

COMPOSITION, SIZE, AND EFFECTIVENESS OF NATIVE PLANT CONSERVATION
PLANTINGS FOR SUPPORTING BENEFICIAL INSECTS

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A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

Entomology – Doctor of Philosophy
Ecology, Evolutionary Biology, and Behavior – Dual Major

2013

ABSTRACT

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Agricultural practices generally create unfavorable environments for beneficial insects, resulting in declines of these insects in agricultural landscapes and risking a loss in valuable ecosystem services, such as pollination and biological control. Previous work has demonstrated that the establishment of flowering plants can provide the necessary resources to support beneficial insects in agricultural landscapes, which can enhance beneficial insect populations in these regions. This dissertation evaluates how patch size and on-farm establishment of wildflower habitat supports beneficial insects and their delivery of ecosystem services.

To investigate the response of insects to wildflower patch size and plant richness, 12 native perennial flowering plant species were established in 25 replicated patches ranging in size from 1 to 100 m². With no significant differences in bloom density or flower richness across patch sizes, in general wild bees were observed at greater densities and higher diversity in larger patches. Conversely, honey bees and hoverflies did not respond to wildflower patch size, but all pollinators were positively influenced by increasing flower richness. Wildflower patch size was also important for natural enemy density, richness, and diversity. In contrast, there was only a slight increase in herbivore density with wildflower patch size.

Through the investigation of pollination services delivered to three wildflower species with different bloom periods, patch area (positively), and floral richness (negatively), significantly influenced seed set of the measured wildflowers planted within the habitat patches.

Comparing population growth of sentinel soybean aphids (*Aphis glycines* Matsumura) across wildflower patch size, aphid colonies were smaller as plot size increased, resulting in higher biocontrol service index values. Thus, providing beneficial insects with flowering resources resulted in significantly more beneficial insects and greater delivery of pollination and biological control services than in smaller habitat patches.

Using highbush blueberry as a model system, wildflower plantings composed of 15 native perennial flowering plants and three native grass species were established adjacent to crop fields and evaluated for their efficacy at enhancing beneficial insect populations and their delivery of ecosystem services to the cropping system. Honey bees visiting blueberry flowers had similar abundance in enhanced and control fields, whereas wild bee abundance after three years was higher than in control fields. Pollination parameters including percent fruit set, berry weight, and mature seeds per berry were significantly greater in fields adjacent to wildflower plantings three and four years after seeding, leading to higher crop yields with value exceeding the cost of establishing and maintaining the plantings. Wildflower plantings also positively affected the density and diversity of some natural enemy groups and enhanced biological control of sentinel pest eggs along the crop edge. Conversely, insect herbivore densities generally were not enhanced by the provision of perennial floral resource plantings.

The general patterns observed here can help guide future efforts in the conservation and support of beneficial insects in the natural and agricultural landscapes. The results from these studies suggest that small modifications to resource-poor, non-cropped areas within farms, such as through the establishment of native flowering plants, can selectively enhance biodiversity, pollination, pest-control, and thus has the potential to optimize multiple ecosystem services.

ACKNOWLEDGMENTS

First and foremost I would like to thank Rufus Isaacs, my graduate advisor. Much appreciation is also given to Doug Landis, Larry Gut, and Carolyn Malmstrom for their participation as my graduate advisory committee. I would also like to thank the rest of the Berry Crops Entomology Lab at MSU, especially Keith Mason and Annie Kirk, for all their help and support over the past five years (including assisting with wildflower planting establishment and keeping me sane). My blueberry grower cooperators, John Calsbeek, Karlis Galens, Dennis Hartmann, Richard J. Rant, and Denny Vanderkooi, were a crucial part of this work and a great group of people to work with. I am also thankful for a great bunch of undergraduate assistants; Kyle Ringwald, Nury Duque-Feghali, Jacob Morden, Marla Greanya, Laurel Lindemann, and Joe Fletcher, for their help in collecting and sorting samples. I must also thank the crew at the Trevor Nichols Research Center for their help in maintaining my research plots and providing me with a comfortable place to stay during the summers. I appreciate the advice and services provided by Ester Durnwald from Michigan Wildflower Farm and Bill Schneider from Wildtype Design, Native Plants & Seed, Ltd. I owe many thanks to caffeine, particularly that from Diet Coke[®], for being delicious and providing me with energy. I am greatly appreciative of the funding support I have received from The Hutson Endowment of the Department of Entomology at MSU, the Sustainable Agriculture Research and Education program of the United States Department of Agriculture, and Project GREEN. I would also like to thank Heather Lenartson-Kluge and the Entomology Business Office for helping me keep on top of all my paperwork. Last, but definitely not least, I would like to thank my lovely wife (Annie), Shalom, Iris, and the rest of my family and friends for all their love and support. Also, thank you for reading this. Enjoy!

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CHAPTER 1.

HABITAT MANAGEMENT TO SUPPORT BENEFICIAL INSECTS AND THEIR PROVISION OF ECOSYSTEM SERVICES IN AGRICULTURAL LANDSCAPES

Introduction

The use of land for settlements and agriculture is essential for our society because they provide the critical resources of shelter and food. Unfortunately, the utilization of natural resources for the sake of human necessities often comes at the expense of degrading the environment, and human activities are dependent on a continually increasing portion of the world's natural resources (Tilman et al., 2002; Foley et al., 2005). Agriculture is the dominant land-use activity across the world, occupying roughly 40% of the terrestrial biome (Foley et al., 2005). Numerous characteristics associated with modern agriculture can make agricultural landscapes poor habitat for beneficial insects. Crop monocultures by design sacrifice vegetative diversity, and consequently can weaken insect pollinator and natural enemy diversity over large areas (Russell, 1989; O'Toole, 1993; Hendrickx et al., 2007). Cropland surrounded by other cropland or structurally simple landscapes, for instance, has significantly fewer insects than farms surrounded by uncultivated, more complex landscapes (Tscharntke et al., 2008), and the number of pollinators (Ricketts, 2004; Ricketts et al., 2008) and insect natural enemies (Woltz et al., 2012) that visit the crop increases with proximity to surrounding natural habitats composed of forests and grasslands. Also, frequent use of pesticides and herbicides harm pollinators (Erickson Jr. et al., 1994) and insect natural enemies (Ruberson et al., 1998).

The increase in agricultural area and intensity of farming to support growing human populations is resulting in a loss of natural vegetation that once supported beneficial insects (Richards, 2001; Kremen *et al.*, 2004a; Zurbrügg and Frank, 2006b). The expansion of agricultural landscape has occurred not only through the destruction of previously natural habitats, but also through the replacement of pastures and non-pollinator-dependent crops (Aizen

et al., 2008). For example, from 1938 to 1991, Britain lost 30% of its hedgerow along field margins, which had provided floral and ground resources for wild bees (Osborne et al., 1991) and insect natural enemies like ground beetles (Asteraki et al., 1995). Thus, a loss of natural vegetation could potentially become devastating to beneficial insect populations.

Although modern agriculture has been successful in increasing food production through the use of synthetic fertilizers, irrigation, and pesticides, these same factors have caused of extensive environmental damage (Matson et al., 1997; Pimm and Raven, 2000; Hoekstra et al., 2005). Agricultural intensification breaks natural habitats into smaller, more isolated patches (MacArthur and Wilson, 1967; With, 2002), which often disturbs the habitat that beneficial insects depend on for resources. The remaining habitat fragments, within an otherwise resource-poor agricultural landscape, likely provide insufficient resources for beneficial insect communities (Fischer and Stöcklin, 1997), therefore leading to reduced pollinator (Aizen and Feinsinger, 1994) and natural enemy (Kruess and Tscharntke, 2000b) abundance and diversity in these habitat patches. This loss of beneficial insect abundance and diversity may in turn lead to a decline in ecosystem services provided by these insects, such as pollination (Bender et al., 1998) and biological control (Kruess and Tscharntke, 1994).

Insect provided ecosystem services

Beneficial insects provide valuable ecosystem services that support human survival and agricultural production through pollination and biological control. Insect pollinators, particularly wild and managed bees, provide an ecosystem service that is exploited considerably by growers worldwide for the pollination of a large diversity of crops (Kremen *et al.*, 2002a; Greenleaf and

Kremen, 2006; Winfree *et al.*, 2007a). Pollinator-dependent crops rely mostly on a single managed pollinator species, the European honey bee, *Apis mellifera* (Winfree *et al.*, 2007b), which means that more than a third of the world's food supply (Klein *et al.*, 2007) is vulnerable due to the challenges this species faces (Neumann and Carreck, 2010). In agricultural systems that are not intensively managed and where crops historically relied on wild, unmanaged bees for pollination, these wild bees can pollinate the crops fully when the cropland is located near natural habitat (Klein *et al.*, 2003a; Winfree *et al.*, 2007a). In other cropping systems that are not necessarily dependent on wild pollinators for pollination, wild pollinators can significantly contribute to crop productivity (Klein *et al.*, 2007), a worldwide service that is valued at over US\$200 billion annually (Gallai *et al.*, 2009).

Biological control (biocontrol) is another important ecosystem service at risk in agricultural systems. Worldwide, pest suppression from insect natural enemies, including predators and parasitoid wasps, is valued at more than US\$400 billion annually (Costanza *et al.*, 1997). The abundance and diversity of these insect natural enemies are generally greater in agricultural landscapes surrounded by uncultivated, natural habitat (Bianchi *et al.*, 2006), whereas insecticide use and scarcity of flowering plants make agricultural systems resource-poor landscapes for natural enemies (Landis *et al.*, 2000; Hendrickx *et al.*, 2007; Geiger *et al.*, 2010). The lack of habitat and resources can cause declines in valuable biological control services and increase potential for pest outbreaks (Chaplin-Kramer *et al.*, 2011; Meehan *et al.*, 2011). Consequently, there has been growing interest in developing approaches to conserve beneficial insects and these strategies often involve integrating floral resource patches into farmland to support beneficial insects and the services they provide (Landis *et al.*, 2000; Bianchi *et al.*, 2006; Isaacs *et al.*, 2008; Letourneau and Bothwell, 2008).

Wildflower habitat to conserve beneficial insects in agricultural systems

A key approach for conserving beneficial insects and stabilizing their populations in an agricultural landscape is to meet the ecological requirements of these insects within or near these environments (Landis et al., 2000), which will require more ecologically-based management practices of the cropland (Matson et al., 1997; Tilman et al., 2002). Thus, one proposed way to mitigate the reduction in quantity and quality of natural habitat in agricultural systems is to re-integrate natural, floral habitat into agricultural landscapes (Landis et al., 2000; Carvalheiro et al., 2012).

Sufficient floral resources and proper vegetation structure are necessary to support diverse populations of insects (Zurbrugg and Frank, 2006b). Consequently management of structurally resource-poor environments through the establishment of flowering plants and grasses within agricultural landscapes is expected enhance beneficial insect populations (Long et al., 1998; Kells et al., 2001; Rebek et al., 2005). Beneficial insects, particularly pollinators and natural enemies, require access to alternate hosts, overwintering habitats, a constant food supply, and appropriate microclimates in order to survive (Johnson and Triplehorn, 2005). These requirements can be fulfilled through the provision of a diverse array of floral resources incorporated adjacent to resource-poor crop fields, which provide the necessary resources to support populations of pollinators and natural enemies throughout the growing season (Landis et al., 2000; Ahern and Brewer, 2002; Carreck and Williams, 2002; Kremen and Miles, 2012), without taking valuable cropland out of production.

Natural habitat with floral resources neighboring crop fields can help support beneficial insect communities in agricultural landscapes (Baggen and Gurr, 1998; Dufour, 2000; Carreck

and Williams, 2002; Fiedler and Landis, 2007a; Fiedler and Landis, 2007b; Tuell et al., 2008), but the majority of the work in this area has focused on non-native annual or biennial flowering plants (Baggen and Gurr, 1998; Dufour, 2000; Carreck and Williams, 2002). Although annual flowers bloom within one growing season, they commonly must be re-sown each year, making it costly to successfully maintain a well-established strip of annual flowers (Fiedler and Landis, 2008; Tuell et al., 2008). Hence there have been other studies that have examined native perennial flowering plant strips for supporting beneficial insects (Fiedler and Landis, 2007a; Fiedler and Landis, 2007b; Tuell et al., 2008), although perennial flowers may require years to first bloom. Native perennial flowering plants may be better than exotic annuals because they are adapted to the local environment, are less likely to become invasive, and have the potential to increase native beneficial insect diversity in agricultural landscapes (Fiedler, 2006; Stephens *et al.*, 2006a).

Beneficial insects respond positively to the addition of floral resources in agricultural systems, but different insect taxa respond to these manipulations in varying ways (Fraser et al., 2008; Osborne et al., 2008; Tschardt et al., 2008), and may also respond to habitat at different scales. For example, in a study by Heard *et al.* (2007), landscape composition influenced bee abundance, but local scale habitat size had no effect on bee density, whereas Meyer *et al.* (2007) observed that pollinator density and diversity responded positively to increasing area of floral habitat. The response of insects to natural habitat area and fragmentation likely depends on their varying abilities to disperse through an environment (Tschardt, 2005). Small bees can forage (Araujo et al., 2004; Bommarco et al., 2010) and parasitoid wasps can disperse (Thies et al., 2005) at a scale ranging from hundreds of meters up to two kilometers, while relatively large bees (Greenleaf et al., 2007; Osborne et al., 2008) and lady beetles (Werf *et al.*, 2000) are

considered stronger dispersing insects. Nonetheless, to support populations of beneficial insects, natural habitats must be situated at distances from each other that even poorly dispersing insects can traverse. For wildflower habitats to be adopted within agricultural systems for the support and conservation of beneficial insects, this approach must be done without increasing insect herbivore populations (Lavandero *et al.*, 2006; Isaacs *et al.*, 2009a).

Potential negative aspects of wildflower habitat

The provisioning of floral resources through wildflower plantings may provide increased benefits to pollinator and natural enemies in agricultural systems, but these resources may also support potential pest herbivores (Lavandero *et al.*, 2006; Wäckers *et al.*, 2007). For example, the Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae), is a major pest of Michigan's fruit crop industries, including blueberry. Beyond feeding on leaves and berries, there is also a zero threshold policy for contamination of blueberries by Japanese beetle, meaning that an infestation by this pest can lead to expensive load rejections for growers. Because the potential for loss, growers may be reluctant to add plants to their farms that may attract or benefit the beetles and other potential pests. Japanese beetles feed sparingly or not at all on common wildflower species used for beneficial insect conservation, such as New England aster and wild bergamot (Fleming, 1972). However, for the sake of grower adoption it is critically important to understand how key herbivore pests respond to the addition of perennial wildflowers in the agricultural system. Monitoring the response of these insects within flower plantings as well as in the adjacent crops is an important element of this project.

Although the modification of agricultural systems for the conservation of beneficial insect biodiversity may provide resources for potential pests, these habitats can potentially provide a range of benefits to farmers, including lower production costs, increased yield, and decreased dependence on pesticide use (Losey and Vaughn, 2006; Cullen et al., 2008). Unfortunately, the establishment of wildflower strips for conservation of beneficial insects also entails initial costs and risks, and may have unintended consequences. Seeds for planting wildflower strips adjacent to field crops can cost thousands of dollars per hectare (Durnwald, 2009), and little research has evaluated the economic costs compared to the benefits of crop pollination and natural pest reduction from conservation biological control (Cullen et al., 2008). Many of the negative aspects of wildflower establishment may be overcome by increasing interest in beneficial insect conservation, expanding government programs to subsidize the cost of habitat establishment in North America (NRCS, 2010) and Europe (EU, 2005), and improve understanding of the costs and benefits of the habitats for agriculture.

Native plant habitat to support beneficial insects and their services in a perennial fruit system in Michigan

Highbush blueberry, *Vaccinium corymbosum* L., a perennial fruit crop native to eastern North America, has a community of wild bees that visit the flowers (Javorek et al., 2002; Tuell et al., 2009), and insect pests that consume leaves, shoots, roots, flowers, and fruit (Isaacs et al., 2004; Liburd and Arévalo, 2005; Isaacs et al., 2009b; Retamales and Hancock, 2012). These factors make highbush blueberry an amenable system to measure the effects of habitat manipulation on the conservation of beneficial insects and their provisioning of ecosystem

services. The scale at which beneficial insects respond is important, because farmers are more likely to maintain or restore natural habitat if there is a measurable benefit at the field-scale (Tilman et al., 2002; Wossink and Swinton, 2007). Conservation of beneficial insect communities at blueberry farms will require natural habitat that is large enough to maintain the structure of the plant-insect interactions (Forup et al., 2008). It is expected that insect abundance and diversity will be greater in larger habitat patches that have more resources to support populations (MacArthur and Wilson, 1967; Slobodkin, 1980), but few studies have examined this pattern in relation to beneficial insects. Local habitat factors (Murray et al., 2012) and floral richness (Marlin and LaBerge, 2001) influence pollinator community composition. However, previous studies did not measure the response of insect pollinator abundance, diversity, or their services to the size of habitat patches. One objective of the research reported in this dissertation is to determine how insect pollinators respond to the area of wildflower habitat by using plants that have been shown to be beneficial for both pollinators and natural enemies (Fiedler and Landis, 2007a; Fiedler and Landis, 2007b; Tuell et al., 2008). Furthermore, it is also important to investigate how patch size and floral richness affect wildflower seed set within habitat patches, as this information can help guide restoration of wildflower habitat for plant conservation.

Natural enemies, as well as herbivores, can benefit from floral resources, so understanding the response of insect natural enemy and herbivore populations to the area of wildflower habitat is important before implementing these plantings at farm settings. While a positive response from insect natural enemies to the size of host patch size has been documented previously (Bach, 1988b; Olson and Andow, 2008), there is little information on the response of natural enemies or herbivorous insects as a function of wildflower patch size. As a way to elucidate the relationship of natural enemies and herbivores with patch size, an objective of this

dissertation is measure insect density and diversity in wildflower patches of different sizes. Since natural enemies also provide the valuable ecosystem service of biological control, it will be important to determine how natural enemies and the biological control services they provide might respond to wildflower patch size.

Floral habitats may act as vital ‘habitat islands’ in agricultural landscapes (Pickett and Thompson, 1978; Letourneau, 1998) by providing resources needed to maintain beneficial insect populations within the landscape. Recent studies indicate that adjacent wild habitat can increase pollinator abundance in almond (Klein et al., 2012) and mango (Carvalho et al., 2012) orchards, but with positive influence on pollination and crop yield only in the latter system where habitat was tailored to support pollinators. There is relatively little information on how local-scale improvement (Murray et al., 2012) of resource-poor areas using optimized mixes of wildflowers will affect pollination services in adjacent crop fields, or the return on investment from the improvement practice. Thus an objective of my research is to determine how wild bees respond to local habitat manipulations planted with native perennial wildflower plants that have been previously shown to be beneficial for both pollinators and natural enemies (Fiedler and Landis, 2007a; Fiedler and Landis, 2007b; Tuell et al., 2008). In addition to the response of these insects, the likelihood of adoption of these tactics will depend on the inclusion of an economic component to determine whether the value of changes in blueberry yield exceed that of the investment in pollinator habitat under different economic scenarios.

Since the wildflower habitat established at blueberry farms also provides resources for natural enemies and potentially for herbivores, the potential for multiple ecosystem services, or possibly negative impacts, from such plantings should be investigated. Thus, another objective of this dissertation is to determine the impact of perennial floral resources on natural enemies and

herbivores and the subsequent level of biological control services they provide in adjacent crop fields.

CHAPTER 2.

LARGER PATCHES OF DIVERSE FLORAL RESOURCES INCREASE INSECT POLLINATOR DENSITY, DIVERSITY, AND POLLINATION OF NATIVE WILDFLOWERS

Introduction

Land use intensification has broken natural habitats into smaller and more isolated patches or islands (MacArthur and Wilson, 1967; With, 2002), often fragmenting the habitat that insect pollinators depend on for survival. Fragmentation can disrupt landscape connectivity, potentially leading to declines in biodiversity and ecosystem services (Bender et al., 1998; Kearns et al., 1998). According to the theory of island biogeography, the restricted population size that small patches or islands can support increases the extinction risk, limiting biodiversity within the fragmented landscape (MacArthur and Wilson, 1967). In fact, the remaining small and isolated habitat fragments within a resource-poor landscape likely provide insufficient foraging and nesting resources for insect pollinator communities (Pickett and Thompson, 1978; Fischer and Stöcklin, 1997), reducing pollinator abundance and species richness (Aizen and Feinsinger, 1994; Cane et al., 2006; Ouin et al., 2006).

The loss of natural vegetation that would otherwise provide floral resources and nesting habitat generally results in simplified landscapes with limited floral diversity, which consequently leads to lower insect pollinator diversity (O'Toole, 1993; Holzschuh et al., 2007). Decreased visitation rates from a compromised pollinator community or fragmented habitat results in reduced pollen dispersal (Wilcock and Neiland, 2002), adversely affecting seed set (Ashman et al., 2004; Dauber et al., 2010). For most flowering plants, including annual and perennial wildflowers, sufficient pollen exchange is an essential process for seed set and population persistence (Larson and Barrett, 2000; Ashman et al., 2004). Consequently, to support pollinator communities by creating lasting wildflower habitats, there must be a match between the resources the established plants provide and the resources the pollinators within the habitat

require. For example, during the early spring, queen bumble bees (*Bombus* spp.) require access to flowering plants to build up enough resources to start a colony (Goulson, 2003), and many early blooming flowering plants depend on the early emerging bumble bees for pollination (Handel, 2000). The establishment of flowering plant species in a habitat does not necessarily guarantee that pollinators will be attracted or supported by such plants (Handel, 2000). If either the bees or the early blooming flowers are not present at the appropriate time, the flower/pollinator mutualism would fail, and neither group would survive. Thus, when creating wildflower habitat, it is essential to include diversity of flower species that bloom throughout the growing season (Isaacs *et al.*, 2009a), and to understand which flower species and floral characteristics are best for attracting and supporting pollinator communities (Tuell *et al.*, 2008).

In agricultural systems, the pollination needs of most pollinator-dependent crops are generally well understood (Delaplane and Mayer, 2000; Klein *et al.*, 2007). Conversely, the pollination needs of many native annual and perennial flowering plants are still unknown (Cane, 2008), but wild bees are the key pollinators for most ecological regions of the world (Axelrod, 1960) and for most plant species (Ollerton *et al.*, 2011). Flowering plants that are primarily pollinated by wild bees, such as bumble bees (Goulson, 2003), often benefit from the capacity to be pollinated by multiple species of pollinators (Waser *et al.*, 1996). Having the functional capacity to be pollinated by multiple species creates a type of pollination redundancy (Blüthgen and Klein, 2011), and despite this potential buffer against the loss in pollinator diversity, the removal of highly generalized bees from an ecosystem is predicted to result in the greatest loss of plant diversity (Memmott *et al.*, 2004). The continued loss of plant diversity may potentially cause a feed-back loop in the system, resulting in a continued loss of pollinator diversity and thus

further loss of plant diversity (Goulson, 2003), which will likely be intensified in fragmented habitats (Cunningham, 2000).

Restoring natural plant diversity through the establishment of native wildflower habitat within bee flight ranges in the otherwise fragmented or resource-poor landscapes may provide the required pollen, nectar, and shelter resources for pollinators throughout the growing season, thus maintaining populations and diversity of wild bees (Carreck and Williams, 2002; Roulston and Goodell, 2011). In fragmented landscapes, the home ranges of pollinators may be spread across multiple “partial habitats” (Westrich, 1996), where required resources and nesting sites are spread across numerous habitat fragments. The addition of wildflower habitat is one strategy for increasing the connectivity of the fragmented habitat (Bender et al., 1998; Donald and Evans, 2006), and thereby improving the availability of resources critical for supporting insect pollinators (Carreck and Williams, 2002).

Species that survive in habitat remnants are confronted with a modified environment, and because species differ in life history strategies, they will likely be affected by habitat fragmentation in distinct ways. Beneficial insect species differ in their ability to disperse through an environment, which will impact their response to the distribution of fragmented natural habitats in the landscape (Tschardt, 2005). Small bees can forage at a scale ranging from hundreds of meters up to two kilometers (Araujo et al., 2004; Bommarco et al., 2010), while relatively large bees may fly up to five kilometers (Greenleaf et al., 2007; Osborne et al., 2008). Nonetheless, most bees forage only up to a few hundred meters from their nest (Zurbuchen et al., 2010), and since most bees must return to a permanent nesting site after foraging for resources, the location of nesting and natural habitats must be within distances that pollinators can traverse.

Preservation of plant and pollinator abundance and diversity requires natural habitat that

is large enough to maintain the structure of the plant-insect interactions (Forup et al., 2008). It is expected that insect abundance will be greater in larger habitat patches that have more resources to support populations (Rosenzweig, 1995; Connor et al., 2000), and the proportion of taxa that are pollinators is expected to increase as the number of resource-rich plants within the habitat increases (Conner and Neumeier, 1995). However, few studies have examined this pattern in relation to beneficial insects. Beneficial insects respond positively to the addition of flowering resources to the environment, but different insect taxa respond to these manipulations in varying ways (Fraser et al., 2008; Osborne et al., 2008; Tschardt et al., 2008), and may also respond to habitat at different scales. Matteson and Langelotto (2010) determined that small scale additions of native plants failed to increase pollinator richness in urban environments. Similarly, in a study by Heard et al. (2007), landscape composition influenced the abundance of *Bombus* spp. bees (Hymenoptera: Apidae), whereas flower patch size had no effect. Conversely, Meyer et al. (2007) observed that increasing flowering strip size increased abundance and diversity of insect pollinators. Local habitat factors influence pollinator community composition (Murray et al., 2012). However, these previous studies did not measure insect pollinator abundance, diversity, and provision of the ecosystem service of pollination in response to patch size.

Native and non-native annual and perennial plants can be used in habitat manipulation to support pollinators (Carreck and Williams, 2002; Blake et al., 2011), however native perennial wildflowers are adapted to the local environment, unlikely to become invasive, and can attract native pollinators that are adapted to interact with the flower morphology (Pontin et al., 2006; Tuell et al., 2008; Hogg et al., 2011). Also, providing a rich variety of native flowers to the habitat may also be important for the persistence of the associated pollinator species (Marlin and LaBerge, 2001). To determine how insect pollinators respond to the area of wildflower habitat

and floral richness, I measured insect abundance and diversity in wildflower patches of different sizes that remained consistent in plant diversity and species composition that were known to support pollinators (Tuell et al., 2008). I tested the hypothesis that density and diversity of insect pollinators increases with the area and species richness of wildflowers. I also predicted that the pollination of wildflowers within the patches would increase correspondingly. To determine whether habitat size and flower richness affect the visitation rates of insect pollinators and subsequently the level of pollination provided to the wildflowers within the patch, the seed set of three wildflower species with three different bloom periods was measured in these plantings.

Methods

Experimental design

In the fall of 2008, at the Trevor Nichols Research Center in Fennville, Michigan, a 1-ha grass field was prepared for 25 square-shaped wildflower patches. The 25 patches consisted of a logarithmic series of five size treatments (1, 3, 10, 30, and 100 m^2) with 5 replicates each. The patches were arranged in a 5 x 5 grid of 15 x 15 m cells, with the center of each patch positioned in the center of a grid cell. The different sized patches were arranged within the grid using a Latin-square design (Fig. 2.1). The 25 patches were mowed and then sprayed twice in the late summer with 1% glyphosate herbicide at 206.7 L/ha (Touchdown®, Syngenta Crop Protection, Inc. Greensboro, NC) to reduce the growth of weeds. At first vegetative growth in the spring of 2009, glyphosate was again applied to all 25 patches two weeks before wildflower seedlings were planted. The patches were not tilled, in order to prevent the exposure of dormant weed seeds.

One-year-old seedlings (Wildtype Native Plant Nursery, Mason, Michigan) of 12 native perennial wildflower species (Table 2.1) were planted in mid-May 2009. Plant species were selected for their known attractiveness to insect pollinators, with overlapping bloom periods that spanned May through October (Fiedler and Landis, 2007a; Tuell et al., 2008). To maintain the same relative abundance of species across the experiment, the seedlings were planted 30-45 cm apart within square groupings of 12 plants (1 from each species), with the relative position of each species randomized within every grouping. With this design 1 m² patches had 1 grouping of 12 seedlings (1 from each species), the 3 m² patches had 4 groupings (48 seedlings), 10 m² patches had 9 groupings (108 seedlings), 30 m² patches had 25 groupings (300 seedlings), and 100 m² patches had 64 groupings (768 seedlings). During the first year, flower buds were removed from the maturing seedlings before bloom to encourage energy storage in the roots in order to enhance establishment.

Table 2.1 List of native Midwestern annual wildflowers and their bloom periods planted at the Trevor Nichols Research Center in Fennville, Michigan, USA.

		Bloom period (month)					
Common Name	Scientific Name	M	J	J	A	S	O
Golden Alexanders	<i>Zizia aurea</i>	X	X				
Foxglove beard-tongue	<i>Penstemon digitalis</i>		X	X			
Sand coreopsis	<i>Coreopsis lanceolata</i>		X	X			
Black-eyed Susan	<i>Rudbeckia hirta</i>		X	X	X	X	
Butterfly milkweed	<i>Asclepias tuberosa</i>			X	X		
Spotted beebalm	<i>Monarda punctata</i>			X	X		
Boneset	<i>Eupatorium perfoliatum</i>			X	X	X	
Blue lobelia	<i>Lobelia siphilitica</i>			X	X	X	
Yellow coneflower	<i>Ratibida pinnata</i>			X	X	X	
Cup plant	<i>Silphium perfoliatum</i>			X	X	X	
Stiff goldenrod	<i>Solidago rigida</i>				X	X	X
New England aster	<i>Symphyotrichum novae-angliae</i>				X	X	X

To combat weed growth, wood chip mulch was added to the patches after planting (5 cm depth). The grass surrounding the patches was mowed approximately once a month during the summer for the duration of this project, and five locations within the grassy areas and away from the patches served as the negative controls (Fig. 2.1).

