EVALUATION OF WILDFLOWERS TO PROVIDE FORAGING RESOURCES FOR MANAGED AND WILD POLLINATORS IN MICHIGAN

By

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ABSTRACT

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Optimizing plant resource selection to support managed and wild bees requires knowledge of taxa-specific bee responses to plant resource availability, and the plant traits that influence these relationships. The primary objectives of this work were to 1) determine the relative attractiveness of 54 drought-tolerant flowering plant species found in Michigan to honey bees, bumblebees, and non-Bombus wild bees in three distinct regions of west Michigan, and 2) determine the flower traits that best predict increased patterns of pollinator visitation to these plants. A common garden experiment utilizing single species plantings of wildflowers was replicated at three sites in Michigan, and data collection included both pollinator visitors and flower traits. Plant species varied in their relative attractiveness to pollinators. Honey bees and bumblebees showed more overlap in plant attraction. Floral area was the most consistent flower trait predicting the abundances of wild bees and hoverflies, as well as wild bee species richness, but was not a significant predictor of honey bee or bumblebee visitation to plant species. Other flower traits had taxa-specific relationships with the pollinator community. The results of this work inform the development of future plant lists for establishing pollinator habitat enhancements in the Great Lakes Region of the United States, and reveal that patterns of pollinator visitation to plants can be predicted by flower traits.

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KEY TO ABBREVIATIONS

SWMREC: Southwest Michigan Research and Extension Center CRC: Clarksville Research Center NWMHRC: Northwest Michigan Horticulture Research Center PERMANOVA: Permutational multivariate analysis of variance PCA: Principal component analysis CHAPTER 1:

INTRODUCTION

Ecosystem services provided by beneficial insects

Humans benefit from the ecological services provided by natural systems (Daily 1997). Collectively, these benefits are called ecosystem services (Daily 1997, Pimentel et al. 1997). Ecosystem services are classified into four main categories: regulating services (benefits provided by the regulation of ecosystem processes in nature) provisioning services (beneficial products that can be extracted from ecosystems), cultural services (non-material benefits obtained from the regulation of ecosystems that contributes to the development and cultural advancement of people), and supporting services (the underlying ecosystem processes necessary for the production of all other ecosystem services) (Millennium Ecosystem Assessment 2005). In agricultural systems, provisioning services rely on a complex web of supporting and regulating services that influence crop production, such as pest control, and pollination (Swinton et al. 2007, Zhang et al. 2007).

Insects are the most diverse group of organisms on the planet and provide regulating services in the form of arthropod mediated ecosystem services (AMES) in agricultural landscapes (Landis et al. 2000, Losey and Vaughan 2006, Isaacs et al. 2009). The two main services provided by beneficial insects include biological control of crop pests, and pollination of crops (Losey and Vaughan 2006). Natural enemies, usually predators and parasitoids, are the primary biocontrol agents and help protect plants from damage caused by insect herbivores (Rodriguez-Sanona et al. 2012). The majority of pollination services are attributed to managed and unmanaged bee species (Klein et al. 2007), although consideration has been given to other types of pollinators, such as hoverflies (Family: *Syrphidae*) (Fountaine et al. 2006). Conservation of the

services provided by beneficial insects generally involves manipulation of the environment to improve the potential of services by enhancing the survival, fecundity, longevity, and behavior of beneficial insects (Landis et al. 2000, Eilenberg et al. 2001, Isaacs et al. 2009).

Importance of pollination services provided by bees

Bees, as a monophyletic group of about 20,000 species, play a vital role in the stability of both natural and managed ecosystems (Ashman et al. 2004, Klein et al. 2007, Kremen et al. 2007, Winfree et al. 2007, Campbell et al. 2017, Sutter et al. 2017). Pollination services are considered one of the most important ecosystem services that positively impact human well-being (Melhim et al. 2016). Nearly 88% of flowering plant species depend directly on the services provided by insect pollination services are provided by bees (Potts et al. 2011). The majority of these pollination services are provided by bees (Potts et al. 2010, Ollerton et al. 2011). Plants that can self-pollinate and do not require insect mediated pollination for reproduction still require outcrossing to maintain flow of genetic materials between members of the same species (Ashman et al. 2004).

