture

Common Name	Scientific Name	% of Mixture
Alfalfa SD Common	*Medicago sativa*	3.25
Alsike Clover	*Trifolium hybridum*	6.52
Birdsfoot Trefoil	*Lotus corniculatus*	4.3
Crimson Clover	*Trifolium incarnatum*	6.43
Sainfoin	*Onobrychis viciifolia*	2.81
Black-Eyed Susan	*Rudbeckia hirta*	9.03
Canada Milkvetch	*Astragalus canadensis*	0.97
Common Milkweed	*Asclepias syriaca*	2.92
Evening Primrose	*Oenothera biennis*	0.79
Ox-Eye Sunflower	*Heliopsis helianthoides*	0.58
Foxglove Beardtongue	*Penstemon digitalis*	0.72
Hoary Vervain	*Vergena stricta*	1.96
Ironweed	*Veronia fasciculata*	0.55
Maximillian Sunflower	*Helianthus maxmilliani*	0.84
New England Aster	*Aster novae-angliae*	0.76
Pale Purple Coneflower	*Echinacea pallida*	0.3
Partridge Pea	*Chamaecrista fasciculata*	0.77
Phacelia	*Phacelia angelia*	4.08
Blue Sage	*Salvia azurea*	0.21
Prairie Cinquefoil	*Potentilla arguta*	2.21
Prairie Coneflower	*Ratibida columnifera*	2.64
Purple Coneflower	*Echinacea purpurea*	0.75
Purple Prairie Clover	*Dalea purpurea*	1.59
Rough Blazingstar	*Liatris aspera*	0.15
Sawtooth Sunflower	*Liatris aspera*	0.68
Shell Leaf Penstemon	*Penstemon grandiflorus*	0.38
Showy Goldenrod	*Solidago speciosa*	0.65
Showy Tick Trefoil	*Desmodium canadense*	0.13
Sky Blue Aster	*Aster azureus*	0.94
Smooth Blue Aster	*Aster laevis*	0.73
Stiff Goldenrod	*Solidago rigida*	1.86
Stiff Sunflower	*Helianthus pauciflorus*	0.09
Tall Boneset	*Eupatorium altissimum*	0.92
White Prairie Clover	*Dalea candidum*	2.2
White Yarrow	*Achillea millefolium*	6.13
Wild Bergamont	*Monarda fistulosa*	1.82

Big Bluestem-Bison	*Andropogon gerardii*	3.54
Canada Wildrye	*Elymus canadensis*	3.29
Little Bluestem-Itasca	*Schizachyrium scoparium*	4.65
Prairie June Grass	*Koeleria cristata*	8.29
Sideoats Grama-Pierre	*Bouteloua curtipendula*	4.1
Western Wheatgrass	*Agropyron smithii*	3.15
Plains Oval Sedge	*Carex brevior*	1.33

Honeybee Seed Mixture

Common Name	**Scientific Name**	**% of Mixture**
Alfalfa SD Common	*Medicago sativa*	7.25
Alsike Clover	*Trifolium hybridum*	13.41
Birdsfoot Trefoil	*Lotus corniculatus*	7.18
Crimson Clover	*Trifolium incarnatum*	5.74
Ladino White Clover	*Trifolium repens*	22.26
Medium Red Clover	*Trifolium pratense*	17.56
Sainfoin	*Onobrychis viciifolia*	2.12
White Blossom Sweet Clover	*Melilotus officinalis*	4.15
Yellow Blossom Sweet Clover	*Melilotus officinalis*	4.15
Hoary Vervain	*Vergena stricta*	0.87
Maximillian Sunflower	*Helianthus maxmilliani*	0.5
Partridge Pea	*Chamaecrista fasciculata*	0.41
Phacelia	*Phacelia angelia*	3.64
Showy Goldenrod	*Solidago speciosa*	0.58
Sky Blue Aster	*Aster azureus*	0.42
Smooth Blue Aster	*Aster laevis*	0.32
Canada Wildrye	*Elymus canadensis*	2.2
Indiangrass-Tomahawk	*Sorghastrum nutans*	2.23
Little Bluestem-Itasca	*Schizachyrium scoparium*	4.98

Table 4.2. List of all predators, total abundances in floral and control margins and floral and control fields, z values, and significance. Bolded values indicate significant difference between treatments (p<0.05).