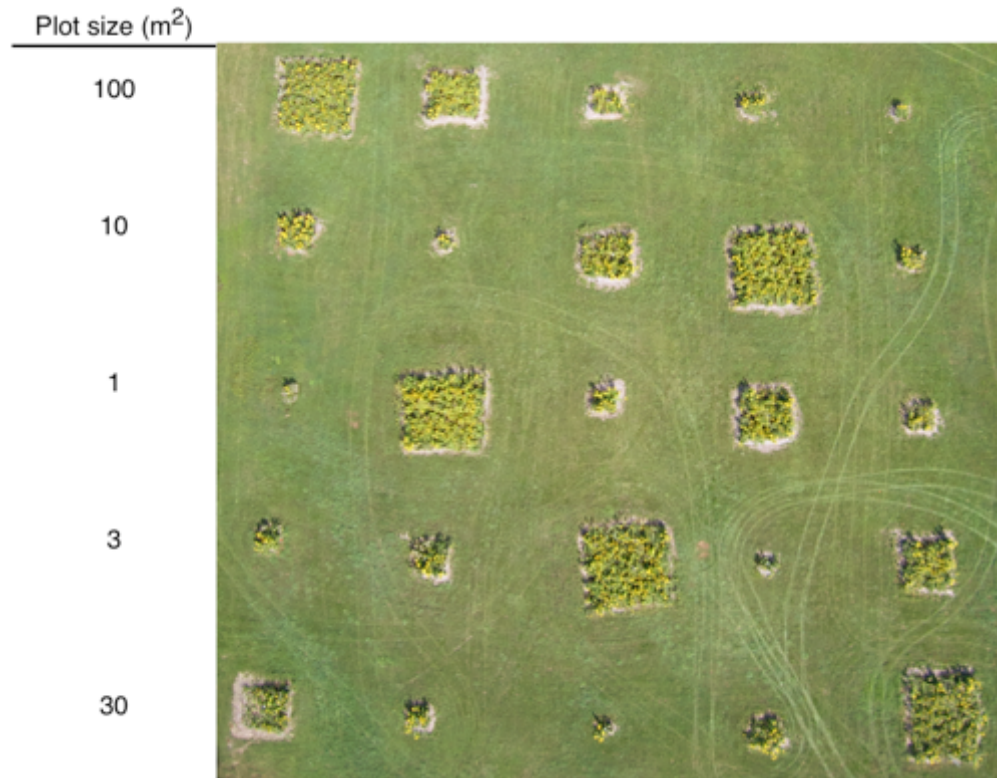


Figure 2.1 Aerial image of wildflower patches. Sized patches were arranged using a Latin-square design, and the sizes (m^2) of the wildflower plantings in the first column are displayed on the left. For interpretation of the references to color in this and all other figures, the reader is referred to the electronic version of this dissertation.

Wildflower assessment

The richness and density of wildflower blooms within the different sized patches were assessed during the same time periods as insect sampling. The number of species of wildflowers

that were in bloom within the 1 m² area during the 5 min insect sampling periods was recorded for each of the 25 wildflower patches for each of the three insect sampling periods. Density of flowers in bloom was measured separately using a 0.1 m² PVC quadrat, which was randomly tossed three times within each of the 25 patches. All the flowers in bloom within the 0.1 m² area were identified, counted, and recorded, with composites and umbels considered as individual flowers.

Bloom richness and density were each averaged for the entire growing season (three sampling periods combined) and were compared separately across the five patch sizes using a generalized linear model (GLM) with Poisson distribution, overdispersion parameter estimated by Pearson Chi-square, and estimated by maximum likelihood (JMP, Version 8, SAS Institute Inc., Cary, NC).

Insect sampling

To measure the effect of wildflower patch size on the insect pollinators, in 2011 three native flower species were selected that had three different bloom periods; early-season (sand coreopsis), mid-season (cup plant), and late-season (New England aster; Table 2.1). During each of the three different bloom periods, on three separate warm, calm, and sunny days between 10:00 and 16:00 h, a 1 m² area (measured with a PVC quadrat) within each patch was sampled for 5 minutes. The insects that visited flowers within the 1 m² area were counted and identified. With the exception of honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.), all other bees and Syrphidae were identified to family. Voucher specimens were deposited in the Albert J. Cook Arthropod collection at Michigan State University (Appendix 2).

The density of each pollinator group (honey bees, wild bees, and hoverflies) was pooled from the entire season, and compared among patch sizes separately using a GLM with Poisson distribution, overdispersion parameter estimated by Pearson Chi-square, and estimated by maximum likelihood (JMP, Version 8). Bee diversity (Shannon's index, H (Wani et al., 2005), of honey bees and wild bees) was compared among patch sizes using an analysis of variance (ANOVA) with square root transformed diversity data. Diversity data were further compared among patch sizes using Student's t test with the alpha level corrected *post hoc* via the Bonferroni method ($\alpha = 0.01$) (Zar, 1999) (JMP, Version 8).

The relationship between the density of each pollinator group and the richness of wildflower species was determined, and repeated for the square-root-transformed bee diversity data using a GLM with normal distribution (JMP, Version 8). The GLM analyses were also conducted using both patch size and wildflower richness in the model. The corrected Akaike's information criteria (AIC_C) were calculated to determine which model (patch size only, wildflower richness only, and patch size + richness) had the lowest AIC_C , and thus was the best at approximating pollinator density and bee diversity (Anderson et al., 2000) (JMP, Version 8).

Pollination services to wildflowers

The effect of wildflower patch size on the pollination of wildflowers was investigated using the three native flower species listed above, each of which has composite inflorescences (pseudanthia). During the bloom periods of each species, six unopened flower buds were tagged at each of the 25 wildflower patches. Two of these buds were designated for each of three treatments to test for pollination limitation: insect pollinator-restricted pollination (bagged), hand pollination, or open pollination (Kearns and Inouye, 1993). To determine if plants could produce

viable seeds in the absence of insect visitors, buds tagged for restricted pollination were enclosed with a fine mesh bag (150 μm , The Cary Company, Addison, IL), and remained unvisited for the duration of the experiment. Buds designated for hand pollination were also bagged, while those intended for open pollination remained unbagged and untreated. When the flowers began to bloom in the hand pollination treatment, freshly collected, conspecific pollen was applied to the open flowers using a paintbrush (Pentel Watercolor Paint Brush, Size 2; Pentel of America, Ltd., Torrance, CA). Hand pollination was conducted three times during one week, only removing the mesh bags from the flowers during the hand-pollination process. Once the plants had set seed, each of the seed heads from each of the three treatments from the 25 patches were collected, placed in individual brown paper bags, and allowed to dry naturally. To evaluate pollination in each of the treatments, each bud was opened and the number of mature seeds inside was recorded. The increase in pollination due to insect visitation was determined by subtracting the number of mature seeds found in the bagged flowers from the number of mature seeds in the unbagged flowers.

The difference in mature seeds between the bagged and unbagged treatments were analyzed across patch sizes using a GML as described above (JMP, Version 8). The number of mature seeds averaged over the entire season was analyzed using a GLM as described above (JMP, Version 8) separately for each model; patch size only, wildflower richness only, and patch size + richness. The GLM analyses were calculated a third time including both patch size and wildflower richness in the model. The AIC_C values from the three potential models were compared to determine which best approximated pollinator density and bee diversity (Anderson et al., 2000) (JMP, Version 8).

Pollination data were further analyzed to determine the relationship between the season-averaged seed set and patch size, wildflower richness, wild bee density, and bee diversity by calculating the Pearson product-moment correlation for these relationships (JMP, Version 8).

Results

Wildflower assessment

Wildflower seedlings were initially planted within the patches at 12 seedlings per square meter, so it was expected that bloom density would be consistent across patch sizes as well. This was proven to be true, with no significant differences among patch sizes for bloom density, that ranged from 12.1 ± 1.5 blooms per square meter in the 1 m^2 patches to 16.6 ± 2.8 blooms per square meter in the 100 m^2 patches ($\chi^2 = 2.2$, d.f. = 4, $P = 0.71$). Likewise, seasonal average wildflower bloom richness ranged from 1 to 4 blooms per m^2 , but was not significantly different across patch sizes ($\chi^2 = 1.94$, d.f. = 4, $P = 0.75$).

Pollinators visiting flower patches

Honey bees were the most abundant pollinator observed visiting wildflowers. In addition, a diverse group of wild, non-*Apis* bees and hoverflies were also observed visiting the wildflower patches (Table 2.2). *Bombus* spp. made up over half of all the non-*Apis* bees observed, and members of the Andrenidae, Halictidae, Megachilidae, and Colletidae families were also noted (Table 2.2).

Table 2.2 Total-season-averaged densities (insects per m² ± SEM) of the unique taxonomic wild bee groups observed per 5 minute sampling period in different sized wildflower patches (GLM with Poisson distribution).

Taxonomic group	Wildflower patch size (m ²)					Total N	χ^2	P
	1	3	10	30	100			
<i>Bombus</i> spp.	1.00 ± 0.30	2.4 ± 0.60	1.80 ± 0.50	2.6 ± 0.70	3.20 ± 0.7	462	9.40	0.052
Andrenidae	0.02 ± 0.02	0.1 ± 0.05	0.20 ± 0.08	0.2 ± 0.07	0.30 ± 0.1	33	10.90	0.027
Other Apidae	0.02 ± 0.02	0.2 ± 0.10	0.20 ± 0.06	0.3 ± 0.10	0.50 ± 0.1	54	17.60	0.002
Halictidae	0.20 ± 0.08	0.4 ± 0.10	0.40 ± 0.10	0.8 ± 0.20	0.70 ± 0.1	118	10.40	0.034
Megachilidae	0.02 ± 0.02	0	0.02 ± 0.02	0	0.05 ± 0.03	5	7.66	0.110
Colletidae	0	0	0	0	0.02 ± 0.02	1	16.10	0.003

The distinctive pollinator groups (honey bees, wild bees, and hoverflies) responded differently to wildflower patch size (Fig 2.2). Honey bees and hoverflies did not respond significantly to the varying sizes of wildflower patches and their densities were relatively similar across the five different sizes (honey bees: Fig. 2.2a, Table 2.3; and hoverflies: Fig. 2.2c, Table 2.3). Wild bees, responded positively to increasing wildflower patch size (Fig. 2.2b, Table 2.3), with wild bee density greatest in the 30 and 100 m² patches than in the smallest 1 m² patches (Fig. 2.2b).

Evaluation of the response of individual wild bee groups to wildflower patch size revealed that bee families have varying responses to resource size. For example, larger sized bees, such as *Bombus* spp. and those in the Megachilidae family had a moderate trend of increasing density with larger patch size (Table 2.2). Conversely, smaller sized bees, generally in the Andrenidae, Halictidae, and other Apidae (non-*Apis* and non-*Bombus* spp.) families showed a significant increase in density with larger patch sizes (Table 2.2). Similarly, the diversity of bees visiting wildflowers during summer also increased with patch size (Fig. 2.3a; $F_{4,195} = 4.44$, $P = 0.002$).

In the analysis of native bee visitors, for all three bloom periods (early, mid, and late-season), the density of native bees visiting flowers increased with wildflower patch size. Compared to the smallest wildflower patches, the 100m² patches had significantly greater densities of native bees at each of the bloom periods [early: Fig. 2.4a; $\chi^2 = 25.11$, d.f. = 4, $P < 0.0001$; mid: Fig. 2.4b; $\chi^2 = 11.61$, d.f. = 4, $P = 0.021$; late: Fig. 2.4c; $\chi^2 = 13.55$, d.f. = 4, $P = 0.0089$]. This finding indicates that native bees are sensitive to the size of wildflower plantings and respond positively throughout the summer to larger areas of floral resource. In contrast, honey bees and hoverflies were not influenced by patch size (Fig. 2.2).

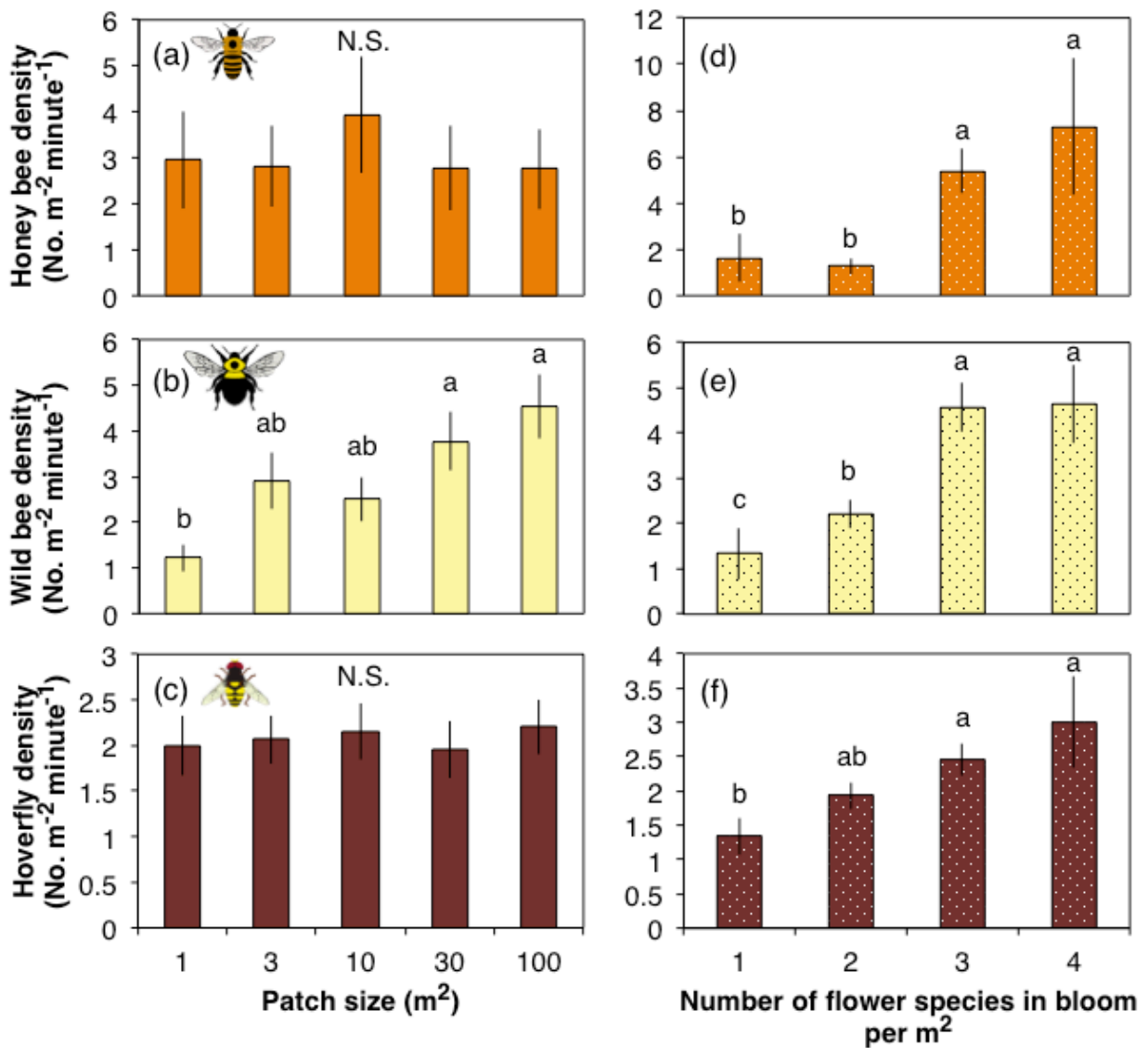


Figure 2.2 Total season average pollinator density (mean \pm SE) for (a) honey bees (N = 686), (b) wild bees (N = 673), and (c) hoverflies (N = 467) compared to patch size, and for (d) honey bees, (e) wild bees, and (f) hoverflies in relation to flower richness. Bars with the same letter are not significantly different (Kruskal-Wallis test followed by comparisons for each treatment using a Mann-Whitney *U* test).

Table 2.3 Results from generalized linear model analysis comparing AIC_C values to determine the best model for describing the pollinator and pollination relationships with patch size and wildflower species richness. Bolded values indicate model with lowest AIC_C.

Model			χ^2	d.f.	<i>P</i>	AIC _C
Dependent	Independent	Relationship				
Honey bee density	Patch size	0	0.95	4	0.92	162.9
	Flower richness	+	26.2	3	<0.0001	152.5
	Patch size + flower richness	+	27.6	7	0.0003	160.1
Wild bee density	Patch size	+	19.4	4	0.0007	270.2
	Flower richness	+	25.9	3	<0.0001	233.8
	Patch size + flower richness	+	52.8	7	<0.0001	258.7
Hoverfly density	Patch size	0	0.37	4	0.98	441.1
	Flower richness	+	14.2	3	0.0027	422.0
	Patch size + flower richness	+	14.4	7	0.045	440.7
Bee diversity	Patch size	+	17.4	4	0.0016	229.9
	Flower richness	+	29.2	3	<0.0001	216.0
	Patch size + flower richness	+	53.0	7	<0.0001	200.8
Mature seeds	Patch size	+	13.5	4	0.0089	200.7
	Flower richness	-	28.8	3	<0.0001	208.2
	Patch size +flower richness	+	47.1	7	<0.0001	216.3

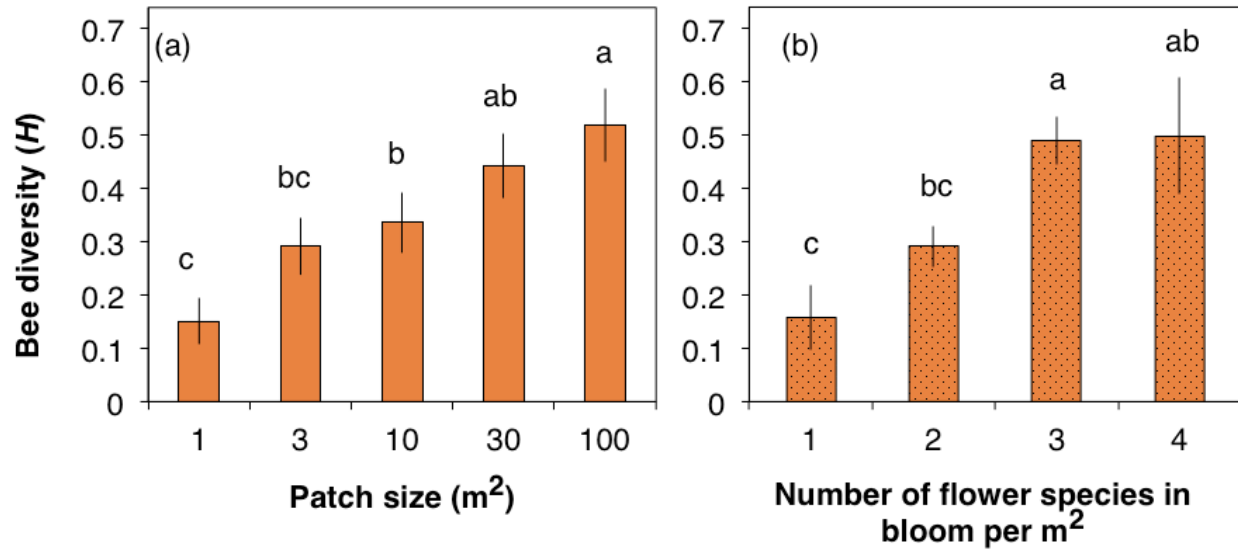


Figure 2.3 Total season average bee diversity (mean \pm SE) as a function of (a) patch size and (b) wildflower richness. Bars with the same letter are not significantly different (ANOVA across treatments and among treatments using Student's t test with the alpha level corrected *post hoc* via the Bonferroni method ($\alpha = 0.01$)).

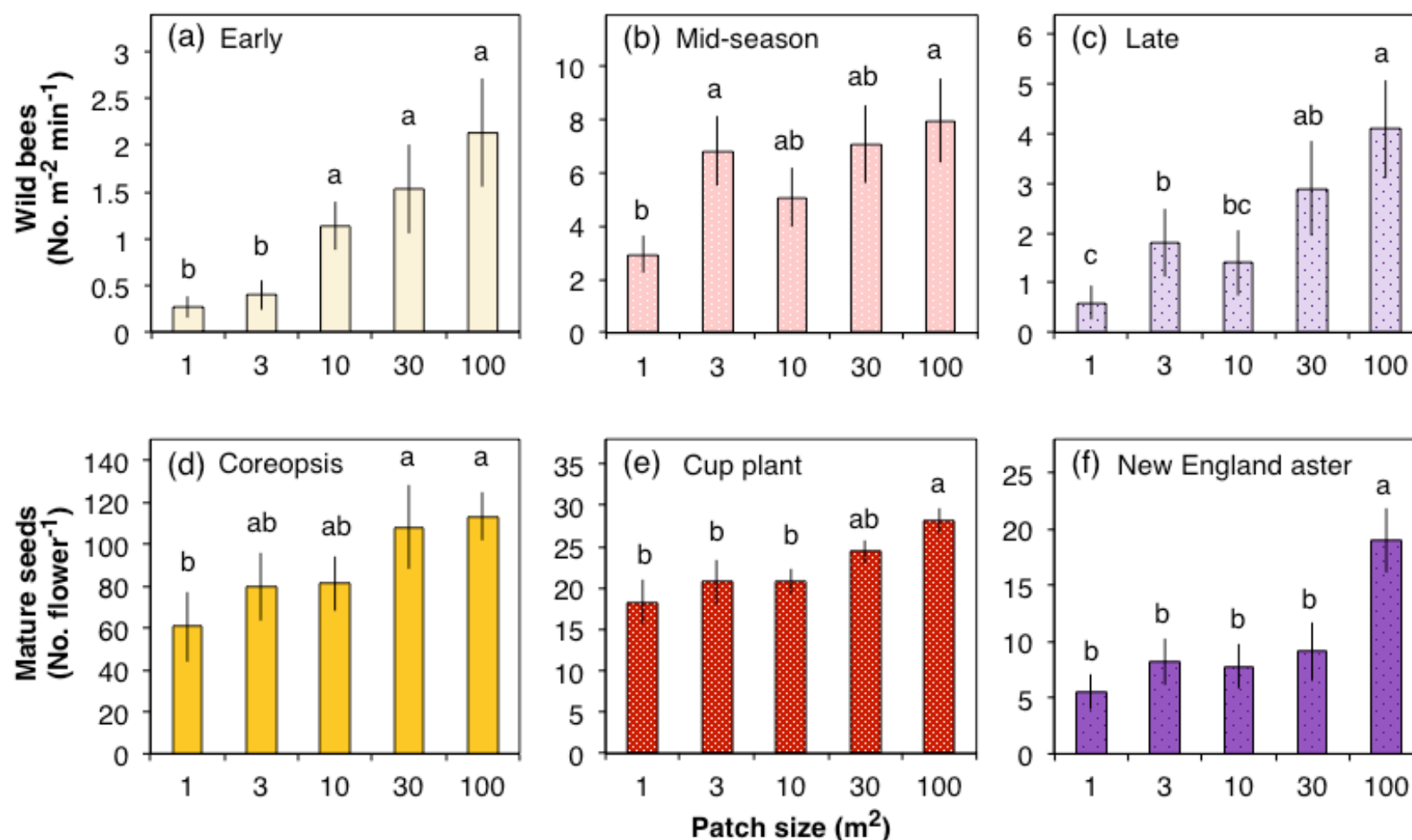


Figure 2.4 Wildflower pollination as a function of patch size. The top bar graph panels compare wild bee abundance (mean \pm SE) with wildflower patch size during three different periods that correspond to the bloom periods for three different wildflower species; (a) sand coreopsis (early-season), (b) cup plant (mid-season), and (c) New England aster (late-season). The bottom graph panels compare the number of mature seeds (mean \pm SE) among different sized wildflower patches for the same three native flower species; (d) sand coreopsis, (e) cup plant, and (f) New England aster. Bars within a graph with the same letter are not significantly different (GLM followed by comparisons for each treatment using a GLM).

Pollinator response to wildflower bloom richness was even greater than the response to patch area, with all pollinator groups (honey bees, wild bees, and hoverflies) responding strongly (Figs. 2.4d-f, Table 2.3). Generally, when three or four wildflower species were in bloom more pollinators visited the wildflower patches than when only one or two species were blooming (Fig. 2.2). Similarly, observed diversity of bees increased with wildflower richness, with increasingly diverse bee visitors found in patches when more species of wildflowers were in bloom (Fig. 2.3b; $F_{3,196} = 10.27$, $P < 0.0001$).

The AIC_C values were used to determine which model (patch size only, wildflower richness only, or patch size + richness) best predicted pollinator density and bee diversity. Wild bee and honey bee densities were best explained by wildflower richness, whereas hoverfly density was best described by wildflower patch size (Table 2.3). The AIC_C value for bee diversity was lowest for the model with both patch size and wildflower richness variables included indicating that bee diversity is most influenced by a combination of patch size and flower richness (Table 2.3).

Pollination services to wildflowers

Unfortunately, the hand-pollination treatments produced very few mature seeds, suggesting a problem with the method of pollen delivery. While we were unable to determine the level of pollen limitation in the three flower species from hand-pollination, in bagged treatments, seeds per flower did not differ across patch sizes (sand coreopsis, range = 0.1 ± 0.1 to 1.0 ± 0.8 seeds, $\chi^2 = 3.71$, d.f. = 4, $P = 0.45$; cup plant, range = 0.1 ± 0.1 to 0.2 ± 0.1 seeds, $\chi^2 = 1.57$, d.f. = 4, $P = 0.81$; and New England asters, range = 1.1 ± 0.4 to 3.0 ± 1.1 seeds, $\chi^2 = 1.59$, d.f. = 4, P

= 0.81). These results indicate the importance of insect pollination of those three native wildflower species.

For two of the three wildflower species (cup plant and New England aster), the number of mature seeds per flower increased with increasing wildflower patch size ($\chi^2 = 12.52$, d.f. = 4, $P = 0.014$ and $\chi^2 = 19.28$, d.f. = 4, $P = 0.0007$, respectively). Cup plant flowers in the largest (100 m²) wildflower patches had over twice as many mature seeds than those in the smallest three patch sizes (1-10 m²) (Fig. 2.4e), and New England aster plants in the largest patches had significantly more seeds than all other sizes (Fig. 2.4f). Although not significantly different among the patch sizes ($\chi^2 = 11.61$, d.f. = 4, $P = 0.055$), the numbers of mature seeds per flower of sand coreopsis were significantly greater in the two largest patches than in the smallest patches (Fig. 2.4d). The increased seed set associated with wildflower patch size corresponded to a concomitant increase in native bees observed visiting flowers during the same time period (Fig. 2.4).

Assessing the relationship of the total season-averaged mature seed set revealed that the number of mature seeds set increased significantly with patch size area and decreased with wildflower species richness (Table 2.3). The AIC_C values show that the model with only patch size included was better at describing seed set than models with wildflower richness or with both patch size and richness variables (Table 2.3).

The number of mature seeds was also significantly, although weakly, positively correlated with native bee density ($r = 0.20$, d.f. = 198, $P = 0.004$) and bee diversity ($r = 0.16$, d.f. = 198, $P = 0.027$). It was also positively correlated with patch size ($r = 0.20$, d.f. = 198, $P = 0.004$), but negatively correlated with wildflower richness ($r = -0.32$, d.f. = 198, $P = 0.0042$), suggesting that additional richness reduces pollinator visitation to specific flower species.

Discussion

This study demonstrates that honey bees, wild bees, and hoverflies all respond positively to increasing flower richness, whereas particular insect pollinator groups respond differently to varying sizes of wildflower habitat. With no significant differences in bloom density or flower richness across wildflower habitat sizes, in general wild bees were observed at greater densities and higher diversity in the 30 and 100 m² patches compared to the smallest areas. Conversely, other insect pollinators, such as honey bees and hoverflies, did not respond to wildflower patch size, with relatively constant densities observed across the five different patch sizes.

Further evaluation of wild bee groups observed visiting wildflower patches revealed that the body size, and thus foraging range of bees might influence their response to the area of floral resources. For example, densities of the generally smaller sized wild bees in the Andrenidae, Halictidae, and other Apidae (non-*Apis* and non-*Bombus* spp.) families increased with wildflower patch size. The body size of bees generally correlates with dispersal range (Greenleaf et al., 2007), and bees with low dispersal range are expected to be especially sensitive to habitat loss and fragmentation (Bommarco et al., 2010). Jha and Vandermeer (2009) determined that small-bodied bees in the coffee production system perceive and respond to floral resources at relatively small spatial scales. Thus adding small patches of wildflower habitat may be an appropriate and important approach for supporting many small bee species that have a relatively small foraging range in an otherwise resource-poor environment.

While small bee species are capable of foraging up to two kilometers from their nesting site (Araujo et al., 2004; Bommarco et al., 2010), most bees forage over very restricted areas and distances (Buchmann and Nabhan, 1996; Zurbuchen et al., 2010). With limited flight distances, it

may take many years for pollinators to discover or colonize a newly established wildflower habitat (Handel, 2000). Alternatively, some bee species, such as *Halictus ligatus*, have been observed utilizing newly restored areas, even at an early stage in establishment (Reed, 1995). The considerable number of small-bodied wild bees observed visiting these plots implies that these bees were already within flight range in the surrounding landscape or that the small bees had already colonized the habitats, as the wildflower patches were two years old.

Larger sized wild bees, such as *Bombus* spp., those in the Megachilidae family, and managed honey bees did not respond to varying sizes of wildflower habitat with a maximum size of 100 m². Large bees are estimated to have the capacity for flight over five kilometers (Greenleaf et al., 2007; Osborne et al., 2008). For example, *Bombus terrestris* has a 10-km potential foraging range (Goulson and Stout, 2001), but it is estimated to actually forage with a range of 0.6 to 2.8 km (Chapman et al., 2003). Similarly, honey bee workers typically fly less than 2 km for floral resources, but have the potential range of 8 km (Visscher and Seeley, 1982). The foraging ranges for bumble bees and honey bees are much greater than the scale at which the wildflower patches in this study were established. In addition, a larger body implies the need for greater energetic inputs, and as such, larger bee species, such as bumble bees, may depend upon resources from multiple patches within the landscape (Bommarco et al., 2010).