As agricultural land use intensifies due to increasing human demands for food production, understanding the factors contributing to bee decline, and developing strategies to support bee conservation, has become ever more necessary (Gunton et al. 2016). In a meta-analysis surveying fruit and vegetable production in 200 countries, 87 crop types, or 75% of the leading food crops, were found to be dependent on insect mediated pollination (Klein et al. 2007). The services provided by insect pollinators are

estimated at over US\$200 billion annually around the world (Gallai et al. 2008) and account for one third of the total global production of foods for human consumption (Losey and Vauhgan 2006, Klein et al. 2007). Furthermore, insect pollinated crops make up 9.5% of the total economic value of world agricultural output related to crops for human consumption (Gallai et al. 2008, Potts et al. 2010). In addition to the clear economic benefits of pollinators, many of the vitamins and other macronutrients that humans rely on for nutritional health are derived from insect pollinated crops (Ellis et al. 2015).

The majority of pollination services to agriculture are provided by the European honey bee (*Apis mellifera*), which is native to Europe but has been used in the United States and around to world to pollinate many insect pollinated crops (McGregor 1976, Williams 1994, Delaplane et al. 2000, Potts et al. 2010). This bee species is capable of increasing yield in 96% of animal pollinated crops (Klein et al. 2007), and the yield of some fruit, seed, and nut crops decrease by more than 90% in fields lacking these pollinators (Southwick and Southwick 1992). Although the services provided by honey bees are worth 5-14 billion dollars per year (Southwick and Southwick 1992), the global stock of domesticated honey bee colonies is growing at a slower rate than the demand for the pollination services provided by them (Aizen 2009), suggesting an increasing need to develop alternative strategies to ensure crop pollination (Pettis and Delaplane 2010).

In addition to managed honey bees, wild bees contribute significantly to the pollination of a wide array of crops (Kremen et al. 2002), and can be more effective pollinators than honey bees on a per flower basis (Garibaldi et al. 2013). Overall, their

pollination services can complement honey bees, or provide pollination insurance in systems experiencing reduced honey bee activity or in systems where honey bees are less effective pollinators (Winfree et al. 2007). In some cropping systems, wild bees interact with honey bees in a way that increases honey bees' pollination efficiency, and thus crop yield (Brittain et al. 2013, Button and Elle 2014, Campbell et al. 2017). One estimate values the services provided by native bees to crop pollination to be nearly \$3.07 billion dollars in the United States alone (Losey and Vaughan 2006). The degree to which wild bees contribute to pollination depends heavily on crop type, wild bee community structure, and biotic and abiotic factors of the surrounding landscape, such as the level of management intensification and the availability of nesting and foraging resources (Kennedy et al 2013, Garibaldi et al. 2014).

Factors affecting pollinator communities and contributing to bee declines

Anthropogenic alterations to natural landscapes have resulted in substantial reductions in the biodiversity of insects (Hunter 2002), and there is increasingly strong evidence that populations of some pollinator species are in decline (Fitzpatrick et al. 2007, Brown and Paxton 2009, Cameron et al. 2011, Bartomeus et al. 2013). There are many hypothesized drivers of pollinator declines, including a number of different pathogens, parasites, and diseases (Roulston and Goodell 2011, McArt et al. 2014, Goulson et al. 2015, Cameron et al. 2016), an increased use of insecticides to manage crop pests (Rortais et al. 2005), invasive plant species (Brown and Paxton 2009), and habitat loss (Winfree et al. 2009). Importantly, these factors often interact, where one

sub-lethal driver of pollinator decline can increase the severity of another (Potts et al. 2010), resulting in increased negative consequences for pollinator populations.

Pesticides

Most of agriculture in the developed world relies on chemical pesticides to control pests (Tilman et al. 2001, Woodcock et al. 2016). Many of these same pesticides can also negatively affect populations of wild and managed bee species (Johansen 1977, Scott-Dupree et al. 2009, Arena and Sgolastra 2014, Goulson et al. 2015, Sanchez-Bayo 2016). Insecticides primarily used to control crop pests can directly kill pollinators (Cresswell 2011, Brittian and Potts 2011), while herbicides, used to control unwanted plant species, can indirectly harm pollinators through the destruction of potential pollen and nectar sources (Goulson et al. 2015). An additional class of pesticides, called fungicides, are commonly found within bees and bee products due to their application to crop flowers during bloom (Mullin et al. 2010, Johnson et al. 2013). Fungicides have been found to have harmful effects on developing honey bee larvae which may have strong implications for colony health (Mussen et al. 2004). Because bees are commonly exposed to multiple insecticides, herbicides, and fungicides during foraging, there is increased potential for multiple routes of transmission of the pesticide into the bee, and an increased likelihood that multiple harmful chemicals might act synergistically on bee health and fecundity (Goulson et al. 2015).