Predator			**Margins**				**Potato Field**			
Order	Family	Genus/Species	Flowers	Control	Z Value	Pr(>|z|)	Flowers	Control	Z Value	Pr(>|z|)
Araneae			427	392	1.4	0.16	79	86	0.17	0.86
	Salticidae		156	212	-0.11	0.91	25	24	0.09	0.93
	Thomisidae		271	180	3.22	0.0013	54	62	0.09	0.93
Coleoptera			222	139	1.13	0.26	1502	1593	0.07	0.94
	Carabidae		218	132	3.68	0.00023	1493	1590	-0.03	0.97
		Lebia grandis	0	0	---	---	0	0	---	---
	Coccinellidae		4	7	1.05	0.29	9	3	1.85	0.064
		Coleomegilla maculata	2	2	---	---	8	2	2.04	0.042
		Hippodamia convergens	2	5	---	---	1	1	---	---
Hemiptera			575	399	2.1	0.036	16	19	-0.18	0.85
	Nabidae	*Nabis* spp	255	232	1.29	0.2	9	14	-0.7	0.49
	Lygaeidae	*Geocoris* spp	77	80	0.88	0.377	3	3	---	---
	Pentatomidae		1	0	---	---	0	0	---	---
		Perillus bioculatus	0	0	---	---	0	0	---	---
		Podisus maculiventris	1	0	---	---	0	0	---	---
	Reduviidae		242	87	5.5	3.70E-08	4	2	---	---
Neuroptera			73	77	-0.21	0.83123	96	135	-0.85	0.3981
	Chrysopidae	*Chrysopa* spp Adult	25	27	-0.24	0.81	33	42	-0.46	0.65
		Chrysopa spp Larvae	48	50	0.24	0.8137	63	93	-1.12	0.2635
Opiliones			232	41	4.71	2.50E-06	252	149	4.05	5.20E-05

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Appendix 1
Seed mixtures used to establish floral plantings

Monarch Seed Mixture

Common Name	Scientific Name	% of Mixture
Alfalfa SD Common	*Medicago sativa*	3.25
Alsike Clover	*Trifolium hybridum*	6.52
Birdsfoot Trefoil	*Lotus corniculatus*	4.3
Crimson Clover	*Trifolium incarnatum*	6.43
Sainfoin	*Onobrychis viciifolia*	2.81
Black-Eyed Susan	*Rudbeckia hirta*	9.03
Canada Milkvetch	*Astragalus canadensis*	0.97
Common Milkweed	*Asclepias syriaca*	2.92
Evening Primrose	*Oenothera biennis*	0.79
Ox-Eye Sunflower	*Heliopsis helianthoides*	0.58
Foxglove Beardtongue	*Penstemon digitalis*	0.72
Hoary Vervain	*Vergena stricta*	1.96
Ironweed	*Veronia fasciculata*	0.55
Maximillian Sunflower	*Helianthus maxmilliani*	0.84
New England Aster	*Aster novae-angliae*	0.76
Pale Purple Coneflower	*Echinacea pallida*	0.3
Partridge Pea	*Chamaecrista fasciculata*	0.77
Phacelia	*Phacelia angelia*	4.08
Blue Sage	*Salvia azurea*	0.21
Prairie Cinquefoil	*Potentilla arguta*	2.21
Prairie Coneflower	*Ratibida columnifera*	2.64
Purple Coneflower	*Echinacea purpurea*	0.75
Purple Prairie Clover	*Dalea purpurea*	1.59
Rough Blazingstar	*Liatris aspera*	0.15
Sawtooth Sunflower	*Liatris aspera*	0.68
Shell Leaf Penstemon	*Penstemon grandiflorus*	0.38
Showy Goldenrod	*Solidago speciosa*	0.65
Showy Tick Trefoil	*Desmodium canadense*	0.13
Sky Blue Aster	*Aster azureus*	0.94
Smooth Blue Aster	*Aster laevis*	0.73
Stiff Goldenrod	*Solidago rigida*	1.86
Stiff Sunflower	*Helianthus pauciflorus*	0.09
Tall Boneset	*Eupatorium altissimum*	0.92
White Prairie Clover	*Dalea candidum*	2.2
White Yarrow	*Achillea millefolium*	6.13
Wild Bergamont	*Monarda fistulosa*	1.82
Big Bluestem-Bison	*Andropogon gerardii*	3.54

Canada Wildrye	*Elymus canadensis*	3.29
Little Bluestem-Itasca	*Schizachyrium scoparium*	4.65
Prairie June Grass	*Koeleria cristata*	8.29
Sideoats Grama-Pierre	*Bouteloua curtipendula*	4.1
Western Wheatgrass	*Agropyron smithii*	3.15
Plains Oval Sedge	*Carex brevior*	1.33