Hoverflies, like the large wild bees and honey bees, did not respond to wildflower patch size. Hoverfly adults can disperse up to a few kilometers from the site of their eclosion (Rotheray et al., 2009), but like small wild bees, do not generally disperse farther than a few hundred meters from floral or prey resources (Lövei et al., 1998; Wratten et al., 2003). Despite hoverflies' tendency to disperse relatively short distances, Steffan-Dewenter and Tscharnkte (1999) observed that hoverfly abundance was not affected by habitat isolation and Ouin et al. (2006)

determined that hoverflies respond to habitat fragmentation at much larger scales than measured in this study. Furthermore, unlike bees, hoverfly larvae are predaceous, and as such at the local scale studies here, hoverfly adults may be responding to prey density or host quality for oviposition (Sutherland et al., 2001). Thus, for hoverflies and large-bodied bees, it is important to better understand how habitat management at the local and landscape levels can help support their populations.

Animal population densities are often positively correlated with larger fragments of habitat (Rosenzweig, 1995; Connor et al., 2000), but it is also important to understand how the area of habitat affects animal diversity. In this study, the diversity of unique bee groups visiting wildflowers significantly increased with patch size. This was expected as Aizen and Feinsinger (1994) observed that when habitat fragmentation created smaller patches, these patches decreased in pollinator diversity. Other research on pollinator diversity in orchard meadows (Steffan-Dewenter, 2003) and in restored quarry habitats (Steffan-Dewenter et al., 2006) found significantly increased bee diversity with increased habitat area. In general, larger habitat patches contain more abundant and diverse resources, and thus they can support more abundant and diverse habitants (Rosenzweig, 1995; Connor et al., 2000; Steffan-Dewenter, 2003). This study demonstrated that diverse groups of pollinators utilize local patches of wildflower habitat, but other factors than size of patches, such as floral richness, may be influencing those pollinators.

Although flower density and richness did not vary with wildflower patch size, blooming flower richness varied from 1 to 4 species throughout the habitat patches. All three pollinator groups evaluated in this study responded positively to increasing flower richness. Significantly greater densities of pollinators were observed visiting wildflower patches that had three or four species of wildflowers in bloom compared to patches that only had one species in bloom. This

pattern remained consistent for bee diversity, with diversity of unique bee groups increasing with floral richness. These results support previous findings that bee diversity is closely linked to floral diversity (Potts et al., 2003) and increased floral richness leads to greater bumble bee abundance (Hegland and Boeke, 2006; Pywell et al., 2006). Bumble bees have also been shown to forage greater distances in order to visit species-rich floral patches (Jha and Kremen, 2013). Thus, floral richness, along with patch size, is clearly important for attracting and supporting a diverse group of pollinators.

Patch size and floral richness are important factors for supporting pollinators, particularly small wild bees, but is one of these factors more important than the other for predicting pollinator density? Honey bees did not respond to wildflower patch area, but were positively influenced by floral richness, and indeed honey bee densities were best explained by wildflower richness when comparing model AIC_C values. Similarly, although patch size was important, wild bee densities were best explained by wildflower richness. Conversely, hoverfly density was best described by wildflower patch size. This result conflicts with previous work that demonstrated that syrphid activity was predicted by plant species richness (Hegland and Boeke, 2006), but as mentioned earlier hoverfly adults may also be responding to prey density or host quality for oviposition (Sutherland et al., 2001), which may be more important than patch size or floral richness at this scale (Ouin et al., 2006). A combination of patch size and floral richness was the best model for predicting bee diversity in the wildflower habitats, presumably because larger habitat patches contain more abundant and diverse resources, which can support greater diversity of bees (Steffan-Dewenter, 2003)

Providing floral resources is important to support wild bee communities, but being able to attract these pollinators is also essential for the persistence of the plants in those habitats. Most

flowering plants depend on insects for sufficient pollen dispersal as their main method of reproduction (Larson and Barrett, 2000; Ashman et al., 2004; Ollerton et al., 2011), and thus decreased visitation rates due to habitat fragmentation result in insufficient pollen dispersal (Wilcock and Neiland, 2002) and decreased seed set (Ashman et al., 2004; Dauber et al., 2010). Previous work has shown that there was no relationship between seed set and habitat size when habitat area was greater than 100 m² (Steffan-Dewenter et al., 2006). In spite of the relatively small scale, this study demonstrates that in general increasing wildflower patch size results in an increase in wildflower seed set of three native wildflowers, corresponding to the increase in pollinator densities within those patches. These results are consistent with findings from Meyer et al. (2007), where small patches of horseshoe vetch had reduced numbers of flower visitors and reduced seed set. Lower pollinator visits and seed set in small habitat patches emphasize the negative impact of habitat fragmentation and loss on insect pollinator communities and the plants that depend on their services (Meyer et al., 2007).

As with pollinator density and diversity, patch area and floral richness influenced seed set of the native wildflowers planted within the habitat patches. Comparing the AIC_C values for wildflower seed set determined that the model with only patch size included was the best for predicting seed set compared to models including wildflower richness alone or both patch size and richness factors. The number of mature seeds was also significantly positively correlated with wild bee density, diversity, and patch size. This was predicted since wild bee density, diversity, and seed set all increased with patch size. Conversely, seed set was negatively correlated with wildflower richness. It is expected that visitation by generalist pollinators in wildflower patches with multiple species of flowers in bloom may result in an increased dispersal of heterospecific pollen among the flowers in bloom, ultimately resulting in

compromised seed set. Furthermore, if certain flower species not measured in this study were more attractive to pollinators than those that were measured, when in bloom with other species, the more attractive species may have been visited by a disproportionate number of pollinators, resulting in a decreased pollination in the studied species with increased floral richness (Ghazoul, 2006). A better understanding of flower species attractiveness, overlapping bloom periods, and the specialization of pollinators is needed to determine how seed set and floral richness are related.

Human land use intensification has broken much of the remaining natural habitats into smaller and more isolated patches or islands (MacArthur and Wilson, 1967; With, 2002), often fragmenting the habitat that insect pollinators depend on for survival. This study revealed that insect pollinators, particularly small-bodied wild bees, and their pollination of wildflowers benefit from the establishment of large patches of native wildflower habitat with diverse floral resources.

Pollination is an ecosystem service that is also significantly exploited by farmers all over the world for production of a large range of crops, which is dependent on pollinators, particularly wild and managed bees (Greenleaf and Kremen, 2006; Winfree et al., 2007a; Ollerton et al., 2011). In agricultural systems, insect pollinators are currently suffering considerable declines in species richness and abundance (Biesmeijer et al., 2006; Potts et al., 2010). One valuable form of field management that may help conserve pollinators in agricultural systems is to establish floral habitat in areas adjacent to the crop fields (Carreck and Williams, 2002; Pywell et al., 2005). These floral habitats may act as vital ‘habitat islands’ in agricultural landscapes (Pickett and Thompson, 1978; Letourneau, 1998) by providing suitable habitat needed to maintain viable pollinator populations within the landscape. Recent studies indicate that adjacent wild habitat can

increase pollinator abundance in almond (Klein et al., 2012) and mango (Carvalho et al., 2012) orchards. Thus, wildflower habitat establishment in agricultural systems may increase connectivity of the landscape linking the habitat patches and the ability of the pollinators to traverse this landscape, which may be particularly important in a system where migration from natural habitat are needed for the pollination services in the neighboring crop (With, 2002).

Conservation of a broad range of beneficial insects is important for providing ecosystem services in agricultural settings (Landis et al., 2000; Kleijn and Sutherland, 2003a; Bianchi et al., 2006). If wildflower plantings are to be used to deliver ecosystem services to crop fields it is essential to determine the optimal patch size and configuration (Brosi et al., 2008). Beyond patches of wildflowers, the complexity of the surrounding landscape may also affect local insect diversity in agricultural systems (Tschamtko et al., 2002), while small-scale habitat manipulation may only attract and concentrate insects that are already present in the surrounding landscape (Gurr et al., 1998). Therefore, future studies should address the combined influence of landscape context and habitat patch size on the distribution and dispersal of beneficial insects to and from crop fields in agricultural landscapes.

The continuing loss of natural vegetation is resulting in simplified landscapes with limited floral diversity, which consequently leads to lower insect pollinator diversity (O'Toole, 1993; Holzschuh et al., 2007). This study concludes that wild pollinators and their pollination services are sensitive to the area of available floral resources. Establishing a diverse set of wildflower species in large patches of habitat will provide nesting sites and pollen resources within foraging range of insect pollinators (Franzén and Nilsson, 2010), which may subsequently increase the habitat connectivity (Donald and Evans, 2006), resulting in an increase in bee density and diversity in the otherwise fragmented landscape. While confounding factors, such as

dispersal ability, patch size, and floral richness, can complicate the understanding of fragmentation effects on pollinators (Ewers and Didham, 2007), the general patterns observed here can help guide future efforts in the conservation and support of plant–pollinator interactions in the natural and agricultural landscapes.

CHAPTER 3.

LARGER WILDFLOWER PLANTINGS INCREASE NATURAL ENEMY DENSITY, DIVERSITY, AND BIOLOGICAL CONTROL OF SENTINEL PREY, WITHOUT INCREASING HERBIVORE DENSITY

This chapter has been published as Blaauw, B.R. and Isaacs, R. (2012) Wildflower plot size influences attraction of natural enemies and their delivery of ecosystem services. *Ecological Entomology*. 37: 386-394

Introduction

Populations of beneficial insects are at risk of decline, particularly in agroecosystems (Biesmeijer et al., 2006; Landis et al., 2008) due to the scarcity of native and flowering plants, insecticide use, and loss or fragmentation of habitat (Landis et al., 2000; Goverde et al., 2002; Carvell et al., 2006). Consequently, there has been growing interest in developing approaches to conserve beneficial insects and these strategies often involve integrating floral resource patches into farmland (Bianchi et al., 2006; Kremen and Chaplin-Kramer, 2007; Isaacs et al., 2008; Letourneau and Bothwell, 2008). For this to be adopted within agricultural systems, support of beneficial insects must be done without increasing negative impacts of herbivore populations (Lavandero 2006; Isaacs et al. 2009).

Sufficient flower abundance and proper vegetation structure are necessary to support a diverse community of insects (Zurbrügg and Frank, 2006a), and therefore manipulation of structurally resource poor habitats through the addition of flowering plants and grasses is expected to help mitigate the loss in beneficial insect diversity in agricultural landscapes (Long et al., 1998; Kells et al., 2001; Rebek et al., 2005). Insect natural enemies, like most beneficial insects, require access to alternate hosts, overwintering habitats, a constant food supply, and appropriate microclimates in order to persist within an environment (Johnson and Triplehorn, 2005; Jonsson et al., 2008). These requirements can be met through the provision of a diverse assemblage of flowering plants, which will provide the resources necessary to support populations of insect predators and parasitoids throughout the season (Landis *et al.*, 2000; Ahern and Brewer, 2002; Büchi, 2002a; Sanchez *et al.*, 2003; Wanner *et al.*, 2006).

Insect population density is expected to be greater in larger habitat patches that have more resources to support populations (Slobodkin, 1980), but few studies have examined this pattern in relation to beneficial insects. While a positive response from insect natural enemies to the size of host patch size has been documented previously (Bach, 1988b; Olson and Andow, 2008), there is little information on the response of natural enemies or herbivorous insects as a function of wildflower patch size. Beneficial insects respond positively to the addition of flowering resources in farmland, but different insect taxa respond to these manipulations in varying ways (Fraser et al., 2008; Osborne et al., 2008; Tschamtkke et al., 2008), and may also respond to habitat at different scales. Meyer et al. (2007) and Olson and Andow (2008) found that larger grassland habitat areas resulted in greater insect abundance and diversity. In a study by Heard et al. (2007), landscape composition influenced bee abundance, but flower patch size had no effect. Conversely, Meyer et al. (2007) observed that increasing flowering strip size increased abundance and diversity of pollinators.

Studies measuring the response of insect herbivore abundance to habitat patch size have also resulted in conflicting observations. Raupp and Denno (1979) observed that herbivore density increased with patch size of salt marsh grasses, whereas Grez and Gonzalez (1995) found that herbivore densities do not differ with patch size of cabbage plants. While the patch size of the host crop may be important, insect herbivores may also be able to take advantage of wildflower plantings in the agricultural landscape. Therefore, understanding how generalist herbivores and potential crop pests respond to wildflower habitat patch size will also be important for future implementation of wildflower plantings to conserve beneficial insects in agricultural landscapes.

To determine how natural enemies respond to wildflower plantings of different sizes, we measured insect density and diversity in wildflower plots of different sizes that remained consistent in plant diversity and species composition. Our hypothesis was that density, richness, and diversity of insect natural enemy groups will increase with the size of wildflower plots, and we predicted that the level of biological control from these insects would increase similarly. To determine whether plot size affected the magnitude of biological control provided by natural enemies, soybean aphid (*Aphis glycines* Matsumura) population growth was measured in the same wildflower plots on sentinel plants. Finally, we also measured the response of herbivorous insects to wildflower plot size to test the hypothesis that the density, richness, and diversity of insect herbivore groups would increase with wildflower plot size.

Methods

Field preparation

A 1 ha grass field was prepared for the experiment in the fall of 2008 at the Trevor Nichols Research Complex in Fennville, Michigan. Twenty-five square plots of varying size were mowed and then sprayed with 1% glyphosate herbicide at 206.7 L/ha (Touchdown®, Syngenta Crop Protection, Inc. Greensboro, NC) twice in the late summer to reduce the growth of weeds. At first vegetative growth in 2009, the same herbicide was applied to all plots two weeks before wildflower seedlings were planted. The plots were not tilled in order to prevent the exposure of dormant weed seeds.

The twenty-five square shaped plots consisted of a logarithmic series of five size treatments with 5 replicates each: of 1, 3, 10, 30, and 100 m². These plots were arranged in a 5 x

5 grid of 15 x 15 m cells, with the center of each plot positioned in the center of a grid cell.

Different sized plots were arranged within the grid using a Latin-square design (Fig. 3.1).

One-year-old plants (Wildtype Native Plant Nursery, Mason, Michigan) of 12 native perennial wildflower species (Table 3.1) were planted in mid-May 2009. Plants were selected for their known attractiveness to natural enemies and had overlapping bloom periods that spanned May through October (Fiedler and Landis, 2007a). The 12 different species were planted 30-45 cm apart within square groupings of 12 seedlings, with the relative position of each species randomized within every grouping. With this design, to maintain the same relative abundance of species across the experiment, 1 m² plots had 1 grouping of 12 seedlings (1 from each species), the 3 m² plots had 4 groupings (48 seedlings), 10 m² plots had 9 groupings (108 seedlings), 30 m² plots had 25 groupings (300 seedlings), and 100 m² plots had 64 groupings (768 seedlings). To combat weed growth, a 5 cm depth of wood chips was added to the plots after planting. The grass surrounding the plots was mowed approximately once a month during the summer for the duration of this project, and five locations within the grassy areas and away from the plots served as the negative controls.

Insect sampling

From May through September 2010 each of the twenty-five wildflower plots were sampled in random order. Once a month on warm, calm, and sunny days between 10:00 and 16:00 h each plot was sampled four times for 30 seconds using a modified reversed-flow leaf blower (BG 56 C-E; Stihl, Waiblingen, Germany) with a fine white mesh bag (150 µm, The Cary Company, Addison, IL) placed over the intake to capture insects (Fiedler, 2006). Suction sampling can underestimate species richness in cross-habitat comparisons as the efficiency of

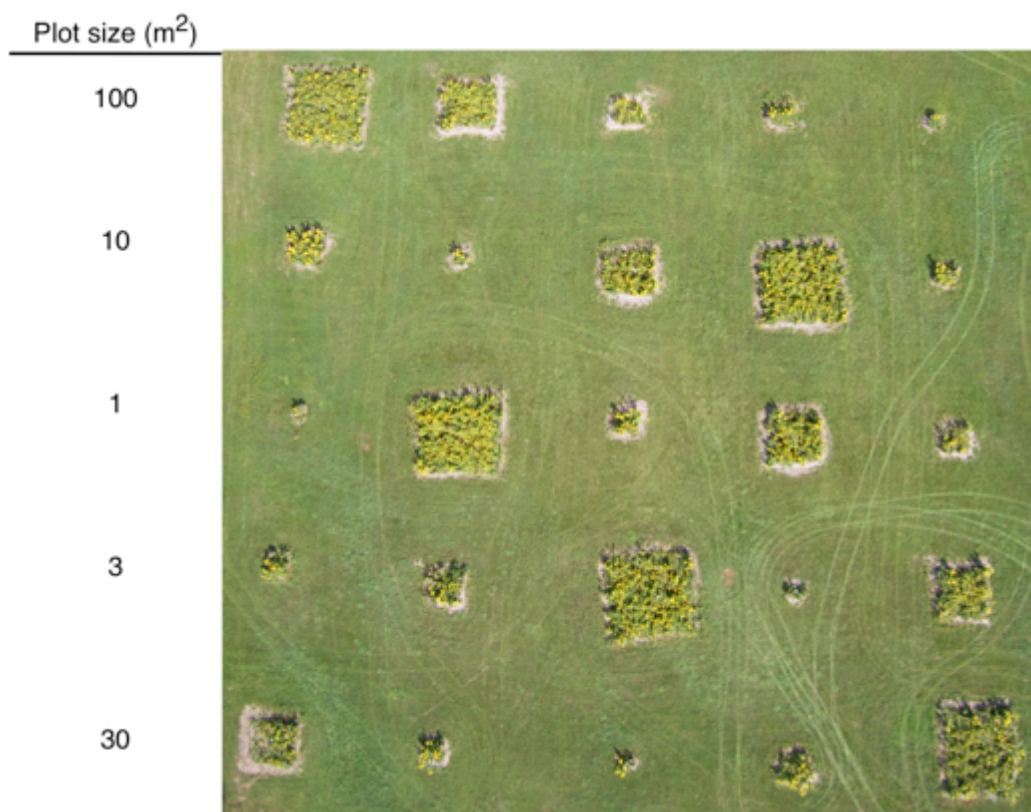


Figure 3.1 Aerial image of wildflower patches. Sized patches were arranged using a Latin-square design, and size (m²) of the wildflower plantings in the first column are displayed on the left.

Table 3.1 List of native Midwestern annual wildflowers and their bloom periods planted at the Trevor Nichols Research Center in Fennville, Michigan, USA.

Common Name	Scientific Name	Bloom period (month)					
		M	J	J	A	S	O
Golden Alexanders	<i>Zizia aurea</i>	X	X				
Foxglove beard-tongue	<i>Penstemon digitalis</i>		X	X			
Sand coreopsis	<i>Coreopsis lanceolata</i>		X	X			
Black-eyed Susan	<i>Rudbeckia hirta</i>		X	X	X	X	
Butterfly milkweed	<i>Asclepias tuberosa</i>			X	X		
Spotted beebalm	<i>Monarda punctata</i>			X	X		
Boneset	<i>Eupatorium perfoliatum</i>			X	X	X	
Blue lobelia	<i>Lobelia siphilitica</i>			X	X	X	
Yellow coneflower	<i>Ratibida pinnata</i>			X	X	X	
Cup plant	<i>Silphium perfoliatum</i>			X	X	X	
Stiff goldenrod	<i>Solidago rigida</i>				X	X	X
New England aster	<i>Symphyotrichum novae-angliae</i>				X	X	X

suction sampling to capture arthropods is higher in shorter vegetation when compared to taller vegetation (Hossain et al., 1999).

Five, 30-second negative control samples were also taken in the same manner from the grassy areas. Sampling focused on flowering portions of the plants where available, and the insect samples were placed in a cooler, returned to the laboratory, and frozen. Insects were later separated from plant matter and identified to major taxonomic groups (Table 3.2) using standard keys (Borror and White, 1998; Johnson and Triplehorn, 2005). Although it is possible that insect abundance data from the suction-samples underestimate the overall abundance of these arthropods, this approach resulted in collection of insects from a wide variety of taxonomic groups, including parasitoids, predaceous insects, and herbivores. Voucher specimens were deposited in the Albert J. Cook Arthropod collection at Michigan State University (Appendix 2).

The density, richness, and diversity (Shannon-Wiener Index, H) of unique taxonomic groups of natural enemies and herbivores (Table 3.2) were compared among plot sizes using analysis of variance (ANOVA) with data averaged from each month during the growing season (May through September) (JMP, Version 5, SAS Institute Inc., Cary, NC). Insect density and group diversity were further compared among treatments by Student's t test with the alpha level corrected *post hoc* via the Bonferroni method ($\alpha = 0.01$) (Zar, 1999). Each observed taxonomic group of natural enemies were also analyzed using ANOVA and Student's t test to determine if specific groups of insects responded positively to wildflower plot size.

Biological control and wildflower plot size

Soybean plants, *Glycine max* (L.) Merr., were grown from seed in the greenhouse and transferred into 15.2 cm square pots. In 2009 and 2010, 50 soybean plants were grown to the V6-stage and two groups of 25 plants were placed in the wildflower plots for each of two repetitions of the following experiment. Soybean plants were placed only in the wildflower plots and not in the grass control areas. To test the background level of predation among plot sizes before flowers started blooming on July 27 and again August 13, 2009, pairs of soybean plants were infested with a combination of 10 (4 adult, 3 mid-instars, and 3 early instars) apterous soybean aphids and placed near the center of each of the twenty-five wildflower plots for two weeks. One control soybean plant in each plot was covered completely, including the pot, with a fine nylon mesh (150 μ m hole size, The Cary Company, Addison, IL) to exclude all natural enemies from the aphids, and the other soybean plant was left uncovered to allow for predation of aphids (Fox et al., 2004; Gardiner et al., 2009). Each potted soybean plant was placed into a separate 15.2 cm square pot attached to a 45 cm stake and placed near the center of each plot, providing support and stability to the potted plants. These pots were painted with fluon (Insect-a-slip, Bioquip Products Inc., Rancho Dominguez, CA) to keep ground dwelling arthropods off the potted plants. The number of aphids on each plant was counted after two weeks. To test the response of predation to plot size after the flowers had started blooming this experiment was repeated on July 30 and August 16, 2010.

To determine the magnitude of biological control provided in 2009 (before flowering) and in 2010 (after flowering), we calculated the relative aphid suppression in different size plots by expressing the change in aphid numbers on open and caged plants as a proportion of aphid

abundance in the absence of predators for each plot. The resulting biocontrol services index (BSI) can vary from 0 to 1, with values increasing as the level of aphid predation increases:

$$BSI = \frac{\sum_{p=1}^5 \frac{(A_{c,p} - A_{o,p})}{A_{c,p}}}{n}$$

where A_c is the number of aphids on the caged plant on day 14, A_o is the number of aphids on the open plant on day 14, p is the plot, and n is the number of replicates for a given plot (Gardiner et al., 2009).

The biological control experiment was conducted twice over a two-month timeframe, so the data were pooled and averaged for these months, and the BSI values and aphid abundance were compared among plot sizes using ANOVA. The BSI values and aphid abundance were then compared among plot sizes using Student's t test with the alpha level corrected *post hoc* via the Bonferroni method ($\alpha = 0.01$) (Zar, 1999). To determine the relationship between aphid abundance on open plants and the populations of natural enemies we calculated the Pearson product-moment correlation of BSI with the natural log transformed ($\log_e + 1$) natural enemy abundance data (Table 2).

Results

Insect natural enemies

The majority of insect natural enemies captured in the wildflower plots included parasitic wasps, spiders, and ants, with other notable collected natural enemies being hoverflies and

minute pirate bugs (Table 3.2). The density (insects/m²) of insect natural enemies increased with plot size (Fig. 3.2a), and was almost twice as high in the 100 m² plots compared with the 1 m² plots ($F_{5,144} = 3.39$, $P = 0.0063$). Natural enemy group richness increased significantly across treatments ($F_{5,144} = 4.99$, $P = 0.0003$), with 30 and 100 m² plots having significantly more unique natural enemy groups (Table 3.2) than the 1 m² plots or the control (Fig. 3.2b). The trend of natural enemy group diversity increased across treatments and was significantly higher in all wildflower plots greater than 1 m² compared to the grassy control plots (Fig. 3.2c; $F_{5,144} = 5.09$, $P = 0.0003$), but did not differ significantly among the different wildflower plot sizes (Fig. 3.2c).

Of the natural enemy groups measured, both predator and parasitoid insects responded positively to plot size. The density of predaceous insects increased with plot size and differed significantly from the control samples ($F_{5,144} = 3.07$, $P = 0.011$). Parasitoid density also increased significantly with plot size ($F_{5,144} = 3.29$, $P = 0.0076$) with significantly more parasitoids being collected in 100 m² compared to the control, 1 m², and 3 m² samples.

Insect herbivores

Plant bugs, leaf hoppers, and aphids were the primary insect herbivores captured in the wildflower plots (Table 3.2). The density of insect herbivores was lower on all wildflower plots than on the control plots (Fig. 3.3a; $F_{5,144} = 13.02$, $P < 0.0001$), but did not differ significantly among wildflower plot sizes. Conversely, herbivore group richness (Table 3.2, Fig. 3.3b; $F_{5,144} = 3.41$, $P = 0.039$) and diversity (Fig. 3.3c; $F_{5,144} = 5.94$, $P < 0.0001$) were significantly higher in all wildflower plots compared to the grassy control plots, but neither showed significant difference among wildflower plot sizes (Fig. 3.3c).

Table 3.2 Numbers of unique taxonomic groups collected in the different sized wildflower plots, grass control areas, and the total abundance of natural enemies and insect herbivores observed in those plots from the four months of sampling.

Taxonomic group	Wildflower plot size (m ²)					
	Control	1	3	10	30	100
Number of individuals collected						
Natural enemies:						
Araneae	60	193	224	225	271	250
Coleoptera						
Coccinellidae	5	11	12	6	11	11
Cantharidae	0	6	15	4	12	22
Dermaptera	0	12	6	1	2	2
Diptera						
Syrphidae	6	34	39	84	102	70
Tachinidae	0	2	5	3	3	1
Dolichopodidae	5	12	15	19	21	26
Asilidae	0	1	0	1	0	1
Hemiptera						
Anthocoridae	4	38	26	45	51	69
Nabidae	29	7	19	11	9	14
Hymenoptera						
Parasitica	319	244	294	378	362	488
Aculeata						
Vespoidea	0	1	1	0	0	0
Formicidae	270	65	78	97	130	152
Neuroptera	4	6	5	20	7	32
Total abundance	702	632	739	894	981	1138
Herbivores:						
Coleoptera						
Scarabaeidae	3	14	11	35	37	52
Chrysomelidae	323	35	53	39	44	60
Curculionidae	44	5	24	53	49	3
Hemiptera						
Miridae	363	232	252	320	412	431
Cicadellidae	1472	162	244	280	365	288
Aphidae	303	110	87	89	102	101
Lygaeidae	3	13	17	33	26	35
Tingidae	6	35	4	47	21	24
Cercopidae	29	21	16	25	40	30
Fulgoroidea	38	2	5	4	3	5
Lepidoptera	69	90	49	58	81	70
Total abundance	2654	719	762	983	1180	1099

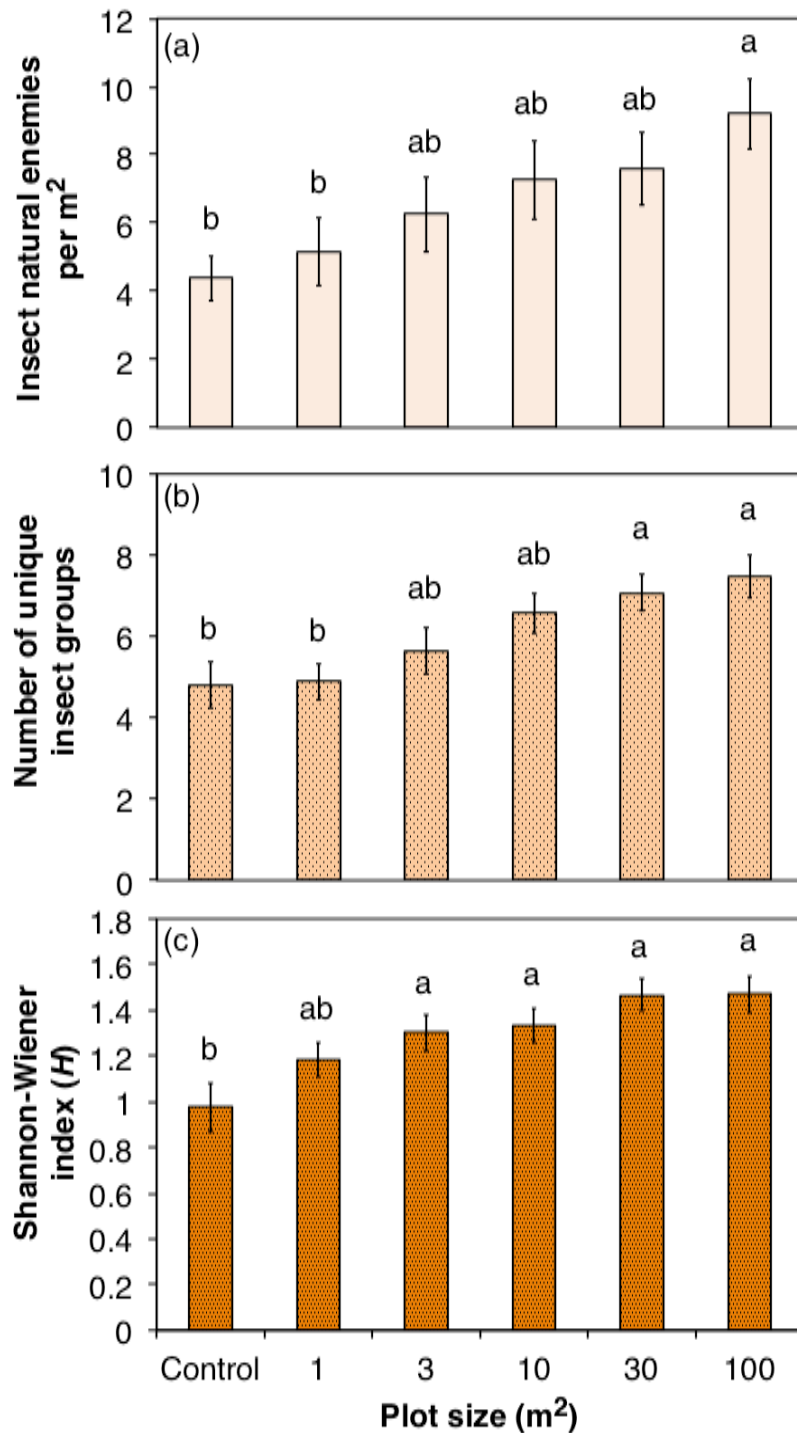


Figure 3.2 (a) Density of insect natural enemies (mean \pm standard error of the mean (SE)) for the different sized flower plots. (b) Insect natural enemy group richness (mean \pm SE) for the different sized wildflower plots. (c) Shannon-Wiener diversity index of insect natural enemy groups (mean \pm SE) for the different sized flower plots. Bars within a graph with the same letter are not significantly different (ANOVA, followed by comparisons for each treatment using Student's t with Bonferroni correction, $\alpha = 0.01$).