The majority of pesticide risk assessments on bees have focused on acute mortality effects of individual pesticides over short periods of time using a median lethal

dosage (LD₅₀) (Desneux et al. 2007). Much less research has been conducted on the sub-lethal effects of pesticides on bee physiology and behavior, although efforts to explore sub-lethal effects of pesticides on bee life history have increased over the past 30 years (Desneux et al. 2007). Furthermore, pesticide assessments generally focus on the negative effects of pesticides on honey bee colonies and foraging workers (Thompson and Hunt 1999, Henry et al. 2012, Pettis et al. 2013), and much less is known about the toxicity of pesticides to wild bees (Blacquiere et al. 2012, Park et al. 2015). Although honey bees have generally been used as "indicator" species for ecotoxicology testing (Heard et al. 2017), there is little consensus about how transferable toxicity findings are to wild bees (Arena and Sgolastra 2014). It is unlikely that wild bees respond to the toxicity of pesticides in similarly ways to honey bees due to their different life history strategies and functional traits (Goulson et al. 2015). Furthermore, since pesticides can act at both the individual and population level (Desneux et al. 2007, Whitehorn et al. 2012), and interact with a variety of life-history traits in bees (Park et al. 2015), it is likely that they directly impact bee community structure (Kevan 1975, McLaughlin and Mineau 1995, Brittain and Potts 2011, Park et al. 2015), and contribute to overall bee declines. Importantly, some of the negative effects of pesticides on bee communities can be mitigated by increasing the proportion of natural habitat within the foraging ranges of bees (Park et al. 2015).

Invasive plant species

The introduction of alien plant species can influence the abundance and diversity of wild bees (Stout and Morales 2009, Schweiger et al. 2010, Fiedler et al. 2012). The

mechanism by which this happens can be complex and system dependent, and the impact of invasive plants on wild bees can occur at different spatial and temporal scales (Stout and Tiedeken 2016). Invasive plants can interact directly with native pollinators by forming new mutualisms with the existing pollinator community (Russo et al. 2014), or indirectly, by altering the structure of existing native plant communities through competition for resources (Kaiser-Bunbury and Muller 2008, Morales and Traverset 2009, Herron-Sweet et al. 2016). The density and abundance of the invader (Herron-Sweet et al. 2016), and whether or not it provides foraging resources for pollinators, both play important roles in determining its effect on existing pollinator communities (Emer et al. 2016, Oduor et al. 2016).

In many cases, the introduction of invasive plants has an overall negative effect on pollinator abundance and species richness (Hanula and Horn 2011, Fiedler et al. 2012). *Centaurea stoebe* ssp. *micranthos* (spotted knapweed) is one example of an exotic invasive plant species that has the potential to impact native and managed plant communities in the Midwest region of the United States. Although valued by beekeepers for its high abundance of nectar during periods of dearth in other species, relatively long bloom time, and abundance in the landscape (Watson and Renney 1974), it is actively removed from the landscape by land managers due to its destructive effects on native plant communities (Carson et al. 2015). In one study, *C. stoebe* was found to be highly attractive to bees, but landscapes dominated by this plant species lacked season long floral availability and diversity, resulting in lower season long bee abundance and species richness (Carson et al. 2016). Alternatively, some studies have shown a net benefit of invasive plant species on pollinator communities. When the invasive thistle

Carduus acanrgoides was provided to bees in addition to native plants in a community context, researchers found a 302% increase in bee abundance and 35% increase in bee species richness overall (Russo et al 2016). These discrepancies in the measureable effects of invasive plant species can lead to challenges in managing environments where invasive plants are abundant (Pimentel et al. 2005).