Honeybee Seed Mixture

Common Name	Scientific Name	% of Mixture
Alfalfa SD Common	*Medicago sativa*	7.25
Alsike Clover	*Trifolium hybridum*	13.41
Birdsfoot Trefoil	*Lotus corniculatus*	7.18
Crimson Clover	*Trifolium incarnatum*	5.74
Ladino White Clover	*Trifolium repens*	22.26
Medium Red Clover	*Trifolium pratense*	17.56
Sainfoin	*Onobrychis viciifolia*	2.12
White Blossom Sweet Clover	*Melilotus officinalis*	4.15
Yellow Blossom Sweet Clover	*Melilotus officinalis*	4.15
Hoary Vervain	*Vergena stricta*	0.87
Maximillian Sunflower	*Helianthus maxmilliani*	0.5
Partridge Pea	*Chamaecrista fasciculata*	0.41
Phacelia	*Phacelia angelia*	3.64
Showy Goldenrod	*Solidago speciosa*	0.58
Sky Blue Aster	*Aster azureus*	0.42
Smooth Blue Aster	*Aster laevis*	0.32
Canada Wildrye	*Elymus canadensis*	2.2
Indiangrass-Tomahawk	*Sorghastrum nutans*	2.23
Little Bluestem-Itasca	*Schizachyrium scoparium*	4.98

Appendix 2

Flower species identified in this study and found in floral and control margins. "X" indicates species was present in a seed mixture, and/or observed in a field margin. Flowers in the column "Neither Mixture" were not present in any seed mixture and grew wild.

Common Name	Scientific Name	Honeybee Mixture	Monarch Mixture	Neither Mixture	Found in Floral Margins	Found in Control Margins
Alfalfa SD Common	*Medicago sativa*	X	X		X	X
Alsike Clover	*Trifolium hybridum*	X	X		X	X
Birdsfoot Trefoil	*Lotus corniculatus*	X	X		X	X
Crimson Clover	*Trifolium incarnatum*	X	X			
Sainfoin	*Onobrychis viciifolia*	X	X		X	
Hoary Vervain	*Vergena stricta*	X	X			
Maximillian Sunflower	*Helianthus maxmilliani*	X	X		X	
Partridge Pea	*Chamaecrista fasciculata*	X	X			
Phacelia	*Phacelia angelia*	X	X			
Sky Blue Aster	*Aster azureus*	X	X		X	X
Smooth Blue Aster	*Aster laevis*	X	X			
Showy Goldenrod	*Solidago speciosa*	X	X		X	X
Ladino White Clover	*Trifolium repens*	X			X	
Medium Red Clover	*Trifolium pratense*	X			X	X
White Blossom Sweet Clover	*Melilotus officinalis*	X			X	X
Yellow Blossom Sweet Clover	*Melilotus officinalis*	X			X	X
Black-Eyed Susan	*Rudbeckia hirta*		X		X	
Canada Milkvetch	*Astragalus canadensis*		X			
Common Milkweed	*Asclepias syriaca*		X		X	X
Evening Primrose	*Oenothera biennis*		X		X	
Ox-Eye Sunflower	*Heliopsis helianthoides*		X		X	
Foxglove Beardtongue	*Penstemon digitalis*		X			
Ironweed	*Veronia fasciculata*		X			
New England Aster	*Aster novae-angliae*		X			
Pale Purple Coneflower	*Echinacea pallida*		X			
Blue Sage	*Salvia azurea*		X			
Prairie Cinquefoil	*Potentilla arguta*		X			
Prairie Coneflower	*Ratibida columnifera*		X		X	
Purple Coneflower	*Echinacea purpurea*		X		X	
Purple Prairie Clover	*Dalea purpurea*		X		X	
Rough Blazingstar	*Liatris aspera*		X		X	
Sawtooth Sunflower	*Liatris aspera*		X			
Shell Leaf Penstemon	*Penstemon grandiflorus*		X		X	
Showy Tick Trefoil	*Desmodium canadense*		X			
Stiff Goldenrod	*Solidago rigida*		X		X	X
Stiff Sunflower	*Helianthus pauciflorus*		X			
Tall Boneset	*Eupatorium altissimum*		X			
White Prairie Clover	*Dalea candidum*		X			
White Yarrow	*Achillea millefolium*		X		X	X
Wild Bergamont	*Monarda fistulosa*		X		X	
Black Medic	*Medicago lupulina*			X	X	X
Bull Thistle	*Cirsium vulgare*			X	X	X
Butter and Eggs	*Linaria vulgaris*			X		X
Butterfly Weed	*Asclepias tuberosa*			X	X	
Canada Hawkweed	*Hieracium canadense*			X	X	X
Canada Thistle	*Cirsium arvense*			X		X
Common Chickweed	*Stellaria media*			X		X
Common Cinquefoil	*Potentilla simplex*			X	X	X
Common Tansy	*Tanacetum vulgare*			X		X
Dandelion	*Taraxacum*			X	X	X
Giant Blue Hyssop	*Agastache foeniculum*			X		X
Harebell	*Campanula rotundifolia*			X		X
Heath Aster	*Symphyotrichum ericoides*			X		X
Hoary Alyssum	*Berteroa incana*			X	X	X
Hoary Puccoon	*Lithospermum canescen*			X	X	
Lanceleaf Coreopsis	*Coreopsis lanceolata*			X	X	
Longleaf Bluets	*Houstonia longifolia*			X		X
Motherwort	*Leonurus cardiaca*			X	X	
Needle Pointed Blue Eyed Grass	*Sisyrinchium mucronatum*			X		X
Northern Bedstraw	*Galium boreale*			X		X
Northern Bog Aster	*Symphyotrichum boreale*			X		X
Philadelphia Fleabane	*Erigeron philadelphicus*			X	X	X
Plains Coreopsis	*Coreopsis tinctoria*			X	X	
Prairie Smoke	*Geum triflorum*			X		X
Pussy Toes	*Antennaria plantaginifolia*			X		X
Raspberry	*Rubus*			X		X
Rough Cinquefoil	*Potentilla norvegica*			X		X
Sheeps Sorrel	*Rumex acetosella*			X	X	X
Silver Conquefoil	*Potentilla argentea*			X	X	X
Small Flowered Flame Flower	*Phemeranthus parviflorus*			X	X	
Spotted Knapweed	*Centaurea stoebe*			X	X	X
Spreading Dogsbane	*Apocynum androsaemifolium*			X		X
Spring Beauty	*Claytonia virginica*			X	X	
White Campion	*Silene latifolia*			X	X	X
Wild Rose	*Rosa acicularis*			X	X	
Wild Strawberry	*Fragaria vesca*			X		X
Yellow Wood Sorrel	*Oxalis stricta*			X	X	