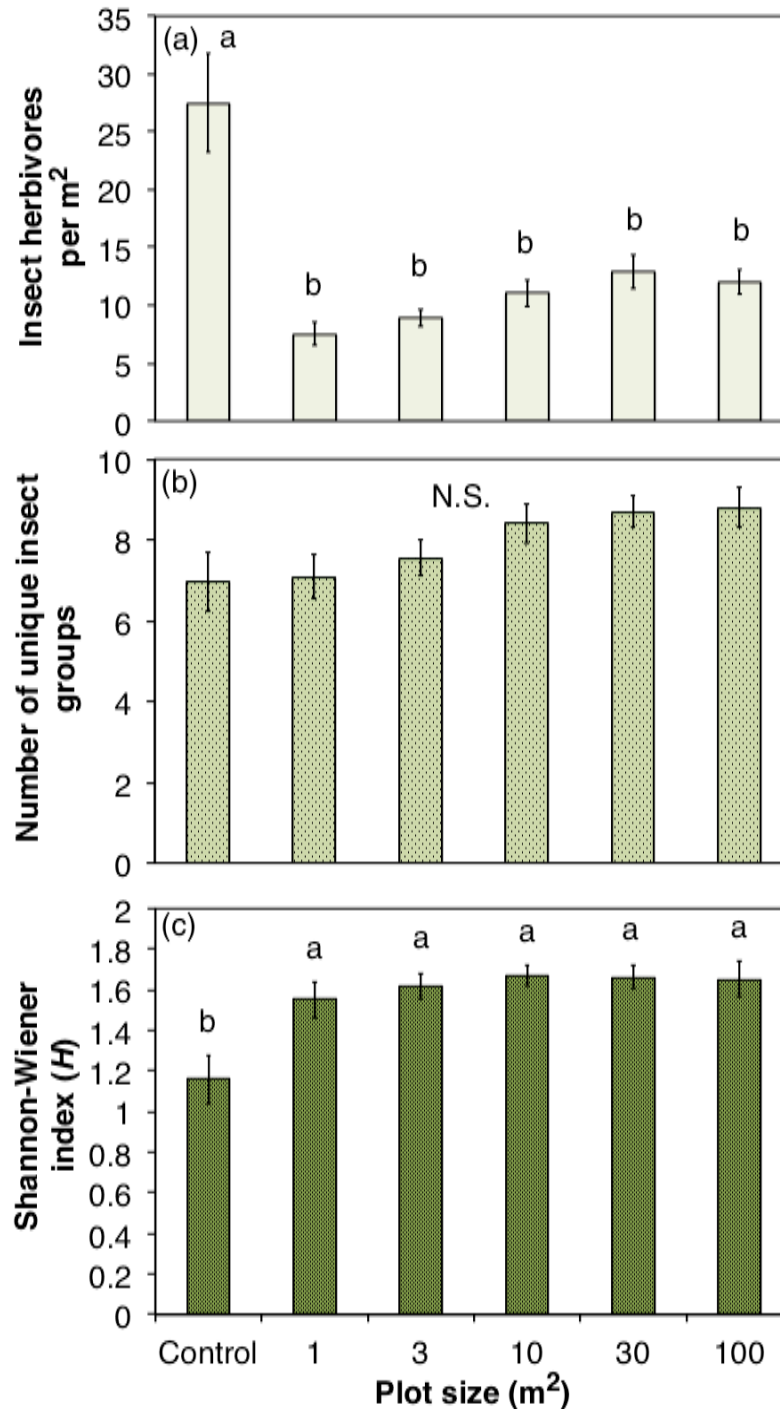


Figure 3.3 (a) Density of herbivorous insects (mean \pm SE) for the different sized flower plots. (b) Insect herbivore group richness (mean \pm SE) for the different sized wildflower plots. There was no significant difference amongst treatments. (c) Shannon-Wiener diversity index of insect herbivore groups (mean \pm SE) for the different sized flower plots. Bars within a graph with the same letter are not significantly different (ANOVA, followed by comparisons for each treatment using Student's *t* with Bonferroni correction, $\alpha = 0.01$).

Biological control

In 2009, in the absence of blooming wildflowers, aphid populations on open soybean plants after two weeks in the field ranged from 15 to 189 aphids per plant and 30 to 203 aphids per plant on caged plants. After wildflower establishment, in 2010 aphid populations on open soybean plants ranged from 7 to 24 aphids per plant and ranged from 54 to 288 aphids per plant on caged plants after two weeks in the field. Adult alate soybean aphids were not observed in either year on open or in caged treatments, suggesting little crowding response.

In 2009, aphid abundance on open sentinel soybean plants was lower, but not significantly different than on those that were caged ($F_{1,98} = 3.78$, $P = 0.055$). Also, neither aphid abundance ($F_{4,45} = 0.94$, $P = 0.45$), nor the BSI value differed significantly among the wildflower plot sizes in 2009 (Fig. 3.4a; $F_{4,27} = 0.25$, $P = 0.91$). In 2010 with the presence of flowers, the average BSI among all 25 plots was significantly higher than that of 2009 (2010, 0.85 ± 0.036 and 2009, 0.69 ± 0.052 ; $F_{1,71} = 6.31$, $P = 0.014$). Also, in 2010 after two weeks in the wildflower plots, aphid colony sizes were much lower on the exposed soybean plants compared to the control plants with the mesh cages ($F_{4,45} = 57.4$, $P < 0.0001$). There was no significant difference in aphid abundance on caged plants among wildflower plot sizes ($F_{4,45} = 3.65$, $P = 0.832$), and as plot size increased the aphid abundance on open plants decreased. The open plants in the 100 m^2 plots had significantly fewer aphids remaining after two weeks than those in the 1 m^2 plots. With increasing plot size there was also an increase in the BSI values. Plots 10 m^2 and larger had significantly greater biological control of soybean aphids than those in the 1 m^2 plots (Fig. 3.4b; $F_{5,44} = 5.62$, $P = 0.0011$). The BSI values were also positively correlated with the density of predaceous insects ($r = 0.499$, $df = 48$, $P = 0.0001$).

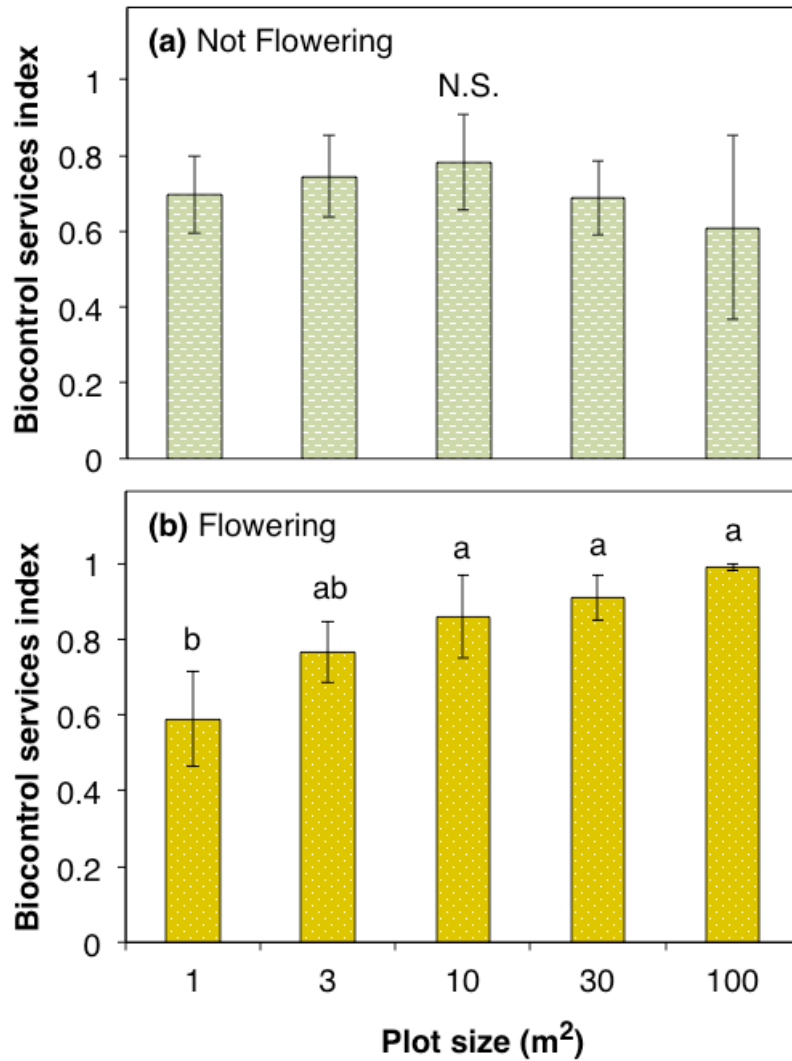


Figure 3.4 The BSI values (mean \pm SE) for predation of soybean aphid, *Aphis glycines*, colonies placed in wildflower plots that varied in size from 1-100 m². (a) 2009. There was no significant difference among treatments. (b) 2010. Bars with the same letter are not significantly different (ANOVA, followed by comparisons for each treatment using Student's t with Bonferroni correction, $\alpha = 0.01$).

Discussion

In this study we show that the density, richness, and diversity of natural enemy groups increase with the native wildflower patch size. The density of predaceous insects in wildflower

plots was also positively correlated with BSI as measured using biological control of soybean aphids in the absence of ground dwelling predators. In contrast, herbivore density did not change with planting area, suggesting that wildflower plantings can selectively support beneficial insects, providing support for their application in agricultural settings to help regulate pest populations.

The increase in natural enemy density with wildflower plot size supports previous results that natural enemies respond positively to plot sizes in different crops, such as maize and mustard (Olson and Andow, 2008; Bezemer et al., 2010). We found that parasitoid wasps (Braconidae and Ichneumonidae), ants (Formicidae), green lacewings (Chrysopidae), and minute pirate bugs (*Orius* spp.) responded positively to wildflower plot size. As these are known to be common insect natural enemies (DeBach and Rosen, 1991), this is a promising result for supporting natural enemies using wildflower plantings because some point during their life cycles, parasitoid wasps (Winkler et al., 2009), ants (Blüthgen and Fiedler, 2004), green lacewing adults and larvae (Silva et al., 2007), and minute pirate bugs (Letourneau and Altieri, 1983) depend on and/or are enhanced by pollen and/or nectar from flowering resources.

As with the density of insect natural enemies, biological control also increased with wildflower plot size. The relative suppression of soybean aphid populations of open versus caged soybean plants was significantly higher in larger wildflower plots. The BSI values were also positively correlated with the density of predaceous insects, further supporting the role of these insects in natural aphid regulation (Costamagna & Landis, 2007). Calculations for BSI are dependent on growth of aphid populations enclosed in a cage of fine mesh. We designed this portion of the study based on the results of Gardiner et al. (2009) and Fox et al. (2004), who both gained insights by comparing open and mesh cage populations of aphids. While mesh cages can

increase temperature and humidity, which may affect aphid populations (Luck et al., 1988), these effects are often either minor (Chambers et al., 1983; Fox et al., 2004) or insignificant (Brosius et al., 2007). Despite those previous reports, we cannot rule out that cage effects influenced aphid growth or survival, potentially affecting the calculated BSI values.

As wildflower plot size increased, so did the total number of flowers per plot, and it has been shown that this is positively correlated with an increase in the level of biological control, particularly parasitism of pest herbivores (Scheid et al., 2011).

Green lacewing larvae and *Orius* spp. are voracious predators of aphids, and their observed increase with wildflower plot size in this study is an additional explanation for the increase in biological control of soybean aphids as planting size increased. From these results, we suggest that providing beneficial insects with larger habitats with densely flowering resources will result in significantly higher densities of natural enemies and subsequently greater pest control within those habitats than provided by small wildflower plots or mown, grass-dominated areas. Hence, larger wildflower plots are more suitable for the conservation of beneficial insects and the natural pest control they provide.

Wildflower plantings may also provide resources for insect herbivores, with the wildflower plantings supporting a significantly higher diversity (but not abundance) of groups of insect herbivores compared to the control areas. The relative density of insect herbivores increased with wildflower plot size in this study. This result supports the predictions of the resource concentration hypothesis (Root, 1973) and is similar to previous studies in which herbivore density increased with host patch size (Thompson, 1978; Raupp and Denno, 1979). Conversely, other studies have found that herbivore densities do not differ with habitat patch size (Maguire, 1983; Bach, 1988a; Grez and Gonzalez, 1995). These conflicting results may stem

from the various sizes and compositions of patches studied, as well as the different organisms observed. Natural enemy retention time is greater in habitats with more abundant prey resources (Vos et al., 1998; Seagraves, 2009), but we did not detect a significant increase in herbivore density among plot sizes. The presence of flowers is likely a more important contributing factor. This is supported by our analysis of the 2009 data where there were no wildflowers in the size plots and we found no difference in the density of open aphid colonies across wildflower plot size. Subsequently, in 2010, in the presence of wildflowers, aphid control was observed on open soybean plants and was significantly higher in the larger plantings.

Beneficial insect abundance and diversity are declining in a variety of landscapes due to habitat loss and agricultural intensification (Goverde et al., 2002; Carvell et al., 2006). Hence, the natural ecosystem services these insects provide are also at risk of decline (Kremen *et al.*, 2002b; Luck *et al.*, 2003). In order to support diverse populations of beneficial insect species in agricultural landscapes that may be able to disperse into crop fields for suppression of pests, it is critical to first understand how beneficial insects and their functions respond to the size of habitat comprised of supportive plants. While our study was not designed to determine a specific size of wildflower habitat needed to conserve beneficial insects, we can conclude that natural enemies and their provision of natural control of herbivores are sensitive to the size of wildflower plantings, even at a relatively small scale. The largest wildflower planting tested in this study was comparatively small in terms of the scale of habitat plantings being established on farms for beneficial insect conservation (EU, 2005; NRCS, 2010), so future examination of larger habitat patches would help illuminate the response of natural enemies to broader ranges of habitat patch size.

Conservation of a broad range of beneficial insects is important for providing ecosystem services in agricultural settings (Landis et al., 2000; Kleijn and Sutherland, 2003a; Bianchi et al., 2006). If wildflower plantings are to be used to deliver ecosystem services to crop fields it is essential to determine the optimal plot size and configuration (Brosi et al., 2008). Beyond patches of wildflowers, the complexity of the surrounding landscape may also affect local insect diversity in agricultural systems (Tschamtke et al., 2002), while small-scale habitat manipulation may only attract and concentrate natural enemies that are already present in the surrounding landscape (Gurr et al., 1998). Therefore, future studies should address the combined influence of landscape context and habitat planting size on distribution and dispersal of beneficial insects to and from crop fields in agricultural landscapes.

CHAPTER 4.

WILDFLOWER PLANTINGS SUPPORT WILD POLLINATOR POPULATIONS AND THEIR POLLINATION SERVICES IN ADJACENT PERENNIAL CROP FIELDS

Introduction

Many arthropods provide valuable ecosystem services, such as those that support human food production. Pollination services have been estimated to be valued at over US\$200 billion annually around the world (Gallai et al., 2009), which includes the contribution from native bees to crop productivity (Klein et al., 2007). However, insect pollinators and the pollination they provide are at risk of decline in agricultural landscapes (Biesmeijer et al., 2006; Potts et al., 2010). Several factors associated with increased farming intensity to support growing human populations can limit the suitability of farm environments for insect pollinators, such as reduction in natural areas, habitat fragmentation, and scarcity of flowering food and nesting resources (Carvell et al., 2006). Monoculture plantings of crops often lack floral diversity and provision of resources for bees throughout the season. Compared to more diverse landscapes, the lack of resources in agricultural landscapes can reduce bee diversity (O'Toole, 1993) and potentially decrease wild bee contributions to crop pollination.

Pollinator-dependent crops rely mostly on the European honey bee, *Apis mellifera* (Winfree et al., 2007b). A high dependence on this single species puts over a third of the world's food supply (Klein et al., 2007) at risk to the challenges facing honey bees (Neumann and Carreck, 2010). In addition to the efforts to sustain honey bee populations, there is growing interest in practices to diversify the sources of crop pollination, such as integrating floral resources into agricultural systems to promote wild pollinator species (Isaacs *et al.*, 2009a; Winfree, 2010). Enhancement of structurally resource-poor environments through the establishment of flowering plants and grasses is expected to create habitat for beneficial insects in agricultural landscapes (Long et al., 1998; Kells et al., 2001). Insect pollinators, require access

to overwintering habitats, a constant food supply, and appropriate microclimates in order to survive and reproduce (Johnson and Triplehorn, 2005). Incorporating flowering plant strips into the agricultural landscape adjacent to the otherwise resource-poor crop fields can fulfill these requirements and help support pollinators throughout the season (Carreck and Williams, 2002; Kremen *et al.*, 2004b; Heard *et al.*, 2007). While native and non-native annual and perennial plants can be used in flowering strips, native perennials are adapted to the local environment, unlikely to become invasive, and are attractive to native pollinators (Pontin *et al.*, 2006; Tuell *et al.*, 2008; Isaacs *et al.*, 2009a; Hogg *et al.*, 2011).

Bees benefit from floral resources at both the landscape and field scales. Larger pollinator habitats can lead to greater bee density and improved pollination of wildflowers (See Chapter 2), and an increasing proportion of natural area within landscapes is associated with improved crop pollination (Kremen *et al.*, 2002b; Holzschuh *et al.*, 2012). For systems in which crop pollination is provided by eusocial or multi-voltine bees, flowering borders within bee flight ranges of crop fields that bloom after the crop may provide the required pollen, nectar, and shelter resources for pollinators throughout the growing season, thereby providing the preconditions for maintaining populations of bees within the agricultural system (Roulston and Goodell, 2011). Recent studies indicate that adjacent wild habitat can increase pollinator abundance in almond (Klein *et al.* 2012) and mango (Carvalho *et al.* 2012) orchards, but with positive influence on pollination only in the latter system where habitat was tailored to support pollinators. There is relatively little information on how local-scale improvement (Murray *et al.*, 2012) of resource-poor areas using optimized mixes of wildflowers will affect pollination services in adjacent crop fields, or the return on investment from the improvement practice.

To determine how wild bees respond to local habitat manipulation with native perennial wildflowers, we measured pollinator abundance and diversity within plantings and adjacent crop fields at blueberry farms in Michigan, USA. We tested the hypothesis that wild pollinator abundance and diversity, crop pollination parameters, and yield would be higher in blueberry fields adjacent to wildflower plantings due to pollinator enhancement from the increase in floral resources compared with fields adjacent to grass control perimeters. Finally, we determined whether the value of changes in blueberry yield could exceed that of the investment in pollinator habitat under different economic scenarios.

Methods

Wildflower planting establishment

In 2009, we established wildflower plantings at five highbush blueberry (*Vaccinium corymbosum* L.) farms in southwest Michigan, USA. Due to decisions made by one of the growers, only four of the blueberry farm sites were sampled in 2012. The plantings ranged from 0.06 to 1.01 ha in size with dimensions that range from 15.2 x 36.6 m to 91.4 x 111.3 m, and were established within 3 m of the crop fields. At each site, the field adjacent to the wildflower planting was paired with a control field that had a perimeter of mown grass without the addition of sown flowers. Control perimeters were adjacent to the same blueberry cultivar and were separated from the enhanced field border by an average distance of 287.4 m that ranged from 175 to 490 m. The landscape at a 1 km radius surrounding the wildflower plantings were composed of an average \pm standard error of 55.3 ± 4.1 percent semi-natural habitat (forest and

grassland), while the proportion of semi-natural landscape surrounding the control perimeters was 59.3 ± 8.1 percent.

Field margins were prepared for the establishment of wildflower plantings with an application of 1% glyphosate herbicide at 200 L/ha (Roundup®, Monsanto, Creve Coeur, MO) in the fall of 2008 and again in early spring 2009. The sites were not tilled, to reduce germination of dormant weed seeds. A perennial wildflower seed mix (Michigan Wildflower Farm, Portland, MI) was selected that consisted of 15 species of Michigan native wildflowers with bloom periods that together span May through October and have been shown to be attractive to bees (Tuell et al., 2008). To reduce competition with invasive plants, provide fuel for potential controlled burnings for future management, and provide nesting habitat for ground nesting bees (Goulson, Lye & Darvill 2008), three native grass species were also included in the seed mix (Table 4.1). The seeds were combined with sawdust at 1:10 ratio, and hand-broadcasted into the prepared sites in early May of Year 1 at 2.25 kg/ha, and the sites were then lightly raked, rolled, or “cultipacked” in order to maximize soil-seed contact. Establishment rates were low in the first year, so in the spring of 2010, we used a hand-operated seed spreader (Earthway Products, Inc., Bristol, IN) to add another 2.25 kg of seed per hectare combined with vermiculite at 1:10 ratio at four of the five sites, for a total of 4.5 kg of native seed per hectare (Table 4.1). The fifth field site was predominately covered with weeds with little germination of native wildflowers in 2009, so this site was treated again with glyphosate in the fall of 2009 and early spring of 2010. This site was reseeded with a total of 4.5 kg/ha of native seed mix (Table 4.1) using a hand-operated seed spreader.

According to standard prairie plant establishment procedures in Michigan, the plantings were mowed (8-12 cm height) two to three times during the first year of establishment to prevent

Table 4.1 List of native Mid-Western perennial wildflowers, grasses, bloom periods, and respective seeding rates for seed mix sown in the wildflower plantings.

Common Name	Scientific Name	Bloom Period (month)						Seeding Rate	
		M	J	J	A	S	O	kg/ha	seeds/m ²
Flowers									
Golden Alexanders	<i>Zizia aurea</i>	X	X					0.07	10.88
Foxglove beard-tongue	<i>Penstemon digitalis</i>		X	X				0.14	64.24
Sand coreopsis	<i>Coreopsis lanceolata</i>		X	X				0.28	19.76
Black-eyed Susan	<i>Rudbeckia hirta</i>		X	X	X	X		0.14	90.94
Swamp milkweed	<i>Asclepias incarnata</i>			X	X			0.28	4.74
Butterfly milkweed	<i>Asclepias tuberosa</i>			X	X			0.14	3.78
Wild bergamot	<i>Monarda fistulosa</i>			X	X			0.07	69.18
Joe pye-Weed	<i>Eupatorium maculatum</i>			X	X	X		0.03	48.94
Boneset	<i>Eupatorium perfoliatum</i>			X	X	X		0.28	39.54
Blue lobelia	<i>Lobelia siphilitica</i>			X	X	X		0.14	61.78
Yellow coneflower	<i>Ratibida pinnata</i>			X	X	X		0.14	14.82
Cup plant	<i>Silphium perfoliatum</i>			X	X	X		0.28	1.38
Stiff goldenrod	<i>Solidago rigida</i>				X	X	X	0.28	20.26
New England aster	<i>Symphyotrichum novae-angliae</i>				X	X	X	0.14	32.62
Smooth aster	<i>Symphyotrichum laevis</i>					X	X	0.28	13.58
Grasses									
Canada wild-rye	<i>Elymus canadensis</i>		X	X	X			0.28	22.61
Indiangrass	<i>Sorghastrum nutans</i>			X	X	X		0.28	11.86
Big bluestem	<i>Andropogon gerardii</i>			X	X	X	X	1.23	9.88

seed set by annual weeds (Stewart 2009). During the second year, half of each planting was mowed two to three times while alternating which half was mowed to allow for weed control as well as for some of the native wildflowers to bloom and set seed. The plantings were not mowed in 2011 or 2012. Establishment of wildflowers within the plantings was assessed once each fall from 2009-2012 by randomly sampling the five wildflower plantings and their corresponding control perimeters using a 1 m² polyvinyl chloride (PVC) quadrat. The quadrat was randomly tossed within the plantings and control perimeters 20 times and all the grasses and forbs within the 1 m² area were counted, identified, and recorded. We determined the density of plant species seeded by us and those not seeded by us (volunteer) per square meter and visually estimated their relative coverage area within the quadrat. Seeded plant density was compared between the flower and control treatments for each individual year using a generalized linear mixed model (GLMM) with treatment (wildflowers or control) as the fixed coefficient, farm site as a random factor, Poisson distribution, and a log link function (Bolker et al., 2009) (SPSS, Version 20, IBM Corp., Armonk, NY). The percent coverage of seeded and volunteer plant species were transformed ($\ln + 1$) and compared separately for each treatment for each of the four years using a GLMM with treatment as the fixed coefficient, farm site as a random factor, linear model, and an identity link function.

The density of wildflower blooms within the plantings and control perimeters was also determined by sampling the wildflower plantings and their corresponding control perimeters using a 1 m² PVC quadrat. As in the previous methods, all the flowers that were in bloom within the 1 m² area were recorded as described above, and composites and umbels were considered individual flowers. These measurements were done once every two weeks from May through September in 2010 and 2011. Bloom density per square meter were averaged from each year and

were compared between the flower and control treatments for each individual year using a GLMM as described above a Poisson distribution and a log link function.

Pollinator sampling

To determine the response of pollinators to wildflower plantings, we sampled the pollinator community within crop fields, wildflower plantings, and control field perimeters during 2009-2012. During peak crop bloom, observations were made on 30 blueberry bushes in each of the crop fields adjacent to the wildflower plantings and the control perimeters. This was done by observing insects visiting blueberry flowers on 15 bushes spaced between 1 and 4 m along the edge of the crop field for 15 min and repeating this sample 15 m into the crop interior parallel to the border for another 15 bushes and 15 min. Observers walked along the 15 bushes stopping and recording the identity and number of insects observed visiting blueberry flowers were recorded during warm, calm, and sunny days between 10:00 and 17:00 h. With the exception of honey bees (*Apis mellifera*) and bumble bees (*Bombus* spp.), all other bees and hoverflies (Syrphidae) were identified to family (Borror and White, 1998; Ascher and Pickering, 2012). Voucher specimens were deposited in the Albert J. Cook Arthropod collection at Michigan State University (Appendix 2).

The abundance of each pollinator group observed visiting blueberry flowers per observation was compared between treatments using a GLMM with treatment (wildflowers or control) as the fixed coefficient, farm site as a random factor, Poisson distribution, and a log link function (SPSS). Data were analyzed separately for each year, pooling the abundance data for observations taken along the crop edge and those taken within the interior for each of the two treatments. The bee community was analyzed by determining the proportion of wild bees out of

all bees observed visiting blueberry flowers using a two-tailed Fisher's exact test (JMP, Version 8). Analysis was done separately for each year, comparing bees observed in fields adjacent to wildflower plantings to those adjacent to control perimeters. The wild bee community visiting blueberry flowers was further analyzed by comparing the diversity (Shannon's index, H (Wani et al., 2005)) of pollinator groups separately for each year between the two treatments using a one-way analysis of variance (ANOVA; JMP, Version 8).

Corresponding with the sampling for wildflower bloom density, in Years 2 and 3 after the establishment of the wildflower plantings, the abundance of pollinators in the wildflower plantings and unplanted control perimeters were sampled once a month from May to September. Each month, the area was sampled using five 30 s (2.5 min total) passes with a modified reversed-flow leaf blower (BG 56 C-E; Stihl, Waiblingen, Germany) with a fine white mesh bag (150 μ m, The Cary Company, Addison, IL) placed over the intake to capture insects (Fiedler, 2006). To limit the bias of sampling due to vegetation height (Hossain et al., 1999), the five 30 s sampling periods were distributed throughout the wildflower planting and control perimeter, sampling from areas that were in bloom. Collected insects were later separated from plant matter and pollinators were identified as described above. The abundance of each pollinator group collected was compared separately for each year between the two treatments using a GLMM as described above.

Diversity (H) of pollinator groups collected via vacuum sampling was compared separately for each year between the two treatments using a Mann-Whitney U test to allow for non-normal distribution of data (SPSS). To determine the relationship between the average number of wild pollinators per sample and the average number of native wildflowers in bloom

per 1 m², we calculated the Pearson product-moment correlation of average wild bees with native wildflower bloom density (JMP, Version 8).

Measuring pollination

In Years 1-4 components of crop yield were measured in the fields adjacent to wildflower plantings and in those adjacent to control perimeters. To measure pollination in each sampled blueberry field 15 bushes along the crop edge and 15 bushes 15 m within the interior of the crop field were randomly selected in each field. Prior to bloom, on each bush one flower cluster was randomly designated to be open pollinated (hereafter, open) while a similar cluster on a separate shoot was excluded from animal pollinators (hereafter, bagged) by enclosing it with a fine mesh bag (150 µm, The Cary Company, Addison, IL) attached to the stem with a twist-tie. The total number of blueberry flower buds in each cluster was counted just prior to bloom each year.