Habitat loss

The effects of habitat loss on biodiversity have been well documented (Foley et al. 2005) and can influence bees through a variety of mechanisms, including the reduction or loss of nesting, breeding, and foraging habitats (Winfree et al. 2009, Tscharntke et al. 2012), and geographical isolation between populations of the same species, i.e. habitat fragmentation (Kennedy et al. 2013). The loss of natural and seminatural habitats is generally thought to be the strongest driver of pollinator declines (Kearns et al. 1998, Sala et al. 2000, Aizen and Feinsinger 2003, Brown and Paxton 2009), and habitat fragmentation has been consistently found to negatively influence wild pollinator community richness and abundance by reducing the availability of floral and nesting resources (Ricketts et al. 2008, Winfree et al. 2009, Kennedy et al. 2013). Both local and landscape scale factors can influence bee populations, and these factors often interact to determine bee community structure (Rundlöf et al. 2008). In the context of the farm, natural habitat configuration and quality, which changes with the degree of land-use intensification, likely influences bee populations by altering the ways in which bees utilize their surrounding habitats (Isaacs et al. 2016). Importantly, observable declines in bee populations are tightly linked to increased anthropogenic land use

(Winfree et al. 2009, Koh et al. 2015). In a review of 54 published studies, researchers found that the effect of habitat loss on wild bee abundance and species richness are most pertinent in landscapes where native habitats have been altered as a result of anthropogenic influences (Winfree et al. 2009, Kennedy et al. 2013). Additional studies demonstrate that the restoration of habitat at the local scale, via the addition of native plant species or the removal of non-native plant species, can also increase wild bee abundance and diversity (Isaacs et al. 2009, Fiedler et al. 2012, Blaauw and Isaacs 2014, Sutter et al. 2017). Considering bees require resources provided to them by their environment, and that resource availability within the environment depends on landscape structure and habitat quality, the link between bee population structure and landscape composition is likely to become more fragile as anthropogenic land use continues to intensify.

Plant resources used by bees

Bees depend almost entirely on the availability of flowering plants to meet their energy and nutritional demands (Michener 2000). As adults, bees collect pollen from the flowers of plants as the primary resource for developing larvae (Muller et al. 2006, Vaudo 2015), and nectar to support their own energy requirements during foraging (Brodschneider and Carilsheim 2010). The quality and quantity of pollen and nectar resources greatly influence bee community structure, abundance, and species richness (Potts et al. 2003, Hines and Hendrix 2005). Furthermore, the quality and quantity of nectar and pollen resources vary considerably between flowering plants species (Roulston and Cane 2000), as well as abiotic conditions and plant age (Peat and

Goulson 2005). In the absence of floral resources, bees experience reduced growth, lower fecundity, and compromised resistance to environmental stressors such as pesticides and pathogens (Di Pasquale et al. 2013). It is likely that bee species-specific nutritional demands, as well as bee community structure, diversity, and richness are influenced by the quantity and quality of pollen and nectar available in the environment.

Pollen

Pollen serves as bees' main source of both proteins and lipids, and contains important micronutrients and phytochemicals (Roulston and Cane 2000, Nicolson 2011, Vaudo 2015). While visiting flowers, adult bees collect pollen from the male floral parts (anthers) and combine it into brood cells as the primary food for developing offspring (Muller et al. 2006). Additionally, many bees are polylectic, foraging from a variety of available plant species. Distinct species of bees can require a diversity of pollen from different plant sources and of different gualities (Muller et al. 2006, Kraemer et al. 2014, Hicks et al. 2016, Kriesell et al. 2017) to maximize fitness of their offspring (Tasei and Aupinel 2008, Vaudo 2015). In fact, pollen requirements for the development of offspring of different solitary bee species can vary significantly; from the total pollen load of 30 flowers to the amount of pollen contained in several thousand flowers (Muller et al. 2006). Furthermore, the quality as well as the amount of pollen contained within flowers can vary significantly by plant species and floral morphology (Vaudo 2015, Hicks et al. 2016). For example, the protein content of pollen from different plant species can range from 2.5% to 60% protein by dry mass (Roulston and Cane 2000). In social bee species, reductions in pollen protein leads to an increase in pollen foraging activity

(Moezel et al. 1987). Because of their complex dietary needs, bees may forage strategically to regulate pollen collection in order to maximize nutritional benefit to their offspring. This form of strategic foraging to maximize nutritional pollen profiles has been observed bumble bees (Vaudo et al. 2014, Kriesell et al. 2017), and may be reflected in floral visitation rates.

Nectar

In addition to pollen, nectar is a dietary resource that is considered to be both a necessity and a reward for foraging bees (Southwick et al. 1981, Nicholson 2007, Nicolson 2011). Being rich in carbohydrates, nectar provides adult bees with the majority of their energy requirements necessary to enhance longevity, reproduction, and to fuel their flight (Corbert 2003, Gonzalez-Teuber and Heil 2009, Brodschneider and Carilsheim 2010, Nicolson 2011, Vaudo et al. 2015, Somme et al. 2016). Additionally, it contains other macronutrients, such as amino acids, lipids, and secondary plant compounds that are sometimes used by bees, and may directly or indirectly have nutritional importance (Somme et al. 2016). Without adequate access to nectar, bee fitness can be negatively affected at both the individual and population levels. In addition to being an important food source, many bees use the water contained in nectar to cool and heat their bodies, depending on external temperatures (Winston 1987, Kuhnholz and Seeley 1997).