Appendix 3

Models and corresponding AIC values for pollinators and predators in field margins and within potato crops.

		Model	AIC	Delta AIC	wAIC
Pollinators	Margin	Treatment	1225.7	3.6	0.099453163
		Cover	1239.2	17.1	0.000116448
		Treatment+Cover	1222.1	0	0.601656576
		Treatment*Cover	1223.5	1.4	0.298773814
	Crop	Treatment	1197.8	12.1	0.00230717
		Cover	1194.9	9.2	0.009835732
		Treatment+Cover	1195	9.3	0.009356038
		Treatment*Cover	1185.7	0	0.97850106
Bees	Margin	Treatment	920.4	18.5	6.43E-05
		Cover	907.3	5.4	4.50E-02
		Treatment+Cover	901.9	0	6.69E-01
		Treatment*Cover	903.6	1.7	2.86E-01
	Crop	Treatment	528.4	3.3	0.145547715
		Cover	535.7	10.6	0.003782949
		Treatment+Cover	529.3	4.2	0.09280532
		Treatment*Cover	525.1	0	0.757864015
Predator	Margin	Treatment	1913.7	0	0.6061309
		Cover	1919.8	6.1	0.02870571
		Treatment+Cover	1915.7	2	0.2229831
		Treatment*Cover	1916.6	2.9	0.1421803
	Crop	Treatment	3445.4	1.1	0.26488204
		Cover	3444.3	0	0.45910759
		Treatment+Cover	3446	1.7	0.19622944
		Treatment*Cover	3447.8	3.5	0.07978094
Foliar	Margin	Treatment	1841.5	0	0.502741
		Cover	1844.5	3	0.1121767
		Treatment+Cover	1843.1	1.6	0.2258961
		Treatment*Cover	1843.8	2.3	0.1591863
	Crop	Treatment	1893.5	0.1	0.3540132
		Cover	1893.4	0	0.3721639
		Treatment+Cover	1895.4	2	0.1369114
		Treatment*Cover	1895.4	2	0.1369114
Epigeal	Margin	Treatment	1323.7	1.4	0.252140573
		Cover	1337.4	15.1	0.000267132
		Treatment+Cover	1323.8	1.5	0.239843533
		Treatment*Cover	1322.3	0	0.507748762
	Crop	Treatment	3293.3	0.4	0.31127478

Cover	3292.9	0	0.38019187
Treatment+Cover	3294	1.1	0.21935163
Treatment*Cover	3295.8	2.9	0.08918172