After bloom, open clusters were also enclosed with mesh bags to control for potential effects of bags on berry maturation. Prior to harvest, when approximately 50% of the fruit per cluster were ripe, the open and bagged berry clusters were collected and the number of fruit recorded to calculate percent fruit set. Berry weight and seed number are directly related to pollination success (Brewer and Dobson, 1969), so average berry weight was determined for each cluster and the largest berry from each cluster was squashed inside a plastic bag and the number of mature seeds recorded. To account for parthenocarpy, the difference in fruit set, fruit weight, and number of mature seeds between open and bagged samples were calculated to estimate the magnitude of pollination provided by insect pollinators. For each year, we compared the changes in pollination parameters (open minus bagged values) between blueberry fields adjacent to wildflower plantings and fields adjacent to control perimeters using a GLMM with

treatment as a fixed coefficient, farm site as a random factor, a linear model, and a identity link function. In Year 4 we compared the change in pollination parameters between treatments (flower and control) for location in the crop along the crop edge and interior with a GLMM as described above.

Using the change in average percent fruit set and fruit weight between open and bagged treatments, and calculating fruit abundance per hectare based on bush spacing and flowers per bush, crop yield for the crop edge and interior were compared between fields adjacent to wildflower plantings and those adjacent to control perimeters. The number of bushes per hectare was calculated individually for each farm and the average number of flowers per bush was determined from previously-collected data for different blueberry cultivars (Jersey = 5556, Duke = 2944, Bluecrop = 3628, and Elliott = 2540 flowers bush⁻¹ (A. Kirk unpublished)). Yield was estimated by multiplying percent fruit set, berry weight, bushes hectare⁻¹, and flowers bush⁻¹. Due to the non-normality of the data, yields from the crop edge and interior were compared between the wildflower planting and control treatments using a GLMM with treatment as a fixed coefficient, farm site as a random factor, a linear model, and a identity link function. Yield data for the edge and interior positions were then combined for each year and crop yield was compared between treatments for each year separately using a GLMM as described above.

Establishment costs and estimated revenue from wildflower plantings

The expenses that growers face when preparing, establishing, and maintaining wildflower plantings to support pollinators are extensive and may impede widespread adoption of this approach. To better understand the costs and benefits of adding these resources to farms, our grower cooperators recorded all the expenses involved in establishment, including site

preparation, wildflower seeds, site maintenance, and labor during the four-year period of this study. We were then able to use the estimated yield calculations to determine the increase in revenue from the establishment of wildflowers over time.

In Michigan, USA, the Conservation Reserve Program (CRP) supported through the Natural Resources and Conservation Service and administered by the Farm Services Agency provides subsidies to establish pollinator habitat within farm landscapes. The State Acres for Wildlife Enhancement (SAFE) provides an incentive payment up to \$124 per 0.4 ha of land planted and an initial 90% cost-share (up to \$600) for the costs of establishing the wildflowers. Additionally, the program requires growers to dedicate at least 0.8 ha of their farmland to wildflower plantings and growers receive \$62 annually in land rental payment per 0.4 ha of wildflower habitat (NRCS 2010).

From grower questionnaires we learned that each hectare of wildflower planting requires on average \$222 to prepare it for wildflower establishment and the seed mix cost \$2,224. At the labor rate of \$10 per hr, site preparation cost \$49 in labor, and on average \$198, \$148, \$99, and \$49 were spent on maintenance in Years 1 through 4, respectively. It is expected that the maintenance costs will be \$49 for the subsequent years with an added \$247 to conduct mid-contract maintenance for each hectare in Year 5. Using these data, we calculated the relative cost of wildflower planting establishment with and without the subsidy ($\text{Cost} = (\text{size of planting} \times \text{site preparation cost per ha}) + (\text{size of planting} \times \text{seed cost per ha}) + (\text{size of planting} \times \text{salary} \times \text{establishment costs for that year})$).

Fruit yield (kg per ha) for field sites was estimated by multiplying percent fruit set, berry weight, bushes per ha, and average number of flowers per bush. Comparing fruit yield from crop fields adjacent to wildflower plantings to those adjacent to control field perimeters we were able

to determine the percent yield change each year due to the addition of wildflower habitat (Percent yield change = (avg. yield flower treatment – avg. yield control treatment) / avg. yield flower treatment). I used the average, maximum and minimum price of US blueberries, \$4.72 per kg (Joshua 2011), along with the estimated yield to calculate the expected revenue for each of our farm sites (revenue = [(yield x price per kg) x (size of crop field x proportion of crop field enhanced) x (1 + percent yield increase)] – [(yield x price per kg) x (size of crop field x proportion of crop field enhanced)]).

To determine the general effect of wildflower plantings on revenue from blueberry fields, I assumed a single standard 0.8 ha wildflower planting (80 x 100 m), a minimum for the CRP-SAFE program (NRCS 2010), adjacent to the shorter edge of a typically-sized 4 ha highbush blueberry field (100 x 400 m). In this study we measured pollination in roughly 4.5% of the 4 ha blueberry field area, so we used this value as a very conservative estimate of the area of crop field enhanced by the adjacent planting. Using these values, along with the US average blueberry price of \$4.72 kg⁻¹ (Joshua 2011), average yield of 6,725 kg ha⁻¹ (Joshua 2011), the measured changes in yield in response to the planting, and the costs associated with establishment (with and without subsidy), I calculated the cumulative revenue for a 4 ha blueberry field in response to establishing a 0.8 ha wildflower planting based on our data. In 2012 there was an average of 61% fruit set in the area sampled within the crop fields adjacent to wildflower plantings. Then, to reach 100% pollination by Year 10, I extrapolated pollination out to Year 10 assuming that the change in percent yield between the wildflower and control treatments decreased by 50% sequentially each year thereafter. These calculations were then repeated using the national US minimum blueberry price of \$3.75 kg⁻¹ (Joshua 2011) without

subsidy and the maximum price of \$7.12 kg⁻¹ (Joshua 2011) with subsidy to highlight the range of possible revenues.

Results

Wildflower planting establishment

In all four years of this study, the density of seeded plants per square meter within the wildflower plantings was greater than the density of seeded plants in the control mown grass field margins (Table 4.2). The percent coverage of the seeded plants was also significantly greater during each of the four years within the wildflower plantings (Table 4.2). The density of the seeded wildflowers was significantly greater in Year 4 than in Year 1 within the wildflower plantings (Flower: $F_{1,7} = 8.8$, $P = 0.021$), but did not change significantly among years for the control field margins ($F_{1,7} = 14.9$, $P = 0.41$). Similarly, the percent coverage for seeded plants was significantly greater in Year 4 in the wildflower plantings compared to Year 1 ($F_{1,7} = 19.2$, $P = 0.003$). The percent coverage of seeded plants did not change significantly from Year 1 to Year 4 in the control treatments ($F_{1,7} = 0.78$, $P = 0.41$). Also, there was no difference in percent coverage of volunteer plants between the two treatments during 2010, whereas in 2011 the control field margins had significantly greater coverage of volunteer plants than the wildflower plantings (Table S1b). The percent coverage of volunteer (weed) plants did not change significantly from year to year for either treatment (Flower: $F_{1,7} = 0.54$, $P = 0.49$; Control: $F_{1,7} = 1.7$, $P = 0.23$). See Appendix 1 for an example of the wildflower planting establishment during the four year period of this study.

Pollinator abundance and community

In Years 1 and 2, there was no significant difference in the number of wild bees observed in blueberry fields adjacent to wildflower plantings compared to fields adjacent to control perimeters (Fig. 1a; $F_{1,38} = 2.1$, $P = 0.16$, and $F_{1,38} = 1.5$, $P = 0.23$, respectively). Thereafter, relative bee abundance increased in the fields adjacent to the plantings and in 2011 enhanced fields had almost twice as many wild bees than fields adjacent to control perimeters ($F_{1,38} = 14.7$, $P = 0.0008$). The average number of wild bees visiting crop flowers did not increase greatly in Year 4, but remained significantly higher adjacent to wildflower plantings ($F_{1,38} = 13.8$, $P = 0.001$). The abundance of hoverflies visiting blueberry flowers exhibited a similar trend where the treatments were not significantly different until Years 3 and 4 (Fig. 1b; Year 1: $F_{1,38} = 1.5$, $P = 0.054$; Year 2: $F_{1,38} = 0.39$, $P = 0.53$; Year 3, $F_{1,38} = 5.1$, $P = 0.03$; Year 4, $F_{1,38} = 13$, $P = 0.001$). Conversely, across the four year period honey bee abundances observed visiting blueberry flowers showed no response to the flower treatment (Year 1: $F_{1,38} = 2.3$, $P = 0.14$; Year 2: $F_{1,38} = 0.088$, $P = 0.77$; Year 3, $F_{1,38} = 1.9$, $P = 0.18$; Year 4, $F_{1,38} = 0.98$, $P = 0.33$).

Blueberry flowers were visited by a variety of wild pollinators, including bumble bees, sweat bees (Halictidae), mining bees (Andrenidae), and hoverflies (Fig. 4.2). Growers stocked fields with honey bees, which were the dominant pollinator visiting crop flowers, comprising at least 74% of the observed visitors. In 2009 when the wildflowers were still seedlings, the proportions of wild pollinators to all pollinators were similar ($P = 0.071$) between treatments (Fig. 4.2; control = 12% and flower = 10%). In 2010, 22% of the pollinators observed visiting blueberry flowers adjacent to the control perimeters were unmanaged, compared with 31% in crop fields adjacent to wildflower plantings ($P = 0.385$). In 2011, the proportion of wild pollinators visiting blueberry flowers was significantly higher in fields adjacent to the wildflower

plantings (25%) compared to the control (17%) ($P = 0.002$). The proportion of wild pollinators decreased in both treatments in 2012 (control = 6% and flower = 11%), but remained significantly higher in the crop fields adjacent to the flower treatment ($P = 0.001$).

Table 4.2 Comparison of the average (\pm SE) number of seeded (“Seed”) plants per m^2 , a comparison of the average percent coverage (\pm SE) of seeded and volunteer (“Vol.”) plants, and the number of flower blooms per m^2 within the flower and control treatments over four years. Bolded values indicate significant difference between treatments ($P < 0.05$).

			Year			
			2009	2010	2011	2012
Plant density/ m^2	Seed	Flower	8.7 ± 1.7	10.1 ± 1.9	11.2 ± 1.8	10.2 ± 1.6
	Seed	Control	0.01 ± 0.003	0	0.01 ± 0.003	0
		$F_{1,8}$	161.6	47.8	49.3	47.9
		P	0.0009	< 0.0001	< 0.0001	< 0.0001
% coverage	Seed	Flower	5.1 ± 1.1	13.6 ± 3.5	24.6 ± 5.1	26.3 ± 5.3
		Control	0.3 ± 0.3	0	0.05 ± 0.05	0
		$F_{1,8}$	19.7	14.9	23.1	24.1
		P	0.002	0.005	0.001	0.003
	Vol.	Flower	42.6 ± 10.1	60.6 ± 6.4	49.7 ± 4.2	42.3 ± 5.8
		Control	86.1 ± 2.0	87.8 ± 2.9	89.3 ± 3.6	88.8 ± 1.2
		$F_{1,8}$	27.3	14.9	57.4	91.1
		P	0.001	0.005	0.0009	0.0007
Bloom density/ m^2	Seed	Flower	-	4.7 ± 0.9	11.5 ± 2.3	-
		Control	-	0.1 ± 0.08	0.03 ± 0.03	-
		$F_{1,8}$	-	62.7	76.7	-
		P	-	< 0.0001	< 0.0001	-
	Vol.	Flower	-	43.8 ± 10.9	90.7 ± 27.9	-
		Control	-	12.9 ± 3.5	22.9 ± 9.9	-
		$F_{1,8}$	-	2.9	11.1	-
		P	-	0.09	0.01	-

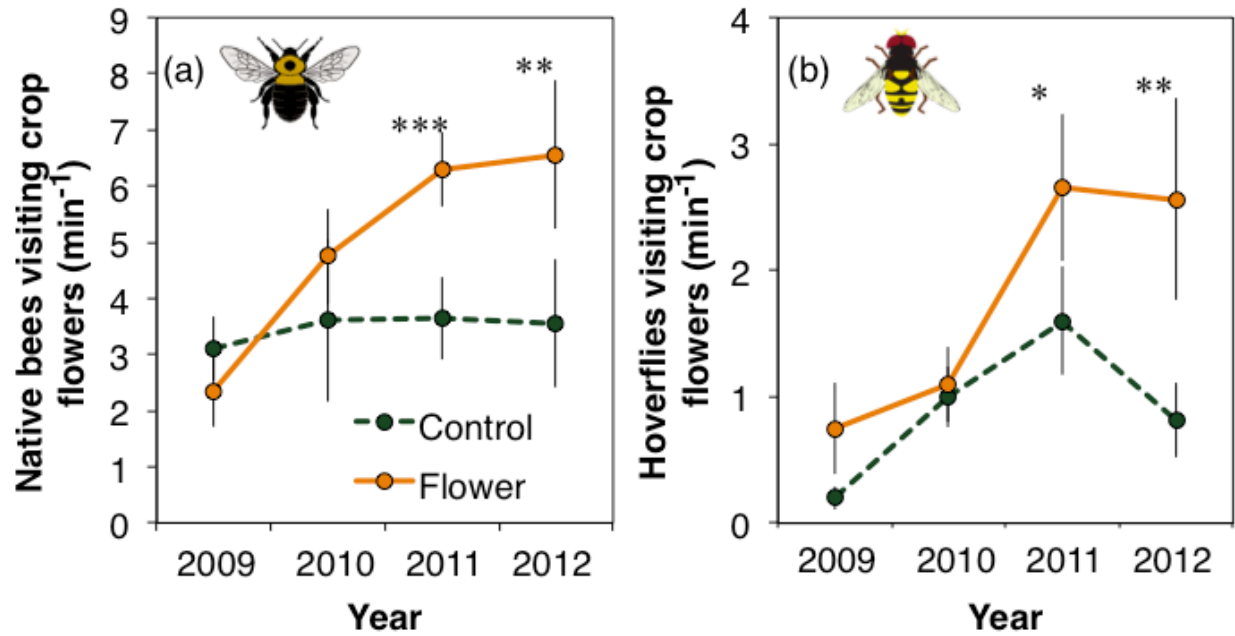


Figure 4.1 Mean \pm SE abundance of (a) wild bees and (b) hoverflies observed visiting blueberry flowers during 15 min observational samples. Asterisks indicate levels of significance (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) for difference between grass control margins and flower treatments.

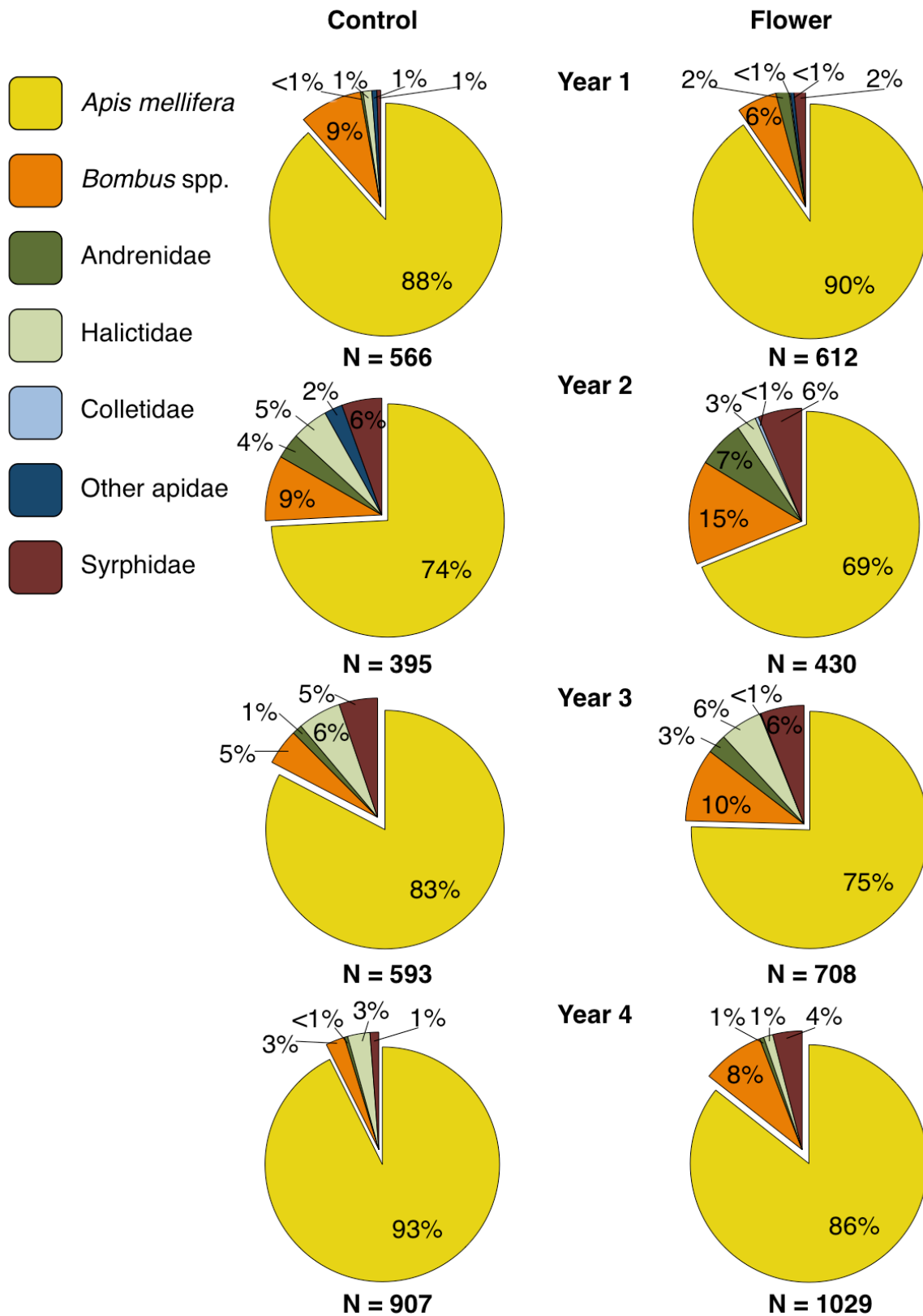


Figure 4.2 Bee community observed in blueberry fields with or without adjacent wildflower habitat over four years.

In 2009, Shannon diversity (see Fig. 4.2 for groups) was similar in blueberry fields adjacent to wildflower plantings or control perimeters ($H = 0.26 \pm 0.10$ and $H = 0.24 \pm 0.10$, respectively; $F_{1,18} = 0.018$, $P = 0.89$). A similar result was found for the following three years ($H = 0.38$ - 0.78 in control fields and 0.55 - 0.90 in enhanced fields; $F < 2.31$, $P > 0.15$).

Vacuum sampling in the areas adjacent to blueberry fields revealed greater abundance of wild pollinators, including bees and hoverflies, in the presence of wildflowers. In 2010 there was an average of 0.4 ± 0.27 wild bees and 2.65 ± 1.59 hoverflies per 2.5 min sampling period within the control perimeters compared with 1.4 ± 0.27 bees and 4.35 ± 1.6 hoverflies within the wildflower plantings. The following year, only 0.48 ± 0.35 wild bees and 1.8 ± 0.92 hoverflies were collected within the control perimeter, whereas 2.16 ± 0.34 bees and 4.12 ± 0.92 hoverflies were collected from the wildflower plantings. In both years, significantly more wild bees were collected in wildflower plantings (2010: $\chi^2 = 6.62$, $P = 0.01$; 2011: $\chi^2 = 14.09$, $P = 0.0002$). Hoverfly abundance was not significantly different in 2010 ($\chi^2 = 0.61$, $P = 0.44$), but in 2011 significantly more hoverflies were collected in the wildflower plantings ($\chi^2 = 3.8$, $P = 0.049$). In 2011 there was a significant positive correlation between the average number of number of seeded flower blooms per square meter within the wildflower plantings and the average number of wild pollinators collected ($r = 0.75$, d.f. = 23, $P < 0.0001$).

Comparing the communities of wild bee groups collected in the two treatments, in 2010 diversity values were not statistically different between the wildflower ($H = 0.1 \pm 0.048$) and control treatments ($H = 0.05 \pm 0.037$; $U = 288$, $P = 0.4$). However, in 2011 bee diversity within the wildflower plantings ($H = 0.26 \pm 0.085$) was significantly greater than that in the control perimeters ($H = 0.03 \pm 0.028$; $U = 225$, $P = 0.011$).

Pollination and yield

In 2009, the difference in average fruit set between open and bagged treatments was greater in blueberry fields adjacent to the wildflower plantings, average berry weight was higher in fields adjacent to the control perimeter, and there was no significant difference in average number of mature blueberry seeds, which indicates no difference in pollen deposition (Table 4.3). With no significant differences between control and flower treatments, the estimated yield was also not significantly different between the treatments (Table 4.3). During 2010, fields adjacent to wildflower plantings had higher pollination parameters but these were not significantly different from the control, and there was no significant difference in yields. In 2011, the increases in percent fruit set, average berry weight, and numbers of mature seeds were significantly greater in blueberry fields adjacent to the wildflower plantings (Table 4.3), and this was consistent in 2012, resulting in higher yield adjacent to wildflower plantings (Table 4.3).

In 2012, the treatments were also analyzed separately by field location, and the average change in percent fruit set was significantly greater along the crop edge adjacent to the wildflower planting ($47.9 \pm 3.6\%$) than the control ($33.4 \pm 3.7\%$; $F_{1,88} = 7.9$, $P = 0.006$). However, these values were numerically greater for the flower treatment, but were not significantly different between treatments for the interior location (flower: $52.8 \pm 4.3\%$; control: $42.7 \pm 4.4\%$; $F_{1,88} = 2.8$, $P = 0.097$). The same trend was observed at the crop edge for the change in average berry weight: 0.64 ± 0.06 g adjacent to the wildflower planting and 0.43 ± 0.06 g next to the control ($F_{1,88} = 6.9$, $P = 0.01$), but there was no significant difference between the treatments 15 m into the crop field (flower: 0.64 ± 0.07 g; control: 0.51 ± 0.05 g; $F_{1,88} = 2.8$, $P = 0.098$). The change in mature seeds per berry was similar at the crop edge adjacent to the wildflower plantings (22.6 ± 1.3 seeds) and the control (20.2 ± 1.8 seeds), and within

Table 4.3 Comparison of the average (\pm SE) changes (open-bagged) in pollination parameters for blueberry fields adjacent to control or flower treatments over four years. Bolded values indicate significant difference between treatments ($P < 0.05$).

Pollination Parameter	Treatment	Year			
		2009	2010	2011	2012
Δ Fruit set	Control	30.1 \pm 2.9	30.9 \pm 2.7	26.5 \pm 3.4	38.1 \pm 2.9
	Flower	37.7 \pm 3.0	32.9 \pm 2.5	37.9 \pm 3.1	50.3 \pm 2.8
	F _{1,294}	3.7	0.29	8.4	9.3
	<i>P</i>	0.056	0.58	0.004	0.003
Δ Berry weight (g)	Control	0.63 \pm 0.08	0.52 \pm 0.03	0.56 \pm 0.05	0.47 \pm 0.04
	Flower	0.52 \pm 0.07	0.53 \pm 0.03	0.62 \pm 0.04	0.64 \pm 0.04
	F _{1,294}	1.1	0.18	1.1	9.4
	<i>P</i>	0.29	0.67	0.3	0.002
Δ Mature seeds	Control	20.7 \pm 1.8	19.5 \pm 0.8	15.0 \pm 1.0	20.1 \pm 1.2
	Flower	21.2 \pm 1.4	19.5 \pm 1.0	19.5 \pm 1.0	23.6 \pm 1.2
	F _{1,294}	0.05	0.001	11	5.1
	<i>P</i>	0.83	0.97	0.001	0.025
Estimated yield (kg/ha)	Control	7291.1 \pm 496.9	4377.1 \pm 218.7	6147.3 \pm 462.9	3171.3 \pm 237.4
	Flower	6887.4 \pm 408.2	4610.62 \pm 224.2	6995.1 \pm 424.4	4148.1 \pm 268.8
	F _{1,294}	0.79	0.65	11	3930
	<i>P</i>	0.37	0.97	0.001	0.003

the crop interior mature seeds were significantly greater next to the flower treatment (flower: 24.7 ± 1.9 seeds; control: 20.5 ± 1.6 seeds) ($F_{1,88} = 1.6$, $P = 0.21$ and $F_{1,88} = 4.4$, $P = 0.039$, respectively).

Estimated blueberry yields were higher in crop fields adjacent to wildflower plantings than controls in 2011 and 2012 (Table 4.3). By examining the two regions of the crop field separately (edge and interior), we also found that the estimated yield followed the same trend as the pollination parameters, being significantly higher along the edge ($U = 2238$, $P = 0.031$), but not within the crop interior ($U = 2609$, $P = 0.44$) in 2011. In 2012 the increase in pollination was more evenly distributed, with significantly greater yield at both regions of the fields adjacent to the wildflower plantings compared to control fields (edge: $U = 1425$, $P = 0.006$; interior $U = 1387$, $P = 0.004$; Fig. 4.3).



Figure 4.3 Estimated blueberry yield (mean \pm SE) for regions of the crop along the field edge and 15 m within the interior in 2012, comparing fields adjacent to wildflower plantings and those adjacent to control perimeters. Asterisks indicate levels of significance (** $P < 0.01$) for difference between control and flower treatments.

Using the estimated yield calculated from the four years of this study along with recorded expenses for establishment and maintenance of wildflower plantings, we compared the costs and revenues, assuming 0.8 ha wildflower plantings placed adjacent to 4 ha highbush blueberry fields over a 10 year period (Fig. 4.4). To determine the potential yield benefits over this time-span, changes in yield in response to wildflower plantings were determined for the first four years based on our field data, with the predicted change in yield decreasing by 20% each year thereafter. Expenses for establishment and maintenance were calculated separately for scenarios with or without cost-sharing for pollinator habitat, and using published prices and yields of highbush blueberry (Joshua 2011). As expected, the time to profit (i.e. positive revenue) is longer for an unsubsidized farm receiving low to average berry prices (4-5 years) than a subsidized farm receiving high prices (3 years, Fig. 4.4).

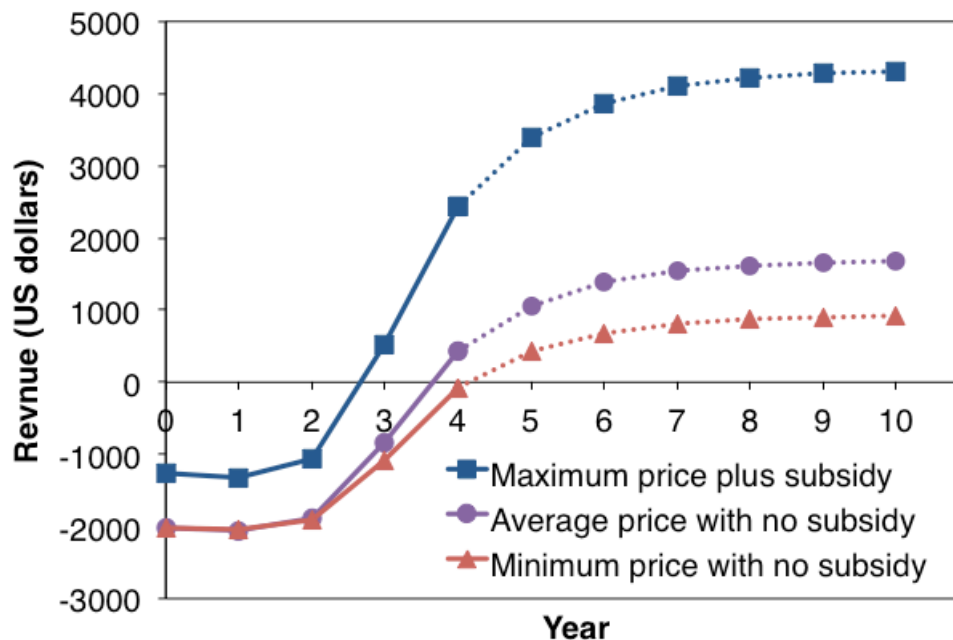


Figure 4.4 Measured (solid line) and predicted (dashed line) revenues from a 4 ha highbush blueberry field adjacent to a 0.8 ha wildflower planting. Scenarios provided are for minimum, average, or maximum price of blueberries (Joshua 2011) and under conditions that are either with or without pollinator habitat subsidy.

Establishment costs and estimated revenue from wildflower plantings

Although not statistically significant, after 2009 there was a 1% decrease in blueberry yield within the area of the crop fields sampled adjacent to the wildflower plantings when compared to the samples taken from the control sites (Table 4.4). The very small decrease in yield along with the initial expenses of the wildflower planting establishment resulted in negative revenue for both unsubsidized and subsidized plantings. The small decrease in yield during the first year may be due to the disturbance of former populations of pollinators and the removal of potential resources during preparation of the sites for wildflower establishment. After 2010, when vegetative and floral resources began to grow back, we found that the percent yield change between flower and control treatments positively favored the enhanced sites, with greater yields being measured for the following two years and extrapolated out to Year 10 for our theoretical 4 ha farm (Table 4.4). The positive changes in yield in response to wildflower plantings result in an overall increase in yield and therefore positive additional revenue for the grower (Fig. 4.4).

The calculated expenses associated with the establishment of a 0.8 ha wildflower planting at a 4 ha highbush blueberry farm is substantially higher at the unsubsidized farm than for the farm receiving assistance. Therefore, while the cumulative revenues based on US average price for highbush blueberries for the unsubsidized and subsidized farms are both expected to make profit during the fourth year, the subsidized farm is expected to have considerably higher revenue (Table 4.4). Either way, within the first four to five years the increase in revenue due to the benefits of wildflower plantings on adjacent crop yield offsets the growers' costs associated with preparation, establishment, and maintenance of wildflower plantings.