Optimal foraging theory suggests that bees will forage in a way that will maximize net yield of energy for the individual and/or the colony (Pyke 1984). As nectar is their primary source for carbohydrates, bees must be able to actively locate it while foraging

(Vaudo et al. 2015). Since most flowering plants require visitation by insect pollinators to reproduce, nectar has evolved as an important floral reward that bees associate with multiple floral characteristics, including visual cues such as floral morphology and color, as well as floral scent (Pichersky and Gershenzon 2002, Cnaani et al. 2005, Potts 2010, Knauer and Schiestl 2015). During foraging, bees can utilize these floral characteristics to optimize their foraging strategies to reap the greatest benefit from each visit. Nectar composition, volume, concentration, and sugar composition are the strongest predictors of host-plant selection in honey bees (Cnaani et al. 2005). As described above for pollen resources, nectar resource diversity, or the variety of nectar volume-concentration combinations available in a floral community, can greatly influence host-plant selection at the community scale (Potts et al. 2004).

Floral traits and bee attraction

Flowers are complex structures that vary greatly in their phenotype, chemistry, and timing of when resources are available to pollinators (Junker and Parachnowitsch 2015). The relationships between floral traits and pollinator visitation have been well documented (Klinkhamer et al. 1989, Mitchell et al. 2004, Ishii 2006, Glaettli and Barrett 2008, Tuell et al. 2008, Brunet et al. 2015), with an overwhelming amount of research supporting the hypothesis that multiple floral traits mediate bee visitation. Important traits include the area of floral display (Mitchell et al. 2004, Ishii 2006, Ishii et al. 2008, Tuell et al. 2008), floral color or hue (Weiss 1990, Gumbert 2000, Reverte et al. 2016, Russell et al. 2016, Ruxton and Schaefer 2016), flower size (Glaettli et al. 2008), the size of the pollen reward retained within a flower (Ishii et al. 2008, Brunet et al. 2015),

and the floral scent produced by the flower (Junker and Parachnowitsch 2015). A larger floral display, floral color, and floral scent indicate resource availability within the flower. Additionally, traits do not influence bee behavior independently of one another. Instead, multiple traits within a single plant can work synergistically to communicate resource availability (Leonard and Masek 2014). Furthermore, plants that share particular traits can overlap in the pollinators that they attract (Bosch et al. 1997, Anderson and Johnson 2009). Interestingly, different bee taxa may "select" flowers using different floral cues. For example, wild bee, and not honey bee attraction to a suite of native wildflowers in Michigan was primarily driven by the amount of floral area produced by a plant species (Tuell et al. 2008), suggesting that unique bee taxa may use different floral ques to guide their visitation patterns.

Plant bee community diversity

The myriad preferences in floral traits of different bee species helped lead to the overall diversity in the plant-pollinator syndromes we see today. Diversity within a community is generally assessed by quantifying the non-redundant components of the community, such as phylogenetic and functional diversity (Devictor et al. 2010, Junker et al. 2014). In plant-pollinator communities, increased plant species richness, contributing to a higher diversity of flowers available in the environment, can lead to an increase in niche overlap among coexisting plant species (von Felton et al. 2009, Venjakob et al. 2016), as well as increased pollinator species richness and diversity (Potts et al. 2003, Ebling et al. 2008, Blüthgen and Klein 2011, Venjakob et al. 2016).

Pollinators vary considerably in the spatio-temporal patterns of their resource use, and species' ability to coexist is due to both specialization and complementarity of plant-pollinator interactions within a plant-pollinator network (Bluthgen and Klein 2011). Specialist bee species tend to visit a subset of plants visited by generalist bees, which in turn, visit many of the plant species available (Vazquez and Aizen 2004, Pawar 2014, Rohr et al. 2014). Specialization and nestedness within a plant-pollinator network increases network resilience to disturbance and thus the likelihood that rarer species of both plant and bees can persist (Pawar 2014, Rohr et al. 2014). In addition, functional complementarity requires a degree of specialization from each species, while generalization within a plant-pollinator network is associated with high niche overlap of functionally distinct bee species (Blüthgen and Klein 2011). Increased functional complementarity in pollinator communities may buffer plant-pollinator networks against the consequences of species loss (Bluthgen and Klein 2011) and often results in a higher diversity of pollinators contributing to increased functional performance of the plant community (Blüthegan and Klein 2011, Junker et al. 2013, Venjakob et al. 2016).