Table 4.4 Estimated costs and revenue from the establishment of wildflower plantings to support pollination in adjacent highbush blueberry fields, over a 10 year period. Costs and revenues were based on grower expenses and US average price (\$4.72 kg⁻¹) and yield (6,725 kg ha⁻¹) for highbush blueberry (Joshua 2011). Change in percent yield between the wildflower and control treatments for the first four years was calculated from our data, thereafter assuming that the change in percent yield decreased by 50% each year. Calculations are made for a 4 ha highbush blueberry field with a 0.8 ha wildflower planting under unsubsidized and unsubsidized scenarios.

	Year	% yield change	Unsubsidized				Subsidized			
			Cost	Cumulative cost	Revenue	Cumulative revenue	Cost	Cumulative cost	Revenue	Cumulative revenue
From data	0	-	2020	2020	-35	-2055	1270	1270	-35	-1305
	1	-1	160	2180	176	-1879	110	1380	176	-1129
	2	3	120	2300	1040	-839	70	1450	1040	-89
	3	18	80	2380	1270	430	30	1480	1270	1180
	4	22	40	2419	1270	430	-10	1469	1270	1180
Extrapolated	5	11	240	2659	635	1065	190	1659	635	1815
	6	6	40	2699	317	1383	-10	1649	317	2133
	7	3	40	2738	159	1541	-10	1638	159	2291
	8	1	40	2778	79	1621	-10	1628	79	2371
	9	1	40	2818	40	1660	-10	1618	40	2410
	10	0.3	40	2857	20	1680	-10	1607	20	2430

Discussion

This study demonstrates that establishment of wildflower plantings to provide season-long floral resources can support wild bees and enhance pollination in adjacent blueberry crop fields. We demonstrate that local-scale habitat manipulation can enhance wild pollinator abundance and provide benefit to food production and farm profitability, which has the potential to complement the positive benefits from high diversity (Holzschuh, Dudenhöffer & Tschamtkke 2012; Klein *et al.* 2012). Similarly, Carvalheiro *et al.* (2012) have recently shown that within large mango farms surrounded by natural habitat, the addition of small patches of native flowers can increase crop yield. Hence, pollinator populations and crop yield can benefit from suitable habitat at different spatial scales.

The enhancement of wild bee abundances from wildflower plantings is likely due in part to the additional nesting and food resources provided, which can support their growth and persistence (Potts *et al.*, 2005; Roulston and Goodell, 2011). Because wild bee populations naturally fluctuate from year to year and take time to colonize habitats (Williams *et al.*, 2001), the abundance and diversity of wild bees observed at wildflower-enhanced farms may be partially dependent on the flower abundance from the previous year. Establishing natural habitat in farms by removing vegetation may initially hinder pollinator populations. Although nesting site densities were not evaluated, the substantial increase in floral abundance, and thus greater food resources (i.e. pollen and nectar), in subsequent years likely explains the observed increase in wild bee abundance in 2011 and 2012.

Floral diversity has also been shown to increase pollinator diversity (O'Toole, 1993), which may explain the increased groups of wild bees collected within the wildflower

plantings compared to those collected in the control perimeters. Although vacuum sampling may not be the most effective method for collecting bees (Buffington and Redak, 1998), our approach was intended to sample the broader insect community within the wildflower plantings, which vacuum sampling has been proven to excel at (Buffington and Redak, 1998). While it is possible that wild pollinator abundance data from the vacuum-samples underestimated the overall abundance and diversity of bees in the wildflower plantings, this method did result in the collection of bees from five families, including Apidae, Halictidae, and Andrenidae, and the same sampling method was used in all sampled locations. Because bee diversity is correlated with increasing pollination (Klein et al., 2003b), identifying collected pollinators to species will help us better understand how wildflower plantings affect pollinator diversity and if agriculturally important species are actually benefitting from these plantings.

As with pollinator abundance and diversity, it took multiple years after wildflower establishment to detect a significant change in pollination within the adjacent blueberry fields. During the third year after establishment, pollination parameters including percent fruit set and berry weight were significantly greater in fields adjacent to wildflower plantings. It is expected that as the wildflower plantings continue to establish, the crop pollination benefits will continue to increase. Over time, even a slight increase in fruit yield in high value crops such as blueberry can cover the costs of establishing and maintaining these wildflower plantings (Table 4.4).

Fruit yield can also be directly or indirectly affected by weather conditions (Retamales and Hancock, 2012). Weather factors, such as wind, solar radiation, and temperature can negatively impact the foraging behavior of bees (Vicens and Bosch, 2000; Peat and Goulson, 2005) and affect pollination processes within the plant. During 2012 of this study, there were cool temperatures during blueberry bloom (Marino, 2012a), which were not ideal foraging conditions

for the dominant honey bees. Fortunately, many wild, non-*Apis* bees are more efficient blueberry pollinators and are less hindered by cool temperatures than honey bees (Javorek et al., 2002).

When evaluating the pollination parameters of only the open treatments from 2012, there was a drop in percent fruit set, berry weight, and consequently crop yield for all blueberry sites adjacent to both wildflower plantings and control perimeters (Table 4.1). During 2012 there were atypically high temperatures and low precipitation during the summer months (Marino, 2011, 2012b), which likely played an important role in the considerable decrease in fruit yield from 2011 to 2012. Despite these conditions, fruit set and berry weight were not as negatively affected by the conditions in the crop fields adjacent to the wildflower plantings, supporting the predictions that increased abundance and diversity of wild bees can provide insurance against potential yield loss from poor pollination conditions (Naeem, 1998; Winfree et al., 2007b).

Conservation of a range of beneficial insects is important for reliably providing ecosystem services in agricultural settings (Naeem, 1998; Kleijn and Sutherland, 2003a). The addition of floral resources enhanced populations of non-*Apis* bees, which are efficient pollinators of blueberry flowers. Furthermore, these floral resources also enhanced the abundance of hoverflies within the system. Although hoverflies are not effective pollinators of blueberry, they are efficient pollinators of other crops (Dag and Gazit, 2001; Jauker and Wolters, 2008), and the larvae of aphidophagous species are also biological control agents of many soft-bodied arthropods (Bugg et al., 2008; Smith et al., 2008). Therefore, the impact of flowering resources will likely change depending on the type of crop, and the plantings are expected to provide a variety of ecosystem services to the surrounding fields. Further work is needed to better understand the extent to which multiple services are affected and which crops are best suited for this approach.

If wildflower plantings are to be used to deliver ecosystem services to crop fields, it is also essential to determine the optimal plot size, configuration, and distribution of these plantings (Brosi et al., 2008). Larger plantings of floral resources are expected to have more resources, and hence higher capacity to support populations of beneficial insects (Slobodkin, 1980; Kruess and Tscharntke, 2000a). Furthermore, increasing the size of the floral habitat can positively impact the services provided by insects supported by the additional floral resources (Blaauw and Isaacs, 2012). Beneficial insects respond positively to the presence of flowering resources, but different insect taxa respond to these manipulations in varying ways (Tscharntke et al., 2007; Osborne et al., 2008), and may also respond to habitat at different scales.

Beyond the addition of patches or strips of wildflowers, the complexity of the surrounding landscape may also affect local insect diversity in agroecosystems (Tscharntke et al., 2002), while small-scale habitat manipulation may only attract and concentrate beneficial insects that are already present in the surrounding landscape (Gurr et al., 1998). At the landscape scale, natural habitat is necessary to support a diverse pool of wild pollinators and their services to crop fields (Carvalho et al., 2010; Klein et al., 2012), while at the field scale the addition of floral resources may locally augment bee density and diversity. Meyer et al. (2007) observed that the density and diversity of insect pollinators increased with the size of flowering habitat. Conversely, Heard et al. (2007) found that the local scale source of floral resources supported a greater abundance of pollinators, but had no effect on pollinator density, rather that landscape composition was the major influence on bee abundance. With these conflicting results on the importance of local scale habitat manipulation, it is crucial that future studies address the combined influence of landscape context and local habitat manipulation on distribution and

dispersal of beneficial insects and their ecosystem services within agricultural landscapes (Murray et al. 2012).

It is possible that wildflower plantings will attract bees away from the control perimeters and the surrounding landscape and thereby increase pollination and yield near the wildflowers. This could negatively affect pollination in the control fields if abundance of pollinators in the surrounding landscape were relatively low. Although I did not detect a decrease in pollination in our control fields, this project was not designed to determine the mechanism of the effect, i.e. whether the plantings are a concentrator versus a source of pollinators. This also means that I was unable to distinguish between conservation of pollinator populations in the agricultural landscape in this study and enhancement of local populations via neighboring wildflower habitat (Kleijn et al., 2011). For other studies to explore whether there is also an increase in pollination similar to that detected here, it will be indicates that important to study pollinator population ecology within landscapes enhanced for pollinators to determine whether bee populations are enhanced or redistributed. .

Independent of scale, there are benefits for pollinators and fruit production from the addition of floral resources in agricultural landscapes, but the costs of establishment and maintenance of those habitats might discourage farmers from adopting such an approach. Even within agricultural landscapes surrounded by natural habitats, blueberry production is highly dependent on managed honey bees for crop pollination (Isaacs and Kirk, 2010). However, we show here that providing forage habitat with season-long floral resources optimized for wild bees can support a diverse group of wild crop pollinators that with time can provide yield benefits whose value exceeds the cost of habitat establishment and maintenance, even where honey bees are supplied for pollination.

CHAPTER 5.

NATIVE WILDFLOWER PLANTINGS ENHANCE NATURAL ENEMIES AND THEIR PROVISION OF BIOLOGICAL CONTROL SERVICES IN ADJACENT CROP FIELDS

Introduction

Beneficial insects provide valuable ecosystem services, including decomposition, pollination, and biological control that support human survival and agricultural production. Worldwide, pest suppression from insect natural enemies, such as predators and parasitoid wasps, is valued at over US\$400 billion annually (Costanza et al., 1997). The abundance and diversity of these insect natural enemies are generally higher in agricultural landscapes surrounded by uncultivated, natural habitat (Bianchi et al., 2006), whereas insecticide use, scarcity of flowering plants, and loss or fragmentation of habitat can all make agricultural systems resource-poor landscapes for natural enemies (Landis et al., 2000; Hendrickx et al., 2007; Wade et al., 2008). The lack of habitat and resources can cause declines in valuable biological control services and increase potential for pest outbreaks (Geiger et al., 2010; Chaplin-Kramer et al., 2011; Meehan et al., 2011).

The decline of natural enemy populations can be lessened by enhancing habitat to provide them with alternate prey or hosts, a constant food supply, and appropriate microclimates. Provision of habitat to support beneficial insects can be used within conservation biological control programs to suppress pest populations and reduce dependence on chemical inputs (Pickett and Bugg, 1998; Landis et al., 2000; Jonsson et al., 2010). The nutritional and habitat requirements of predatory and parasitic insects can be fulfilled with a diverse assemblage of flowering, non-crop plants placed within or around crop fields, to provide the pollen and nectar necessary to support their populations throughout the season (Landis et al., 2000; Wanner et al., 2006; Jonsson et al., 2008). Floral resources are utilized by natural enemies as primary and alternative food sources (Wäckers et al., 2005; Jonsson et al., 2010), which can enhance their

longevity, fecundity, and potential control of pests (Büchi, 2002b; Berndt and Wratten, 2005; Lee and Heimpel, 2008).

In crop systems with limited habitat resources for natural enemies, increasing plant abundance and diversity through the addition of flowering plants and grasses is expected to increase natural enemy populations (Rebek et al., 2005) and enhance their provision of biological control services (Letourneau et al., 2009; Letourneau et al., 2011). Natural enemy density and diversity, and their provision of pest control services increase with the area of floral resources available (Blaauw and Isaacs, 2012), so increasing the proportion of natural habitat near to crop fields is expected to support populations of natural enemies in resource-poor landscapes (Bianchi *et al.*, 2006; Zurbrügg and Frank, 2006a).

Floral resources have been used to increase parasitoid populations and enhance parasitism of crop pests (Jonsson et al., 2010). For example, Irvin et al. (2006) found increased parasitism rates and decreased densities of light-brown apple moth, *Epiphyas postvittana* (Walker) (Lepidoptera: Tortricidae) in apple orchards close to plantings of buckwheat (*Fagopyrum esculentum* Moench) and sweet alyssum (*Lobularia maritima* L. Desv.). Similarly, Lavandero et al. (2005) determined that parasitoid wasps fed on buckwheat nectar caused increased parasitism of diamond back moth, *Plutella xylostella* (L.) (Lepidoptera: Plutellidae), larvae in nearby broccoli plantings. Several studies support the importance of floral resources for enhancing parasitoid life histories and their provision of biological control services, but most of these projects have been short-term and have used exotic, annual flowers, such as buckwheat and sweet alyssum (Fiedler et al., 2008). In contrast, native perennial flowering plants are adapted to the local environment, provide long-term support of beneficial insects, are less likely to become invasive, and may increase native biodiversity in agricultural landscapes (Stephens *et al.*, 2006b;

Fiedler and Landis, 2007b). Conservation plantings that use a mix of native perennial flowering plant species that provide floral resources for an extended period of time (Fiedler and Landis, 2007a; 2007b) are expected to enable natural enemies to remain near crop fields even when prey/host densities are low (Olson et al., 2005). This approach fits well in perennial cropping systems that have key insect pests that are suppressed by natural enemies.

Highbush blueberry, *Vaccinium corymbosum* L., a perennial fruit crop native to eastern North America, has a community of important native and exotic insect pests (Retamales and Hancock, 2012). Populations of the blueberry aphid, *Illinoia pepperi* (MacGillivray) (Hemiptera: Aphidae), can be suppressed by insect natural enemies such as syrphids and coccinellids (Whalon and Elsner, 1982). The blueberry maggot, *Rhagoletis mendax* Curran (Diptera: Tephritidae), is another key pest of this crop with larvae that develop inside the berries causing major damage and rendering the fruit unmarketable (Liburd et al., 1998). In Michigan, parasitism rates of *R. mendax* larvae by the parasitoid, *Diachasma alloeum* Muesebeck (Hymenoptera: Braconidae) can reach 50% in unmanaged fields (Stelinski et al., 2004). Increased ground cover and reduced-risk insecticides can enhance ground beetle abundance and lead to increased prey removal in blueberry fields (O'Neal et al., 2005a; O'Neal et al., 2005b), and these may be components of a conservation biological control strategy. As highbush blueberry has numerous pests and is often under intensive chemical management, providing resource-rich habitat for natural enemies outside of the crop field may be needed to avoid non-target effects of insecticides on natural enemy populations. Thus, highbush blueberry is a suitable system to measure the effects of habitat manipulation on natural enemies and pest suppression.

Assessing natural pest control in the field can be challenging due to insecticide use to control pests (Kidd and Jervis, 2007; Sarvary et al., 2007). However, surrogate pest organisms

that can be attacked or consumed by insect natural enemies can be used to assess predator activity within field settings. For example, sentinel leafroller larvae have been used to assess natural enemy-inflicted mortality in apple orchards (Sarvary et al., 2007). Using sentinel corn earworm eggs, *Helicoverpa zea* (Boddie) (Lepidoptera: Noctuidae), Werling et al. (2011) determined that predation was strongly related to generalist predator activity, which was enhanced as plant diversity increased within the landscape surrounding the sentinel eggs.

Numerous native flowering plant species have been evaluated for their relative value and benefit to insect natural enemies and herbivores as resources in habitat management (Fiedler and Landis, 2007a; Fiedler et al., 2008), but there are few studies on how a mixture of these species established for perennial wildflower habitat affects insect populations within adjacent crops over time. It is important to note that additional food resources provided by the establishment of wildflower plantings to help conserve natural enemy populations may provide resources and refuge to insect herbivores (Wäckers et al., 2007).

To determine the impact of perennial floral resources on insect natural enemies and the level of biological control services, I measured insect natural enemy abundance and diversity within native wildflower plantings and adjacent crop fields, and also measured the removal of sentinel prey items placed in adjacent crop fields. I also tested the hypothesis that artificially-planted native wildflower habitats would reduce the naturally occurring herbivore populations in adjacent crop fields.

Methods

Site preparation

In 2009, wildflower plantings were established at five highbush blueberry (*Vaccinium corymbosum* L.) farms in southwest Michigan, USA. The plantings ranged from 0.06 to 1.01 ha in size, and were established within 3 m of blueberry fields. At each site, the field adjacent to the wildflower planting was paired with a control field of the same cultivar and management program but with a perimeter of mown grass without the addition of sown native wildflowers. Wildflower plantings and control perimeters were separated from the enhanced field border by an average distance of 287.4 m (range 175 to 490 m). The landscape at a 1 km radius surrounding the wildflower plantings were composed of an average \pm standard error of 55.3 ± 4.1 percent semi-natural habitat (forest and grassland). Similarly, the proportion of semi-natural landscape surrounding the control perimeters was 59.3 ± 8.1 percent.

Field margins were prepared for the establishment of wildflower plantings with an application of 1% glyphosate herbicide at 200 L/ha (Roundup®, Monsanto, Creve Coeur, MO) in the fall of 2008 and again in early spring 2009. The sites were not tilled to prevent the exposure of dormant weed seeds. A perennial wildflower seed mix (Michigan Wildflower Farm, Portland, MI) was selected that consisted of 15 species of Michigan native wildflowers with sequential bloom periods that together span May through October and have been shown to be attractive to natural enemies (Fiedler and Landis, 2007a) (Table 5.1). To reduce competition with weed grasses and invasive plants, and to provide fuel for potential controlled burns, three native grass species were also included in the seed mix. The seeds were combined with sawdust at 1:10 ratio, and hand-broadcasted into the prepared sites in early May of 2009 at 2.25 kg/ha, and the

Table 5.1 List of native Mid-Western perennial wildflowers and grasses used for the seed mix sown in the wildflower plantings, with their bloom periods and respective seeding rates.

Common Name	Scientific Name	Bloom Period (month)						Seeding Rate	
		M	J	J	A	S	O	kg/ha	seeds/m ²
Flowers									
Golden Alexanders	<i>Zizia aurea</i>	X	X					0.07	10.88
Foxglove beard-tongue	<i>Penstemon digitalis</i>		X	X				0.14	64.24
Sand coreopsis	<i>Coreopsis lanceolata</i>		X	X				0.28	19.76
Black-eyed Susan	<i>Rudbeckia hirta</i>		X	X	X	X		0.14	90.94
Swamp milkweed	<i>Asclepias incarnata</i>			X	X			0.28	4.74
Butterfly milkweed	<i>Asclepias tuberosa</i>			X	X			0.14	3.78
Wild bergamot	<i>Monarda fistulosa</i>			X	X			0.07	69.18
Joe pye-Weed	<i>Eupatorium maculatum</i>			X	X	X		0.03	48.94
Boneset	<i>Eupatorium perfoliatum</i>			X	X	X		0.28	39.54
Blue lobelia	<i>Lobelia siphilitica</i>			X	X	X		0.14	61.78
Yellow coneflower	<i>Ratibida pinnata</i>			X	X	X		0.14	14.82
Cup plant	<i>Silphium perfoliatum</i>			X	X	X		0.28	1.38
Stiff goldenrod	<i>Solidago rigida</i>				X	X	X	0.28	20.26
New England aster	<i>Symphyotrichum novae-angliae</i>				X	X	X	0.14	32.62
Smooth aster	<i>Symphyotrichum laevis</i>					X	X	0.28	13.58
Grasses									
Canada wild-rye	<i>Elymus canadensis</i>		X	X	X			0.28	22.61
Indiangrass	<i>Sorghastrum nutans</i>			X	X	X		0.28	11.86
Big bluestem	<i>Andropogon gerardii</i>			X	X	X	X	1.23	9.88

sites were then lightly raked, rolled, or “cultipacked” in order to maximize soil-seed contact. In the spring of 2010, a hand-operated seed spreader was used (Earthway Products, Inc., Bristol, IN) to add another 2.25 kg seed/ha combined with vermiculite at 1:10 ratio at four of the five sites to help increase native wildflower density. The additional seeding increased the total amount of seed used to 4.5 kg per hectare (Table 5.1). There was poor germination at the fifth field site, so it was treated again with glyphosate in the fall of 2009 and again in early spring of 2010. This site was reseeded with a total of 4.5 kg/ha of native seed mix in 2010 (Table 5.1) using a hand-operated seed spreader.

According to standard prairie plant establishment procedures in Michigan, the plantings were mowed (8-12 cm height) two to three times during the first year of establishment to prevent seed set by annual weeds (Stewart, 2009). During the second year, plantings were mowed two to three times by alternating the half that was mowed to allow for weed control as well as for some of the native wildflowers to bloom and set seed. The plantings were not mowed in 2011 or 2012.

To determine if more seeded flowering plants were found in the flower treatments compared to the control, the establishment of wildflowers within the plantings was assessed once each fall during 2009 to 2012 by randomly sampling the five wildflower plantings and their corresponding control perimeters using a 1 m² PVC quadrat. The density per square meter of plant species hand-seeded and of those species not hand-seeded (volunteers) was determined, and the relative coverage within the quadrat was visually estimated at 5% increments. For complete data and analysis of wildflower establishment, see Chapter 4.

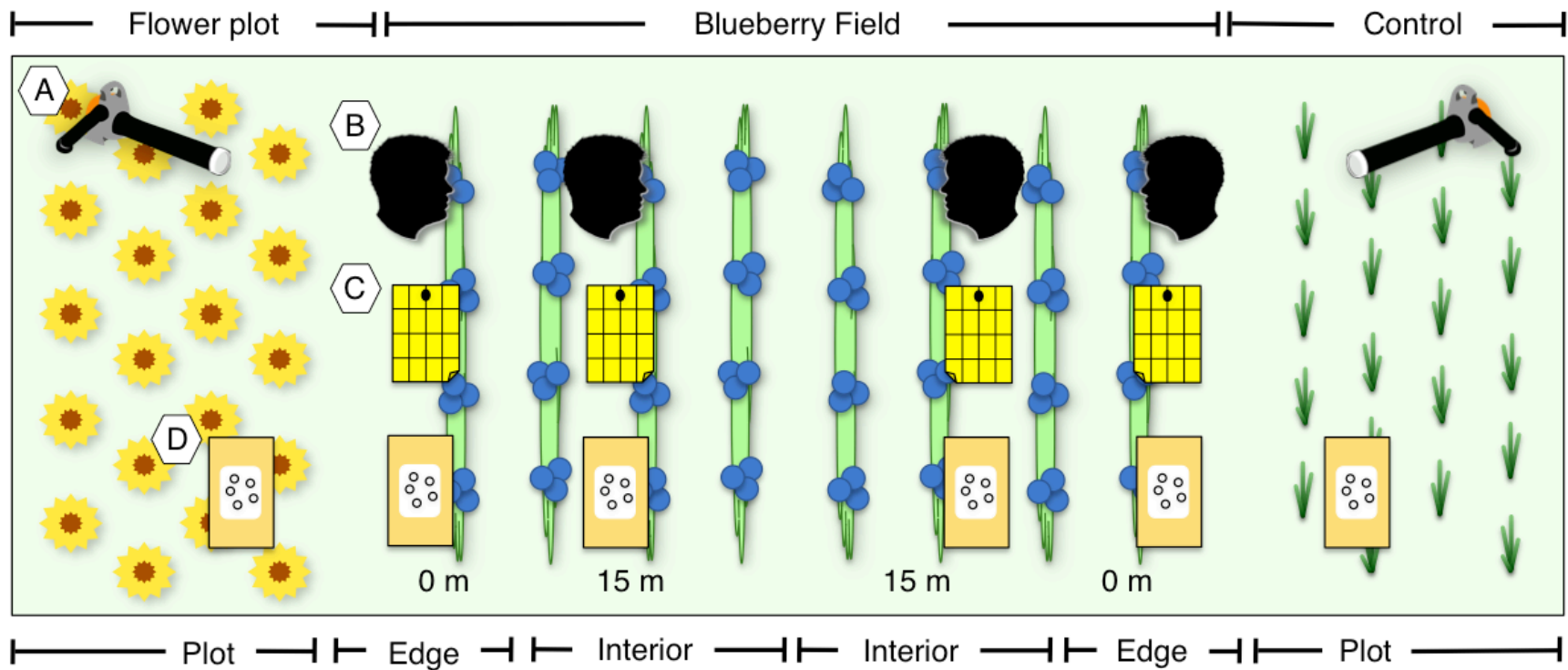


Figure 5.1 Experimental layout for natural enemy and biological control assessment at highbush blueberry farms illustrating the location of (A) vacuum sampling, (B) observational samplings, (C) yellow sticky trap sampling, and (D) corn earworm card placement.

Natural enemies and herbivores in field perimeters

Natural enemies and insect herbivores in the wildflower plantings and in the unplanted control perimeters were vacuum sampled once each month from May to September (Fig. 5.1a). Each site was sampled five times for 30 seconds each (2.5 min total) on each sampling date using a modified reversed-flow leaf blower (BG 56 C-E; Stihl, Waiblingen, Germany) with a fine white mesh bag (150 μm , The Cary Company, Addison, IL) placed over the intake to capture insects (Fiedler, 2006). To limit the bias of sampling due to vegetation height (Hossain et al., 1999) the five 30 s sampling periods were distributed throughout the wildflower plantings and mown control perimeters, being sure to sample from areas that were in bloom. The number of natural enemies and insect herbivores collected via vacuum samples were recorded and identified to family, with the exception of parasitoid wasps (grouped as Parasitica) and *Orius* spp. natural enemies, as well as the specific blueberry pests Japanese beetle, *Popillia japonica* Newman (Coleoptera: Scarabaeidae); cranberry fruitworm, *Acrobasis vaccinii* Riley (Lepidoptera: Pyralidae); cherry fruitworm, *Grapholita packardii* Zeller (Lepidoptera: Tortricidae); and blueberry maggot, *R. mendax*. Only the most commonly collected and/or agriculturally important natural enemies and insect herbivores from the three-year period were used for abundance analyses (Table 5.2). Voucher specimens were deposited in the Albert J. Cook Arthropod collection at Michigan State University (Appendix 2).

Because the wildflower plantings were at different stages of establishment in each year, the densities of natural enemies and insect herbivores (dependent variables) collected per 2.5 min vacuum samples in the wildflower plantings or control perimeters were compared separately for each year between the two treatments (independent variable) using a generalized linear model (GLM) with Poisson distribution, overdispersion parameter estimated by Pearson Chi-square/DF,

and estimated by maximum likelihood (JMP, Version 8, SAS Institute Inc., Cary, NC). The diversities of natural enemy and insect herbivores (Shannon's index, H (Wani et al., 2005)) from vacuum samples were also compared separately for each year between the two treatments using a Mann-Whitney U test to allow for non-normal distribution of data (SPSS, Version 20, IBM Corp., Armonk, NY).

Natural enemies and herbivores in the crop fields

To determine the effect of floral resource plantings on natural enemies and herbivores in the adjacent crop fields, visual samples were taken every two weeks from May through September during 2009-2011 (Fig. 5.1b). At each field, 10 blueberry bushes (8 bushes in 2009) along the crop edge were observed for 1 min each, repeating this sampling 15 m into the crop interior parallel to the border for another 10 bushes (8 bushes in 2009). Insect sampling was done for fields adjacent to the wildflower plantings as well as those adjacent to the control field perimeters. The number of natural enemies and insect herbivores observed on the blueberry plants was recorded and identified as described above for the vacuum samples.

Additional natural enemy and insect herbivore sampling was conducted with yellow sticky traps deployed for seven days each month from May-September in each year of the project (Fig. 5.1c). Each of the crop fields adjacent to wildflower plantings and those adjacent to control perimeters received eight yellow sticky traps: four traps along the crop edge and four 15 m into the interior, placed within bush canopies. After one week deployed in the field, traps were collected and taken back to the laboratory for evaluation. Insects were identified to major taxonomic groups as described above.

Natural enemy and insect herbivore densities observed on blueberry plants per 10 min samples (8 min in 2009) as well as the densities of insects collected per sticky trap were compared between treatments using a GLM as described above (JMP, Version 8). Data were analyzed separately for each year, pooling the abundance data taken along the crop edge and those taken within the interior for each of the two treatments. The Shannon diversity for the natural enemy and insect herbivore communities from observation and sticky trap samples were compared separately for each year between the two treatments using Mann-Whitney *U* tests (SPSS, Version 20).

Biological control services

To determine how wildflower plantings affect biological control in crop fields, in 2011 and 2102 corn earworm eggs, *Helicoverpa zea* Boddie (Lepidoptera: Noctuidae) were used as a sentinel prey item. Eggs were obtained from a commercial insectary (French Agricultural Research, Lamberton, MN, USA), where the eggs had been oviposited on sheets of paper towel. Using methods similar to Werling et al. (2011), standard-sized egg clusters were created by cutting 1 x 2 cm strips of paper towel containing approximately 30 eggs each (range: 15–50). The paper towel strips were then glued to 3 × 5 cm pieces of cardstock using water-soluble glue (Elmer's Glue-All[®], Borden, Inc., Columbus, OH, USA). The number of eggs per card was counted and recorded. Eggs were freeze-killed to prevent hatching and then deployed at the five blueberry farms by stapling the cards to the underside of blueberry foliage at roughly 1 m height (Fig. 5.2). At each site, three egg cards were placed at each of three positions: in the wildflower planting, along the edge of the crop field, and 15 m into the interior of the crop field (Fig. 5.1d). One of the egg cards at each position was covered with a fine white mesh bag (150 µm, The

Cary Company, Addison, IL) to exclude predators, whereas the other two egg cards remained open and exposed to potential predators. Using the same methods, egg cards were also placed at the three corresponding positions in crop fields adjacent to the control perimeter at each site.



Figure 5.2 Example of a sentinel corn earworm ‘egg card’ after four days within the field deployed in a blueberry bush; stapled to the underside of blueberry leaf (June 2011).

Biological control services were measured by comparing the number of eggs present before being placed into the field with the number of eggs (after egg predation by natural

enemies in the field) after four days. The resulting biocontrol services index (BSI) (Gardiner et al., 2009) can vary from 0 to 1, with values increasing as the level of predation increases:

$$BSI = \frac{\sum_{p=1}^5 \frac{(A_{c,p} - A_{o,p})}{A_{c,p}}}{n}$$

where A_c is the proportion of eggs remaining on “bagged” egg cards on day four, A_o is the proportion of eggs remaining on the “open” egg cards, p is the egg card position, and n is the number of replicates for a given position. This approach was used to measure biocontrol services during 4-day periods in June, July, and August in 2011 and 2012.

Biological control services were evaluated by taking the mean of the BSI values across the three sample dates to determine season-averaged egg predation for each sample location. The season-averaged BSI values were compared separately for each year between treatments and field locations using a Mann-Whitney U test to allow for non-normal distribution of data (SPSS, Version 20, IBM Corp., Armonk, NY).

Results

Wildflower planting establishment

Throughout the duration of this study, the density per square meter and the percent cover of seeded plants was greater within the wildflower plantings than in the control mown grass field margins. Please see Chapter 4 for the complete data and results for wildflower establishment.

Natural enemies and herbivores in field perimeters

Vacuum sampling along the crop perimeters revealed that in 2010 the density of natural enemies was significantly lower in wildflower plantings than in the control perimeters (Table 5.2). This trend reversed in 2011, with the density of natural enemies collected in the wildflower plantings being a little higher than that in the grassy control perimeters, although the treatments were not significantly different (Table 5.2). Evaluating the recorded natural enemies, in 2010 the densities of Coccinellidae, Parasitica, and Staphylinidae were significantly greater in the control treatments (Table 5.3). During 2011, the overall abundance of natural enemies collected in wildflower plantings increased, with significantly greater densities of Araneae, Cantharidae, and Syrphidae being collected in the plantings compared to the control perimeters. Staphylinidae were the only natural enemy group to remain significantly greater in the control treatment (Table 5.3). When comparing the natural enemy communities collected in the two types of field perimeters, the diversity index (H) was slightly greater for the flower plantings during both years, but not significantly different from the grassy perimeters (Table 5.4).

A diverse community of insect herbivores and pests was also collected via vacuum sampling from the wildflower plantings and control perimeters. The densities of herbivore groups collected from the perimeters were not significantly different between the two treatments in either of the two years of this study (Table 5.2). When assessing the recorded insect herbivores, in 2010 the densities of Cercopidae and Chrysomelidae were significantly greater in the flower treatments (Table 5.3). In 2011, Cercopidae densities were again greater in wildflower plantings, whereas Chrysomelidae and Cicadellidae densities were greater in control perimeter samples (Table 5.3). Of the agriculturally important blueberry pests monitored during this study (*P. japonica*, *A. vaccinii*, *G. packardii*, and *R. mendax*), only *P. japonica* were collected in the

Table 5.2 Comparison of total natural enemy and herbivore densities (mean \pm SEM) at fields with or without wildflower plantings in field perimeters. Insect were collected via vacuum sampling (per 2.5 min) in field perimeters or by observational samples (per min) and yellow sticky traps (per trap) within crop fields adjacent to control or flower treatments. Bold values indicate significant difference between treatments ($P < 0.05$).

Insect type	Sample location	2010				2011			
		Control	Flower	χ^2	<i>P</i>	Control	Flower	χ^2	<i>P</i>
Natural enemies									
Vacuum	Perimeter	59.6 ± 11.4	31.4 ± 4.6	6.14	0.013	30.1 ± 4.9	36.9 ± 4.5	1.05	0.31
Observations	Crop	8.6 ± 0.7	11.6 ± 1.1	5.65	0.017	7.1 ± 0.6	10.2 ± 0.9	8.57	0.0034
<u>Sticky traps</u>	<u>Crop</u>	<u>38.1 ± 3.6</u>	<u>50.7 ± 3.5</u>	<u>6.35</u>	<u>0.012</u>	<u>47.7 ± 2.1</u>	<u>62.7 ± 3.2</u>	<u>15.86</u>	<u>0.0001</u>
Herbivores									
Vacuum	Perimeter	28.1 ± 5.4	20.2 ± 2.9	1.77	0.18	163.1 ± 23.9	136.5 ± 20.6	1.50	0.22
Observations	Crop	4.6 ± 0.6	3.6 ± 0.5	1.86	0.17	7.3 ± 2.4	6.9 ± 2.2	0.009	0.92
Sticky traps	Crop	46.7 ± 4.9	57.9 ± 6.0	2.06	0.15	53.5 ± 5.5	57.7 ± 5.9	0.27	0.61

Table 5.3 Comparison of specific insect groups collected via vacuum sampling (mean \pm SEM per 2.5 min) from control field margins or within wildflower plantings over a two year period. Bolded values indicate significant difference between treatments ($P < 0.05$).

Insect type	2010				2011			
	Control	Flower	χ^2	<i>P</i>	Control	Flower	χ^2	<i>P</i>
Natural enemies								
Araneae	5.7 \pm 1.4	8.0 \pm 1.7	2.89	0.09	5.3 \pm 0.9	10.2 \pm 2.0	5.43	0.02
Cantharidae	0.1 \pm 0.1	2.3 \pm 1.7	3.82	0.049	0.2 \pm 0.1	2.2 \pm 1.2	5.99	0.01
Carabidae	0.4 \pm 0.2	0.6 \pm 0.3	0.67	0.41	0.1 \pm 0.07	0.3 \pm 0.2	1.61	0.20
Chrysopidae	0.1 \pm 0.1	0.3 \pm 0.1	1.76	0.18	0.2 \pm 0.1	0.4 \pm 0.1	1.17	0.28
Coccinellidae	1.2 \pm 0.4	0.2 \pm 0.1	4.04	0.04	0.5 \pm 0.1	0.7 \pm 0.2	0.51	0.47
Formicidae	6.9 \pm 2.3	3.2 \pm 1.5	0.94	0.33	5.0 \pm 1.2	5.1 \pm 1.1	0.01	0.94
<i>Orius</i> spp.	2.5 \pm 0.9	0.7 \pm 0.4	2.60	0.11	1.8 \pm 0.5	4.6 \pm 1.8	2.84	0.09
Parasitica	59.6 \pm 11.4	25.2 \pm 4.5	4.66	0.03	30.1 \pm 4.9	36.9 \pm 4.5	1.05	0.31
Staphylinidae	1.2 \pm 0.6	0.08 \pm 0.05	6.22	0.01	0.8 \pm 0.3	0.08 \pm 0.05	10.52	0.001
Syrphidae	2.6 \pm 1.2	3.5 \pm 1.6	0.58	0.45	1.8 \pm 0.5	4.0 \pm 1.2	4.62	0.03
Herbivores								
Aphidae	5.9 \pm 2.1	4.3 \pm 1.2	0.05	0.82	19.1 \pm 7.7	11.9 \pm 2.9	0.85	0.36
Cercopidae	0	0.12 \pm .07	9.07	0.003	0.8 \pm 0.3	2.8 \pm 0.9	5.43	0.02
Chrysomelidae	0.2 \pm 0.1	1.4 \pm 0.4	12.35	0.0004	2.8 \pm 0.9	1.0 \pm 0.3	4.97	0.03
Cicadellidae	18.6 \pm 4.9	8.2 \pm 2.4	2.08	0.15	91.3 \pm 15.5	40.6 \pm 6.7	10.70	0.001
Miridae	3.3 \pm 0.7	2.0 \pm 0.5	0.65	0.42	57.9 \pm 11.6	74.2 \pm 16.4	0.68	0.41
Cucurlionidae	0.05 \pm 0.05	0.2 \pm 0.1	2.18	0.14	5.7 \pm 1.4	5.6 \pm 2.0	0.00	0.97
<i>Popillia japonica</i>	0	0	-	-	0.4 \pm 0.3	0.4 \pm 0.2	0.05	0.81

vacuum samples, and only in 2011, and their densities were similar in the two treatments (Table 5.3). Comparing the insect herbivore communities collected from the two types of perimeters, insect diversity tended to be slightly higher each year in the flower treatment, but there was never a statistically significant difference (Table 5.4).

Natural enemies and herbivores in the crop fields

During 2009 there was no discernible difference between treatments in the densities of natural enemies observed in crop fields adjacent to the control or flower treatments (Control: 6.1 ± 0.8 insects/min; Flower: 6.1 ± 0.6 insects/min; $\chi^2 = 0.0006$; $P = 0.98$). During the following two years significantly greater densities of insect natural enemies were observed in fields adjacent to the wildflower plantings compared to fields adjacent to the control perimeters (Table 5.2). In 2010, the greater natural enemy densities observed in crop fields adjacent to wildflower plantings were dominated by Coccinellidae, Parasitica, and Syrphidae, whereas in 2011, Cantharidae, Parasitica, and Syrphidae had significantly greater densities (Table 5.5). In neither year were there any natural enemy groups significantly greater in crop fields adjacent to the control perimeters than the flowering perimeters. Assessing the diversity of natural enemies observed in crop fields in 2009, there was no difference between the two treatments (Control: $H = 0.8 \pm 0.05$; Flower: $H = 0.8 \pm 0.05$; $U = 2933$; $P = 0.36$), but natural enemies were significantly more diverse in crop fields adjacent to wildflower plantings in 2010 and 2011 (Table 5.4). In addition to observation sampling, natural enemies were sampled in crop fields using yellow sticky traps. As seen in the observation data, in 2009 there was no difference in the density of natural enemies collected per sticky trap in fields adjacent to either treatment (Control: 7.9 ± 0.4 insects/trap; Flower: 8.5 ± 0.4 insects/trap; $\chi^2 = 1.26$; $P = 0.26$). More natural enemies were

collected in crop fields with significantly greater densities being collected in fields adjacent to the flower treatments in 2010 and 2011 (Table 5.2).

Evaluating the recorded natural enemy groups collected via sticky traps, in 2010 the densities of Carabidae, Coccinellidae, Parasitica, and Syrphidae were significantly greater in crop fields adjacent to the flower treatments (Table 5.6). Similarly, in 2011, Carabidae, Parasitica, Staphylinidae, and Syrphidae were the natural enemy groups that had significantly greater densities in the crop fields adjacent to the wildflower plantings compared to control fields (Table 5.6). In contrast to the natural enemy observation results described above, the diversity of natural enemies collected with sticky traps was similar in the two treatments in 2009 (Control: $H = 0.9 \pm 0.03$; Flower: $H = 0.9 \pm 0.04$; $U = 19686$; $P = 0.79$) and thereafter (Table 5.4).

Observations of insect herbivores in crop fields indicated that the density of herbivores observed per minute did not differ between the two treatments in 2009 (Control: 2.0 ± 0.7 insects/m²; Flower: 3.6 ± 0.7 insects/m²; $\chi^2 = 0.045$; $P = 0.83$), 2010, or 2011 (Table 5.2). Consistent with the overall insect herbivore density in 2010, there were no individual herbivore groups that responded significantly between treatments. Conversely, in 2011 significantly more Cercopidae were observed in fields adjacent to the wildflower plantings, and of the agriculturally important blueberry pests monitored during this study, only *R. mendax* was observed to have significantly lower densities in crop fields adjacent to the flower perimeters (Table 5.5).

Assessing the diversity of the observed insect herbivore community, there was no significant difference between the two treatments in 2009 (Control: $H = 0.2 \pm 0.04$; Flower: $H = 0.3 \pm 0.04$; $U = 3089$; $P = 0.68$) or in 2010, whereas in 2011 a less diverse community of insect herbivores was observed in fields adjacent to the flower perimeters (Table 5.4).

Table 5.4 Comparison of insect diversity (H , mean \pm SEM) collected via observational and yellow sticky trap sampling methods within crop fields adjacent to control (mown) or flower planting perimeters, and insects collected via vacuum sampling from control field margins or within wildflower plantings over a two year period. Bolded values indicate significant difference between treatments ($P < 0.05$).

Insect type	Sample location	2010				2011			
		Control	Flower	<i>U</i>	<i>P</i>	Control	Flower	<i>U</i>	<i>P</i>
Natural enemies									
Vacuum	Perimeter	1.07 ± 0.09	1.3 ± 0.07	134.0	0.07	1.2 ± 0.08	1.3 ± 0.08	272.5	0.44
Observations	Crop	0.9 ± 0.05	1.2 ± 0.05	2254.0	0.001	1.0 ± 0.05	1.2 ± 0.04	2525.0	0.021
<u>Sticky traps</u>	<u>Crop</u>	<u>0.8 ± 0.02</u>	<u>0.08 ± 0.03</u>	<u>18928.0</u>	<u>0.350</u>	<u>0.7 ± 0.02</u>	<u>0.8 ± 0.02</u>	<u>19364.5</u>	<u>0.58</u>
Herbivores									
Vacuum	Perimeter	1.3 ± 0.1	1.4 ± 0.06	162.0	0.30	1.3 ± 0.07	1.4 ± 0.1	276.5	0.48
Observations	Crop	0.3 ± 0.3	0.3 ± 0.04	2915.5	0.28	0.5 ± 0.05	0.3 ± 0.05	2637.0	0.045
Sticky traps	Crop	0.8 ± 0.02	0.8 ± 0.02	18267.5	0.13	0.8 ± 0.03	0.9 ± 0.02	17344.0	0.022

Insect herbivore density and diversity in crop fields were also measured with yellow sticky traps, and these were similar between treatments in 2009 (Control: 21.3 ± 2.6 insects/traps; Flower: 25.7 ± 3.3 insects/traps; $\chi^2 = 1.13$; $P = 0.29$). The similarity between treatments continued in the subsequent years (Table 5.2). Although the total herbivore density was not different between the two treatments in 2010, the density of Chrysomelidae was significantly greater in crop fields adjacent to wildflower plantings and the density of *P. japonica* was lower in fields adjacent to the wildflower perimeter (Table 5.5). Similarly, in 2011 significantly greater densities of Chrysomelidae, as well as Cercopidae were observed in fields adjacent to the wildflower plantings, and *P. japonica* and *R. mendax* were observed to have significantly lower densities in crop fields adjacent to the flower perimeters (Table 5.5). Assessing the diversity of the insect herbivore community collected via sticky trap sampling, there was no significant difference between the two treatments in 2009 (Control: $H = 0.3 \pm 0.02$; Flower: $H = 0.3 \pm 0.02$; $U = 19846.5$; $P = 0.89$) or in 2010 (Table 5.4). In contrast to the observation results, in 2011 a more diverse community of insect herbivores was collected in fields adjacent to the wildflower plantings (Table 5.4). Although insect herbivores were still present, conservation strips did not significantly increase herbivore abundance in adjacent crops fields.

Biological control services

In 2011, significantly higher levels of biological control (BSI) of corn earworm eggs were measured within the wildflower plantings and along the crop edge adjacent to the wildflower plantings than those in the corresponding positions in the grass control perimeter (Fig. 5.3; $U = 273.5$, $P = 0.012$ and $U = 237$, $p = 0.001$, respectively). Although BSI values were

Table 5.5 Specific insect groups observed (mean \pm SEM per 1 min) within crop fields adjacent to control or flower treatments over a two year period. Bolded values indicate significant difference between treatments ($P < 0.05$).

Insect type	2010				2011			
	Control	Flower	χ^2	P	Control	Flower	χ^2	P
Natural enemies								
Araneae	1.1 \pm 0.1	1.3 \pm 0.2	1.63	0.20	1.6 \pm 0.1	1.8 \pm 0.2	0.83	0.36
Cantharidae	0	0.01 \pm 0.01	2.77	0.10	0	0.06 \pm 0.05	4.10	0.04
Carabidae	0.01 \pm 0.01	0	2.77	0.10	0	0.01 \pm 0.01	2.77	0.10
Chrysopidae	0.3 \pm 0.05	0.4 \pm 0.06	0.03	0.86	0.5 \pm 0.2	0.9 \pm 0.2	2.28	0.13
Coccinellidae	0.2 \pm 0.05	0.4 \pm 0.07	4.15	0.04	0.06 \pm 0.03	0.1 \pm 0.04	0.94	0.33
Formicidae	2.9 \pm 0.4	4.1 \pm 0.6	2.23	0.14	3.7 \pm 0.5	3.9 \pm 0.5	0.05	0.82
<i>Orius</i> spp.	0.01 \pm 0.01	10	2.77	0.10	0	0	0	0
Parasitica	0.2 \pm 0.05	0.5 \pm 0.1	9.77	0.002	0.3 \pm 0.06	0.6 \pm 0.1	8.58	0.003
Syrphidae	0.7 \pm 0.1	1.9 \pm 0.2	29.27	0.0001	0.9 \pm 0.2	2.8 \pm 0.4	19.21	0.0001
Vespidae	0.1 \pm 0.05	0.03 \pm 0.02	3.46	0.06	0.03 \pm 0.02	0.03 \pm 0.02	0.00	1.00
Herbivores								
<i>Acrobasis vaccinii</i>	0.8 \pm 0.3	0.5 \pm 0.2	0.71	0.40	0.7 \pm 0.4	0.3 \pm 0.2	1.25	0.26
Aphidae	0.8 \pm 0.3	0.9 \pm 0.3	0.03	0.86	0.3 \pm 0.1	0.9 \pm 0.4	3.16	0.08
Cercopidae	0	0	0.00	1.00	0.01 \pm 0.01	0.1 \pm 0.07	5.52	0.02
Chrysomelidae	0.01 \pm 0.01	0	2.77	0.10	0.01 \pm 0.01	0	2.77	0.10
Cicadellidae	0.3 \pm 0.08	0.3 \pm 0.09	0.10	0.76	0.5 \pm 0.1	0.4 \pm 0.1	3.16	0.08
Cucurliionidae	0.03 \pm 0.02	0.06 \pm 0.03	1.37	0.24	0.01 \pm 0.01	0.01 \pm 0.01	0.00	1.00
<i>Grapholita packardi</i>	0.3 \pm 0.09	0.3 \pm 0.1	0.01	0.93	0.3 \pm 0.1	0.3 \pm 0.1	0.00	1.00
Miridae	0.4 \pm 0.1	0.3 \pm 0.06	0.25	0.62	0.3 \pm 0.08	0.2 \pm 0.08	0.18	0.67
<i>Popillia japonica</i>	1.8 \pm 0.4	1.1 \pm 0.3	1.76	0.18	5.0 \pm 2.3	4.6 \pm 2.1	0.02	0.89
<i>Rhagoletis mendax</i>	0	0	0	0	0.04 \pm 0.03	0	5.04	0.02

Table 5.6 Comparison of specific insect groups collected via yellow sticky traps (mean \pm SEM per trap) within crop fields adjacent to control or flower treatments over a two year period. Bolded values indicate significant difference between treatments ($P < 0.05$).

Insect type	2010				2011			
	Control	Flower	χ^2	P	Control	Flower	χ^2	P
Natural enemies								
Araneae	1.1 \pm 0.2	1.2 \pm 0.2	0.63	0.43	0.8 \pm 0.1	1.2 \pm 0.2	2.81	0.09
Cantharidae	0.06 \pm 0.02	0.08 \pm 0.03	0.19	0.66	0.2 \pm 0.04	0.3 \pm 0.05	2.50	0.11
Carabidae	0.1 \pm 0.02	0.2 \pm 0.03	6.73	0.01	0.1 \pm 0.02	0.2 \pm 0.04	9.11	0.02
Chrysopidae	0.2 \pm 0.03	0.1 \pm 0.03	0.85	0.36	0.1 \pm 0.03	0.2 \pm 0.03	0.73	0.39
Coccinellidae	0.5 \pm 0.1	1.2 \pm 0.2	15.96	<0.0001	0.4 \pm 0.06	0.5 \pm 0.08	0.16	0.69
Formicidae	0.5 \pm 0.07	0.7 \pm 0.1	4.46	0.03	1.1 \pm 0.1	1.1 \pm 0.1	0.00	1.00
<i>Orius</i> spp.	0.6 \pm 0.09	0.6 \pm 0.08	0.20	0.65	0.6 \pm 0.08	0.6 \pm 0.08	0.01	0.93
Parasitica	27.2 \pm 3.2	40.8 \pm 3.1	8.94	0.003	33.9 \pm 1.6	49.5 \pm 2.9	22.70	<0.0001
Staphylinidae	0.2 \pm 0.05	0.3 \pm 0.04	0.70	0.40	0.2 \pm 0.03	0.4 \pm 0.06	13.36	0.003
Syrphidae	0.9 \pm 0.1	1.3 \pm 0.1	4.19	0.04	1.1 \pm 0.1	1.5 \pm 0.2	4.02	0.04
Vespidae	0.02 \pm 0.01	0.01 \pm 0.01	0.20	0.65	0.05 \pm 0.02	0.04 \pm 0.01	0.35	0.55
Herbivores								
Aphidae	30.1 \pm 4.3	39.1 \pm 5.6	1.62	0.20	37.4 \pm 5.2	37.9 \pm 5.4	0.00	0.94
Cercopidae	0.1 \pm 0.03	0.2 \pm 0.04	2.63	0.10	0.1 \pm 0.03	0.2 \pm 0.04	6.94	0.01
Chrysomelidae	0.2 \pm 0.04	0.8 \pm 0.2	16.90	<0.0001	0.2 \pm 0.04	0.8 \pm 0.2	15.13	0.001
Cicadellidae	15.5 \pm 1.5	16.7 \pm 1.1	0.41	0.52	14.7 \pm 1.5	17.4 \pm 1.2	1.96	0.16
Cucurlionidae	0.1 \pm 0.03	0.2 \pm 0.04	1.45	0.23	0.1 \pm 0.02	0.2 \pm 0.02	2.96	0.09
Miridae	0.7 \pm 0.1	0.9 \pm 0.1	3.09	0.08	0.7 \pm 0.1	1.1 \pm 0.1	4.44	0.04
<i>Popillia japonica</i>	0.01 \pm 0.01	0	5.57	0.01	0.01 \pm 0.007	0	5.57	0.02
<i>Rhagoletis mendax</i>	0.02 \pm 0.01	0.02 \pm 0.01	0.12	0.73	0.2 \pm 0.07	0.02 \pm 0.01	9.22	0.002

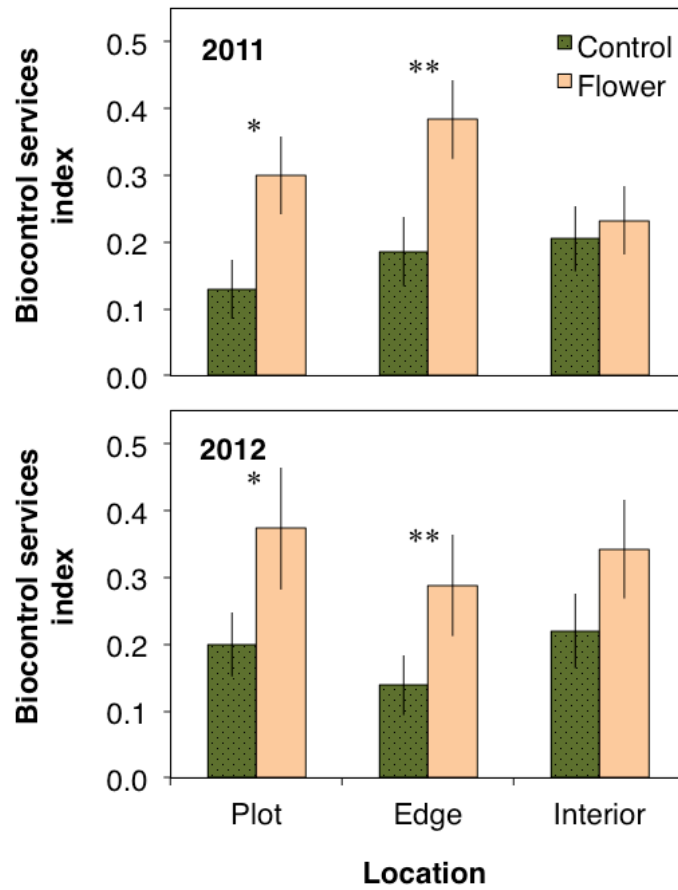


Figure 5.3. Evaluation of biological control services through the measurement of corn earworm egg removal from sentinel egg masses (mean BSI \pm SEM) located at three positions (control/flower plot, crop edge, and crop interior) and two treatments (control and flower). Asterisks indicate levels of significance (* $P < 0.05$, ** $P < 0.01$) for difference between treatments.

higher adjacent to flower treatments, there was no significant difference at the field interior position (Fig. 5.3; $U = 386.5$, $p = 0.34$). The same trend was also measured in 2012, with significantly greater BSI values within the wildflower plantings and along the crop edge adjacent to the plantings (Fig. 5.3; $U = 192.5$, $p = 0.048$ and $U = 128$, $p = 0.001$, respectively), but not within the interior positions (Fig. 5.3; $U = 208.5$, $p = 0.10$).

Discussion

In this study I demonstrated that the establishment of wildflower habitat in areas adjacent to blueberry fields positively affected the density and diversity of some natural enemy groups and enhanced biological control of sentinel pest eggs along the crop edge. In contrast, insect herbivore densities were not enhanced by the provision of perennial floral resource plantings and some declined, suggesting that local-scale habitat manipulation through the establishment of native wildflower plantings can selectively enhance beneficial insects and provide support for the regulation of pest populations.

Sampling of insects in the wildflower planting and the blueberry crop fields revealed that two to three years after wildflower establishment, natural enemy populations were generally enhanced, but the results for individual natural enemy groups varied depending on the sampling method used. Vacuum samples from the crop perimeters detected a lower abundance of natural enemies in 2010 within the flower treatments, but there was no significant difference between the two treatments in 2011. This contrasts with the observational and sticky trap data from samples collected within the adjacent crops where in both 2010 and 2011 significantly greater densities of natural enemies were measured in crop fields adjacent to wildflower plantings

(Table 5.2). One might expect that if greater densities of natural enemies were found in crop fields adjacent to wildflower plantings then there would also be more collected within the nearby plantings than in fields without the enhancement. This discrepancy may be due to the vacuum sampling method, which has been shown to be more efficient at sampling in shorter vegetation, such as was found in the mown control field perimeters (Hossain et al., 1999). Recently, Sanders and Entling (2011) demonstrated that vacuum sampling can underestimate species richness in cross-habitat comparisons and misses many ground dwelling arthropods. Because of this, it is possible that vacuum samples underestimated the overall abundance of arthropods in the wildflower plantings compared to the control samples that were taken from the shorter vegetation of the mown grass control perimeters. Additionally, some natural enemies remain mostly within the cropping system (Duelli et al., 1990), while others utilize resources in the adjacent natural habitats (Landis et al., 2000), so it is possible that the smaller natural enemy abundances in the wildflower plantings were partially due to the insects leaving the plantings to redistribute into the adjacent crop fields. Even with the potential under-estimation in density and diversity, in 2011 greater numbers of Araneae, Cantharidae, Staphylinidae, and Syrphidae were collected within the wildflower plantings (Table 5.3).

Although the density and diversity of arthropods may have been underestimated by the vacuum sampling method, given time for flower establishment, natural enemies were more abundant in wildflower habitats than in mown grass margins and significantly more abundant in crop fields adjacent to wildflowers compared to fields adjacent to mown grass field margins. This supports the established pattern of naturalized non-cropped habitats supporting greater abundance and diversity of beneficial insects compared with simple agricultural landscapes (Thomas et al., 1991; Lee et al., 2001). Another important aspect of this study was to determine

whether floral habitats can in turn increase specific natural enemies within the adjacent crop fields. The finding that Parasitica and Syrphidae were at significantly greater densities in 2010 and 2011 within crop fields adjacent to the wildflower plantings than in fields adjacent to the control perimeters supports the hypothesis that adding flowering plant habitat back into intensively managed cropland can increase agriculturally-important natural enemies. The mechanism of this enhancement is likely to be the increased availability of nutritional resources, since parasitoid wasps (Winkler et al., 2009) and hoverflies (White et al., 1995) depend on and are enhanced by pollen and nectar. Creating a floral habitat that increases the carrying capacity of insect natural enemies will enhance the degree of predator spillover and their impact on pest insects within the adjacent crop field (Holt and Hochberg, 2001).

Coccinellidae, which also benefit from access to pollen and nectar (Lundgren, 2009), were sampled in significantly greater abundance in 2010 from fields adjacent to wildflower plantings, but this trend did not continue into 2011. Coccinellid populations commonly undergo large and unpredictable fluctuations in abundance from year to year (Elliott and Kieckhefer, 1990a, b), so it is not surprising that the response of Coccinellidae to wildflower plantings was not consistent between years. Another notable natural enemy group that can respond positively to non-cropped land are the Carabidae, or ground beetles (Lee et al., 2001). These beetles often go unnoticed because they are generally active at night and hunt near the ground (Lövei and Sunderland, 1996), but the sticky trap sampling revealed significantly greater ground beetle captures in blueberry fields adjacent to wildflower plantings. This supports previous work by O'Neal et al. (2005a) who showed that other conservation practices such as increased ground cover and reduced-risk insecticides, can enhance ground beetle abundance in blueberry fields.

Wildflower plantings established to help conserve natural enemy populations may provide resources and habitat for insect (Lavandero et al., 2006; Wäckers et al., 2007) and vertebrate herbivores (Briner, 2005). In this study, insect herbivore density was never significantly different between the two treatments using vacuum, observational, or sticky trap sampling. Although insect herbivores were potentially underestimated in the wildflower plantings due to the decreased efficiency of vacuum sampling in tall vegetation (Hossain et al., 1999; Sanders and Entling, 2011), the result is consistent across methods. In 2011, insect herbivores were more diverse in crop fields adjacent to the control perimeters than in fields adjacent to the wildflower plantings. Only Cercopidae and Chrysomelidae abundances were significantly influenced by the addition of floral resources. Although these families are not considered important pests of highbush blueberries, they may be pests of other crops (Evans, 1972; Stenberg, 2012). Wildflower habitats have the potential to enhance pest populations, so it is essential to understand how habitat manipulations affect generalist and specialist herbivore populations and their ability to disperse into neighboring crop fields, with understanding of the crop-specific community of insects that can act as either pests or natural enemies.

There is relatively little information on the magnitude of effect for wildflower plantings supporting natural enemies, but these floral habitats clearly provide resources that help support natural enemies in adjacent crop fields. In a review by Bianchi et al. (2006), the increase in natural enemy populations with natural habitat translated directly into enhanced pest suppression in adjacent crop fields in 45% of studies evaluated. In my study, sentinel corn earworm egg predation was significantly greater within wildflower plantings, as well as along the adjacent crop edge compared to those from the control treatments (Fig. 5.3). Although greater numbers of eggs were removed from the crop interior in fields adjacent to the wildflower plantings, the BSI

values for this position were not significantly greater than the control. This is supported by a recent study from Hassan et al. (2012) who found greater abundance of Carabidae in cereal fields surrounded by more natural grassland, but their abundance in the crop decreased rapidly with distance from the strip. Similarly, Eilers and Klein (2009) found that parasitoid densities were greatest along margins of almond orchards with significantly fewer parasitoids detected within the orchard interior. These results suggest that the edges of crop fields adjacent to floral resources will experience the greatest benefit from natural enemies compared to the crop interior (Walton and Isaacs, 2011). Incorporating floral resources in cropping systems where pest pressure is highest along field edges, such as cranberry fruitworm, (*A. vaccinii*) in highbush blueberry (Mallampalli and Isaacs, 2002), may substantially reduce the pest populations in those systems.

The lower densities of Japanese beetle (*P. japonica*) and blueberry maggot (*R. mendax*) observed and/or collected via sticky traps in blueberry fields adjacent to the flower plantings (Tables 5.5 and 5.6) suggests there is increased control of these two pests when floral resources are available. Fewer collected pests may also be a response to the vegetation structure, since for example, Japanese beetle females oviposit in areas with short, sparsely distributed vegetation (Potter and Held, 2002), similar to the vegetation found within the control field perimeters. This suggests that flower plantings may reduce populations of some pests by removal of suitable oviposition habitat. It is important for future research to explore the mechanisms underlying how these plantings affect potential pest populations and pest management.

Pest management is often studied at the field scale, and even though there is evidence that local-scale vegetation diversity enhances pest control by a modest amount (Letourneau et al., 2011), it is also evident that processes critical to natural enemy conservation and pest control

also occur at larger scales (Thies and Tscharntke, 1999; Gardiner et al., 2009; Meehan et al., 2011). Larger plantings of floral resources are expected to have more resources, and hence higher capacity to support populations of beneficial insects (Slobodkin, 1980; Kruess and Tscharntke, 2000a). Furthermore, increasing the size of the floral habitat can positively impact the services provided by beneficial insects (Blaauw and Isaacs, 2012), although different insect taxa respond to these manipulations in varying ways (Tscharntke et al., 2007; Osborne et al., 2008), and may also respond to habitat at different scales. The complexity of the surrounding landscape may also affect local insect abundance and diversity in agricultural systems (Tscharntke et al., 2002), while small-scale habitat manipulation may only attract and concentrate natural enemies that are already present in the surrounding landscape (Gurr et al., 1998). Although the landscape surrounding the crop fields was not analyzed in this study, it was dominated by a mix of forest and additional blueberry fields. A more thorough investigation of how landscape complexity affects the response of natural enemies to the addition of floral resources would be needed to examine the relative importance of local and landscape-scale factors. For example, Woltz et al. (2012) determined that generalist predator abundance was higher in floral strips than in control field margins and was higher in adjacent crop fields that were surrounded by more semi-natural vegetation in the landscape. Although there was not a significant interaction between local habitat manipulation and landscape variables, soybean aphid suppression and predator abundance responded positively to landscape factors (Woltz et al., 2012). Similarly, previous studies have shown that complex landscapes can have higher natural enemy diversity compared to simpler agricultural landscapes (Purtauf et al., 2005; Schmidt et al., 2005) and that the quality and proportion of non-cropped vegetation within agricultural landscapes can significantly affect pest control (Thies and Tscharntke, 1999;

Gardiner et al., 2009). If wildflower plantings are to be used to deliver ecosystem services to crop fields it is essential to determine the optimal plot size and configuration of these plantings (Brosi et al., 2008) and to determine the combined influence of landscape context and habitat planting size on distribution and dispersal of beneficial insects to and from crop fields in agricultural landscapes.

Increasing biological diversity within the agricultural landscape through the provision of additional floral resources to conserve natural enemies and their services may also enhance or maintain other ecosystem services (Isbell et al., 2011; Kremen and Miles, 2012), such as bird habitat (Vickery et al., 2009), erosion control (Markwardt, 2005), native pollinator conservation (Gurr and Wratten, 1999), and enhancement of crop yield (Carvalheiro et al., 2012). For example, Syrphidae larvae are excellent biological control agents of many soft-bodied arthropods (Bugg et al., 2008; Smith et al., 2008), and although they are not effective pollinators of blueberry, they are efficient pollinators of other crops (Dag and Gazit, 2001; Jauker and Wolters, 2008).

The costs associated with the establishment of wildflower plantings are not trivial, government programs (EU, 2005; NRCS, 2010) and potentially crop yield enhancement (see Chapter 4), may compensate for those initial costs making this strategy more economically appealing for grower adoption. Thus, this study demonstrates that small modifications to resource-poor non-cropped areas within farms, such as adding native flowering plants, can enhance biodiversity and pest-control, and has the potential to optimize multiple ecosystem services. Further work is still needed to better understand the extent to which multiple services are affected, the economic costs and returns, and which systems are best suited for this approach.

CHAPTER 6.

CONSERVATION PLANTINGS FOR SUPPORTING BENEFICIAL INSECTS: CONCLUSIONS AND FUTURE DIRECTIONS

Agriculture is one of the dominant activities across the world that shapes the physical structure of landscapes, in part through its reliance on mechanization and pesticides (Robinson and Sutherland, 2002; Foley et al., 2005). Intensification of these agricultural practices breaks the once natural habitats into smaller, more isolated patches (MacArthur and Wilson, 1967; With, 2002). The remaining habitat fragments may not provide adequate resources for beneficial insect communities (Fischer and Stöcklin, 1997), and therefore result in reduced pollinator (Aizen and Feinsinger, 1994) and natural enemy (Kruess and Tscharntke, 2000b) abundance and diversity in these habitat patches. This loss of beneficial insect abundance and diversity may in turn lead to a decline in ecosystem services provided by these insects (Kruess and Tscharntke, 1994; Bender et al., 1998).

Re-introduction of flowering plants or other landscape enhancements can provide the necessary resources for beneficial insects in agricultural landscapes, such as nectar, pollen, alternate prey, shelter, and nesting sites, which can significantly increase wild pollinator and natural enemy diversity in these regions (Baggen and Gurr, 1998; Dufour, 2000; Carreck and Williams, 2002; Fiedler and Landis, 2007a; Fiedler and Landis, 2007b; Tuell et al., 2008).

Previous studies have demonstrated that natural and semi-natural habitats in agricultural landscapes can increase pollinator (Carvalho et al., 2012; Klein et al., 2012) and insect natural enemy (Bianchi et al., 2006; Woltz et al., 2012) abundances within neighboring crop fields.

Where natural habitats are broken into isolated patches or islands (With, 2002), the addition of floral habitat within agricultural systems may help increase connectivity of the landscape by linking the habitat patches and the ability of the beneficial insects to traverse the landscape.

Studies in this dissertation were concerned with the conservation of beneficial insects and their services in agricultural systems. Using highbush blueberry as a model agricultural system, I

demonstrated that the establishment of native wildflower plantings that provide season-long floral resources support diverse populations of wild bees and insect natural enemies along the border of the adjacent crop fields as well as within the plantings. After four years, fruit set and berry weight were significantly greater up to 15 m into the crop fields adjacent to the wildflower plantings than in those with a grass field margin. Moreover, biological control of sentinel pest eggs was greater along the edge of blueberry fields adjacent to the wildflower habitat. In contrast, insect herbivore densities were not enhanced by the provision of perennial floral resource plantings and some herbivore groups even declined. These results suggest that local-scale habitat manipulation through the establishment of native wildflower plantings can selectively enhance beneficial insects, such as pollinators and natural enemies, and provide support for pollination (MacArthur and Wilson, 1967) as well as the regulation of pest populations (Carvalho et al., 2012).

With declining biodiversity (Landis et al., 2000; Haddad et al., 2009; Haenke et al., 2009), there is growing concern about the associated loss of ecosystem services (Kruess and Tschardtke, 1994; Pimm and Raven, 2000; Bianchi et al., 2006). In response, government agencies, such as the United States Department of Agriculture's (USDA) Farm Services Agency (FSA) and Natural Resources Conservation Services (NRCS), have developed programs including the Conservation Reserve Program (CRP) to provide cost-sharing, land rental payments, and implementation incentives to agricultural landowners who adopt practices to reduce soil erosion, improve water quality, and increase wildlife habitat. In Europe, similar agri-environment measures were designed to enhance agricultural production methods to help protect and maintain the countryside (Isbell et al., 2011). Recently, programs with emphasis on restoring habitat to support beneficial insect conservation, such as the FSA's State Acres for Wildlife

Enhancement (CRP-SAFE) program (EEC, 1992) have been initiated. While it is expected that these programs result in increased biodiversity, relatively little work has been done to measure their effects on biodiversity conservation (reviewed by NRCS, 2010). With currently nearly 1,200 acres of land dedicated for wildlife enhancement solely in the Michigan pollinator SAFE program (Kleijn and Sutherland, 2003b), it is crucial to understand how these landscape enhancement approaches benefit biodiversity.

One motivation for performing the studies in this dissertation was to evaluate the effects of establishing patches of native wildflower habitat in a manner that would most likely be adopted by growers. The wildflower habitats in this dissertation were established in accordance to the requirements of the CRP-SAFE program to increase the relevance of this work, particularly for Michigan agricultural landowners. Over four years, the studies reported in this dissertation have revealed that insect pollinators, particularly small-bodied wild bees, and their pollination of wildflowers benefit from the establishment of large patches of native wildflower habitat composed of diverse floral resources. Similarly, the density, richness, and diversity of natural enemy groups increased with the patch size of native wildflower habitat. The density of predaceous insects in wildflower plots was also positively correlated with the biological control services index (FSA, 2013) as measured through the evaluation of sentinel soybean aphid control. In contrast, overall insect herbivore density did not increase with planting area, suggesting that wildflower plantings can selectively support beneficial insects, providing support for their application in agricultural settings to help regulate pest populations. Based on the research in this dissertation, the establishment of wildflower habitat can help conserve pollinators, natural enemies, and support the services they deliver.

The establishment of wildflower habitat may be an appropriate approach for conserving

beneficial insects in the fragmented environment, but the costs associated with the establishment of wildflower plantings are not trivial (see Chapter 4). Incentive programs, such as those that provide financial support for landowners who undertake practices to restore habitats to support beneficial insect conservation (Gardiner et al., 2009; NRCS, 2010), are making the establishment of native wildflower habitat in agricultural landscapes more economically feasible. Funding programs along with the potential crop yield enhancement and reduction in crop pests, may outweigh the establishment costs, making this strategy more economically appealing to growers (EEC, 1992).

The results from this dissertation support the hypothesis that larger wildflower patches with diverse floral resources support beneficial insects and their services, but if these plantings are to be used to sustain ecosystem services in neighboring crop fields, it is also essential to determine the optimal size, configuration, and distribution of these plantings within the agricultural landscape to best support these insects and their services (Kennedy et al., 2013). Growers are generally risk-averse to new and costly methods, and hence are unlikely to abandon time-tested practices (Brosi et al., 2008). While incentive payments and cost-share programs help with the economic struggles for grower implementation of this strategy, better understanding of how these habitats are to be established is still needed. I suggest that future work should focus on evaluating different sizes of wildflower habitat at farms to investigate how large-scale ($> 100 \text{ m}^2$) wildflower habitat impacts beneficial insects and their delivery of services. Testing current habitats established in the CRP-SAFE program in Michigan, which range from 0.25 to roughly 60 acres, would allow for studies to be done on a broad range of sizes and configurations of plantings that have already been established. Thus, determining the importance of size,

configuration, and distribution of these plantings within the agricultural landscape is crucial to address growers' economic concerns.

Another aspect of this approach to beneficial insect conservation that may increase the likelihood of growers adoption is if this approach is relatively simple to establish and maintain (Pannell, 1999). Growing and managing wildflowers is not the same as cultivating most crops, and therefore it may not be appealing to some potential growers. Wildflower seeds can vary dramatically in size and shape, and although they can be hand-sown, they require specific mechanical seeders that growers may not already have at their disposal (Pannell, 1999). Choosing the seeds to sow can be complicated if one is not familiar with these plants. Currently, growers interested in planting wildflowers for this approach must create their own seed mix, choose species from a list of recommended species (Gilbert and Anderson, 1998), or use pre-made "pollinator" mixes found at specialist nurseries. While having pre-determined seed mixes is convenient for growers to choose from, most of these pollinator seed mixes have not been tested for their efficacy at supporting pollinators, natural enemies, or their delivered ecosystem services. Furthermore, agricultural land is variable and different wildflower species require specific soil types. Choosing seed mixes because they are pollinator "friendly" without knowing the growing conditions of the flower species will likely lead to poor germination, resulting in inadequate wildflower establishment. Subsequent to proper seed selection, from my experience with the studies in this dissertation, effective site preparation is key to the subsequent success of the planting. An area of land intended for wildflower habitat may take multiple seasons to prepare adequately for seed establishment (NRCS, 2010). This dissertation demonstrated that when prepared correctly, wildflower habitat specifically designed for the conditions at the farm sites is attractive to both pollinators and natural enemies, and can enhance their populations. For

this approach to be adopted in other systems, further work is needed to evaluate tailored seed mixes and establishment methods for their ability to support beneficial insects and their feasibility for grower adoption.

Apart from being costly to establish, wildflower habitats also have the potential to enhance pest populations. No blueberry-specific herbivore pests were significantly influenced by the addition of wildflower habitat, but a few generalist herbivore groups (Cercopidae and Chysomelidae) were more abundant in fields adjacent to the wildflower plantings. Although these families are not considered economically-important pests of highbush blueberry, crops that are more affected by generalist herbivores might be more heavily impacted by herbivores that show an affinity for flowering plant strips (Gilbert and Anderson, 1998; Norris and Kogan, 2005; Wäckers et al., 2007). Enhancement of specific herbivore groups highlights the crop-specific nature of potential positive and negative effects of the plantings, and highlights that future research should explore the mechanisms underlying how these plantings affect potential pest populations and pest management, to understand how the crop-specific community of insects can act as either pests, natural enemies, or pollinators.

As demonstrated in Chapter 5, the establishment of wildflower habitat adjacent to highbush blueberry fields can enhance biological control within crop fields, but the majority of insect pest management in this crop will likely remain dependent on insecticides in the near future. Even by creating a refuge for beneficial insects within the adjacent land, the proximity of the wildflower habitat to the crop fields could potentially be harmful to the beneficial insect inhabitants due to pesticide drift from adjacent crop fields (Olson and Wäckers, 2007). For example, Walton and Isaacs (1994) observed reductions in natural enemy abundance after pesticide applications in crop fields as well as in the adjacent flower habitat, implying potential

negative impacts of drift. Encouragingly, their results also suggest that floral habitats adjacent to crop fields allow beneficial insects to re-colonize the fields more quickly after the application of pesticides compared to fields without the habitat. These results further emphasize the need for additional work on the long-term effects of pesticide drift on the beneficial insects exploiting these habitats and their impact on ecosystem services.

The studies in this dissertation were evaluated at the field scale, and even though there is previous evidence that local-scale habitat management enhances pollination (Walton and Isaacs, 2011) and pest control (Carvalho et al., 2012), it is also evident that processes critical to beneficial insect conservation and ecosystem services also occur at larger scales (Thies and Tscharntke, 1999; Gardiner et al., 2009; Letourneau et al., 2011; Klein et al., 2012). The complexity of the surrounding landscape may also affect local insect diversity in agricultural systems (Tscharntke et al., 2002; Heard et al., 2007), while local-scale habitat manipulation may only attract and concentrate natural enemies that are already present in the surrounding landscape (Tscharntke et al., 2005).

Although not assessed here, the landscape complexity surrounding a 1 km radius around the highbush blueberry fields evaluated in this dissertation research was relatively similar, comprised mostly of forested areas and other highbush blueberry fields. Because these landscapes are likely the initial source of beneficial insects that are impacted by the addition of floral habitat, it is possible that my results are landscape-specific. Tscharntke et al. (1998) proposed that because resources are lacking in low complexity landscapes, the abundance of beneficial insects is too low to be enhanced by additional resource patches, whereas in high complexity landscapes, the resources are in excess and therefore additional resource patches would not necessarily increase insect populations. Thus, landscapes of intermediate complexity

would present circumstances where the addition of floral habitat would provide the necessary resources that can be exploited by beneficial insects to enhance their populations and delivered services (Tscharntke *et al.*, 2005). Recent studies testing this hypothesis for natural enemies in annual crop systems have demonstrated conflicting effects of landscape complexity on local management practices (Haenke *et al.*, 2009; Isaacs *et al.*, 2009a; Winqvist *et al.*, 2011), but a current synthesis by Kennedy *et al.* (2012) on bee abundance and diversity in farmland suggests that local management through the maintenance of high-quality habitat may compensate for the negative effects of low complexity agricultural landscapes. A more thorough investigation of how landscape complexity affects the response of beneficial insects to the addition of floral resources should be conducted in perennial fruit crops such as blueberry, by establishing habitat plantings at similarly managed fields over a gradient of surrounding landscape complexity. This would provide greater insight into the relative importance of local and landscape-scale factors in this system. Therefore, future studies should address the combined influence of landscape context and habitat enhancement distribution and dispersal of beneficial insects to and from crop fields within agricultural landscapes.

Despite the high value of ecosystem services provided by beneficial insects and the importance of flowering resources, as illustrated in this dissertation, for supporting these insects and their services in agricultural settings, the spatial extent of their benefit is still not well understood. For optimal deployment, it is crucial to understand how the establishment of wildflower habitat affects the distribution of both beneficial and pest insects in agricultural landscapes. Knowledge of insect movement patterns could support optimal placement of wildflower plantings and improve understanding of beneficial insect community structure, pollination, and pest management in relationship to floral resources. Previous studies have

commonly relied on a variety of mark-release-capture methods to understand insect dispersal. Typically, laboratory-reared or field collected insects of interest are marked, released from known sites, and trapped elsewhere in the environment to determine their movement patterns (Kennedy et al., 2013). As reviewed by Hagler and Jackson (2006), common marking techniques include tagging insects with fluorescent paint or powders, genetic markers, radioactive-isotopes, trace elements, genetically engineered markers, or identifying pollen that the insects collect. While these techniques have their advantages, most are expensive and involve marking a small population in the laboratory and releasing them at known points to extrapolate movement patterns of natural populations (Hagler and Jackson, 2001). In order to understand the effects of wildflower plantings on the movement patterns of naturally occurring beneficial and pest insects in the agricultural landscape, an inexpensive method like that of Jones et al. (2001) is needed that allows for direct marking of wild insects in the field, collection in the field, and then testing for marker presence in the laboratory. Spraying one area with a solution of inexpensive protein, allowing time for insect visitation and departure, and then collecting insects in other areas of the landscape would allow for a relative easy evaluation of insect dispersal in agricultural systems with and without wildflower habitat (Jones et al., 2006).

Another important aspect for future research is to focus on insect species diversity, and how the different insect species that are influenced by the addition of floral resources interact with each other within wildflower plantings and the adjacent crop. The studies in this dissertation quantified primarily insect groups and generally identified insects to family. Since different taxa respond to habitat manipulations in varying ways (Jones et al., 2006; Osborne et al., 2008), evaluating species-level responses to wildflower plantings would provide a better understanding of which species this approach benefits. Additionally, the interactions of certain insect species

with the wildflower plantings or with other insect species may impact the level of benefit from the floral resources. For example, depending on their bloom time the additional floral resources may compete for pollination with the crop flowers (Tscharntke et al., 2007) or alternatively, the increased abundance of wild pollinators may increase the efficiency of the managed honey bees during crop pollination (Brown and Mitchell, 2001). Negative interactions may also occur with natural enemy conservation if one predator species attracted by the wildflower habitat disrupts the ability of others to access their prey/host, resulting in weaker or no positive change in pest suppression with increasing natural enemy biodiversity (Brittain et al., 2013). While these negative effects have been documented in the field (Finke and Denno, 2005; Straub et al., 2008), numerous other studies have shown greater prey suppression when predators coexist in the natural enemy community (Aquilino et al., 2005; Wilby et al., 2005; Straub and Snyder, 2006). Until further research is conducted, the safest approach may be to implement habitat enhancement strategies that directly target the conservation of key pollinators and/or natural enemy species.

The mechanisms by which different insect taxa respond to wildflower habitat are still generally unknown, as is the full potential of these habitats for supporting ecosystem services. Increasing biological diversity within agricultural landscapes through the provision of additional floral resources to conserve beneficial insects and their services may also enhance or maintain other ecosystem services (Snyder et al., 2006; Kremen and Miles, 2012). These may include carbon sequestration (Isbell et al., 2011) and erosion control (Syswerda et al., 2011). There is growing evidence that these habitat enhancement techniques also contribute to the general protection of biodiversity, resilience to extreme weather events, improved soil and water quality, and enhanced farm aesthetics (Markwardt, 2005; Wratten et al., 2012). Additionally, some of the

insects that are enhanced by the floral resources may provide multiple services as well. For example, hoverfly adults, although not effective pollinators of blueberry, are efficient pollinators of other crops (Dag and Gazit, 2001; Kremen and Miles, 2012), and their larvae are effective biological control agents of many soft-bodied arthropods (Bugg et al., 2008; Jauker and Wolters, 2008). In order to achieve benefits to multiple ecosystem services, it may be most important to manage habitat at the landscape scale (Smith *et al.*, 2008). Thus, when habitat establishment is conducted on a local scale, it will likely be more effective when adopted over a wide range of areas, thereby increasing the landscape complexity (Fiedler et al., 2008). This emphasizes the importance of extension and outreach to increase grower and public knowledge and perception of beneficial insect conservation, because without their support and the adoption of habitat across networks of adjacent plantings, this approach is unlikely to succeed.

In a perennial cropping system, wildflower habitat can be in place from year to year, but for annual cropping systems future research needs to focus on the effects of crop rotation, tillage regimes, and other aspects of management practices not addressed in this dissertation (Merckx et al., 2009). Additional studies can be conducted to better understand the extent to which multiple services are affected and which crops are best suited for this approach, but the general patterns observed here can help guide future efforts in the conservation and support of beneficial insects in natural and agricultural landscapes. Modifications to resource-poor non-cropped areas within farms, such as through the establishment of native flowering plants, can enhance biodiversity, pollination, and pest-control, and this approach has the potential to optimize multiple ecosystem services to support agricultural production.

APPENDICES

APPENDIX 1

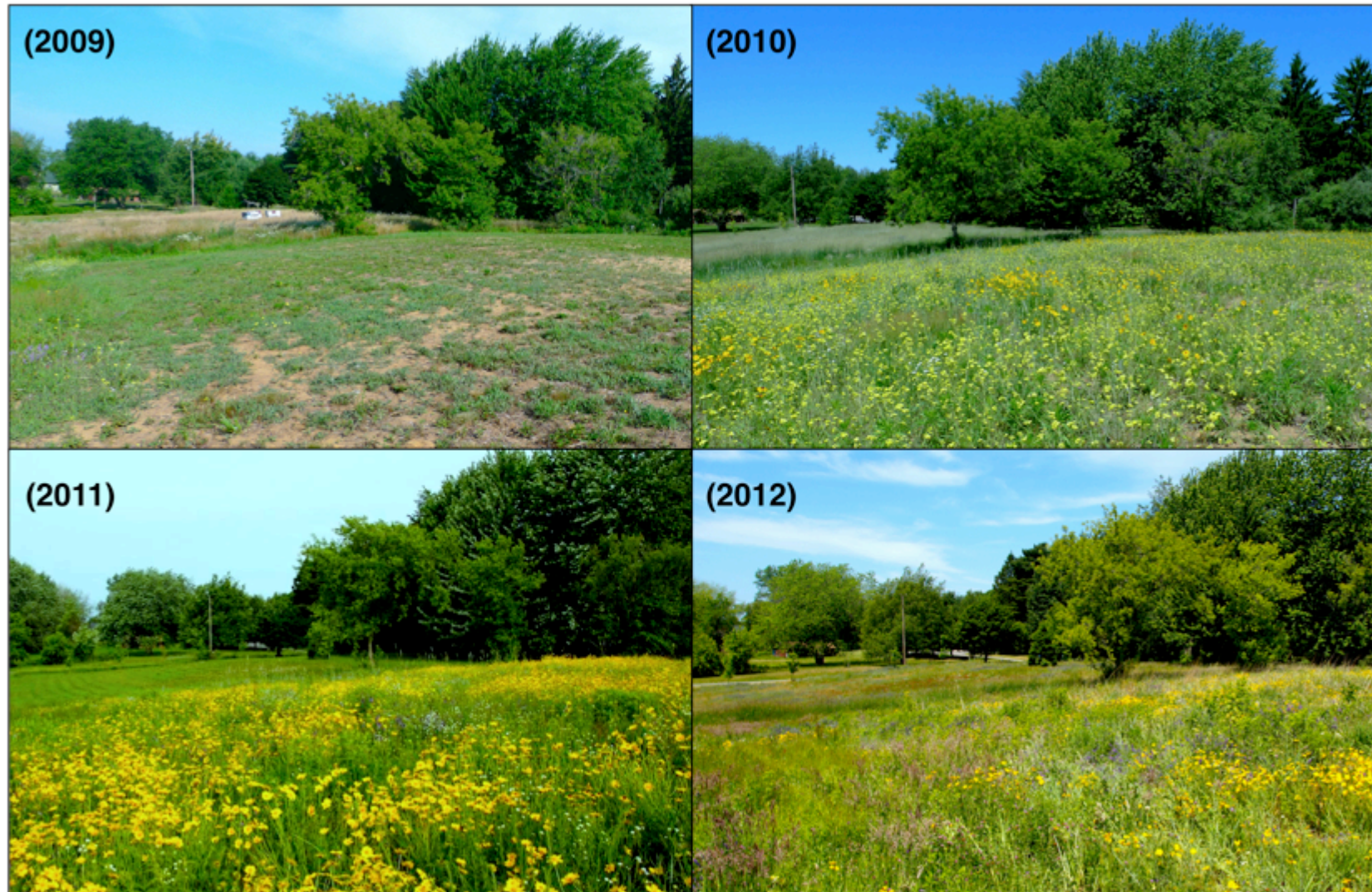


Figure A.1 Example of wildflower habitat establishment over time. All photographs were taken at the same location in June during the indicated year

APPENDIX 2

RECORD OF DEPOSITION OF VOUCHER SPECIMENS

The specimens listed below have been deposited in the named museum as samples of those species or other taxa, which were used in this research. Voucher recognition labels bearing the voucher number have been attached or included in fluid preserved specimens.

Voucher Number: 2013-02

Author and Title of thesis: Brett R. Blaauw - Composition, size, and effectiveness of native plant conservation plantings for supporting beneficial insects

Museum(s) where deposited:

Albert J. Cook Arthropod Research Collection, Michigan State University (MSU)

Table A.2 Examples of insects collected during projects in this dissertation and deposited as voucher specimens.

Order	Family	Genus-Species	Life Stage	Quantity	Preservation
Araneae			Adult	7	Pinned
Coleoptera	Cantharidae		Adult	4	Pinned
Coleoptera	Carabidae		Adult	2	Pinned
Coleoptera	Chrysomelidae		Adult	2	Pinned
Coleoptera	Coccinellidae		Adult	5	Pinned
Coleoptera	Curculionidae		Adult	4	Pinned
Coleoptera	Scarabaeidae	<i>Popillia japonica</i>	Adult	2	Pinned
Coleoptera	Staphylinidae		Adult	1	Pinned
Dermaptera			Adult	2	Pinned
Diptera	Dolichopodidae		Adult	4	Pinned
Diptera	Syrphidae		Adult	4	Pinned
Diptera	Tachinidae		Adult	2	Pinned

Table A.2 (cont'd)

Hemiptera	Anthocoridae	<i>Orius</i> spp.	Adult	4	Pinned
Hemiptera	Aphidae		Adult	2	Pinned
Hemiptera	Cercopidae		Adult	4	Pinned
Hemiptera	Cicadellidae		Adult	6	Pinned
Hemiptera	Fulgoroidea		Adult	1	Pinned
Hemiptera	Lygaeidae		Adult	4	Pinned
Hemiptera	Miridae		Adult	7	Pinned
Hemiptera	Nabidae		Adult	2	Pinned
Hemiptera	Tingidae		Adult	4	Pinned
Hymenoptera	Andrenidae		Adult	1	Pinned
Hymenoptera	Apidae	<i>Apis mellifera</i>	Adult	5	Pinned
Hymenoptera	Apidae	<i>Bombus</i> spp.	Adult	6	Pinned
Hymenoptera	Apidae	<i>Ceratina</i> spp.	Adult	3	Pinned
Hymenoptera	Apidae	<i>Xylocopa</i> spp.	Adult	1	Pinned
Hymenoptera	Apidae		Adult	2	Pinned
Hymenoptera	Colletidae		Adult	2	Pinned
Hymenoptera	Halictidae		Adult	6	Pinned
Hymenoptera	Megachilidae		Adult	2	Pinned
Hymenoptera	Parasitica		Adult	7	Pinned
Hymenoptera	Vespidae		Adult	1	Pinned
Hymenoptera	Formicidae		Adult	5	Pinned
Lepidoptera			Adult	3	Pinned
Neuroptera	Chrysopidae		Adult	4	Pinned

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