Any shift in the structure (i.e. the diversity of traits and/or the availability of floral resources) of a plant community will likely affect the associated pollinator community by altering the spatio-temporal dynamics of plant-pollinator interactions (Ebeling et al. 2008, Hudewenz et al. 2012, Venjakob et al. 2016). In studies where plant diversity has been manipulated to investigate plant-pollinator interaction networks, researchers have found that increased plant species richness supports the spatial and temporal complementarity of flower visitation and niche complementarity of bees (Potts et al. 2003, Roscher et al. 2004, von Felton et al. 2009, Ebeling et al. 2008). In general, an

increase in the complexity of a plant community will lead to an increase in bee abundance and species richness (Potts et al. 2003, Kennedy et al. 2013, Isaacs et al. 2016).

Habitat management to support bees

As a result of agricultural intensification, much of the world has experienced a reduction of biodiversity within agricultural systems, and a net loss of the ecosystem services attributed to beneficial insects (Kremen et al. 2002, Klein et al. 2009, Potts et al. 2010, Landis 2017). This is especially true for pollinators, where agricultural intensification has reduced the amount of available habitat for both foraging and nesting (Kremen et al. 2002, Carvell et al. 2006, Potts et al. 2010). Habitat management utilizes tools to improve the habitats of beneficial or native organisms by increasing the availability of resources necessary for optimal performance (Landis et al. 2000). Insects can benefit substantially from habitat management within agricultural landscapes when management strategies involve increasing the season long availability of diverse floral resource (Landis et al. 2000, Michener 2000, Klein et al. 2007, Blaauw and Isaacs 2014, Blaauw and Isaacs 2015, Williams et al. 2015). This is primarily because simplified landscapes generally lack the resources necessary for survival and reproduction. Increasing the diversity and longevity of these resources provides insects with access to the nutrients retained in pollen and nectar (Tuell et al. 2008, Carvell et al. 2006, Fiedler and Landis 2007, Menz et al. 2011, Williams et al. 2015), shelter (Gurr et al. 1998), favorable micro-climates, and alternative prey or hosts. Additionally, habitat management can economically benefit society as a whole by contributing to sustainable pest management strategies, increased pollination services, and increased crop yield.

(Blaauw and Isaacs 2014, Blaauw and Isaacs 2015, Feltham et al. 2015, Sidhu and Joshi 2016).

As the human population continues to grow, so does the need for highly productive, yet sustainable, agricultural systems (Garnett et al. 2013). In the wake of a global decline of wild pollinators (Kremen et al. 2002, Potts et al. 2010) and increased environmental and anthropogenic threats to managed honey bees (Goulson et al. 2015), efforts to sustainably intensify agricultural landscapes have led to increases in the design and implementation of habitats within agricultural landscapes that support pollinators (Godfray and Garnett 2014, Gunton et al. 2016). These efforts include the planting of floral enhancements containing mixtures of flowering forbs or shrubs along field edges, where resources are limited and pollination services are needed most (Garibaldi et al. 2014). Multiple studies have shown that increasing floral resource abundance and diversity within agricultural landscapes can support pollinator abundance, species richness, specialist species, and increase the overall persistence of pollinators (Kremen and M'Gonigle 2015, Sutter et al. 2017). Associated with positive influences on pollinator communities, some studies also document increases in crop yield (Carvalheiro et al. 2012, Garibaldi et al. 2014, Blaauw and Isaacs 2014, Venturini et al. 2016, Campbell et al. 2017), providing further incentives to growers to incorporate habitat enhancements into their overall land management strategies.

Habitat management to support pollinators has been encouraged by both federal and state agencies (Dicks et al. 2016). For example, the 2008 Farm Bill ignited nationwide interest in pollinator conservation and listed it as a nationwide priority for the United States Department of Agriculture (USDA). Since then, millions of US dollars

have been spent on the development of agri-environmental schemes to support bees as part of the National Resource Conservation Service (NRCS), and the Farm Service Agency (FSA), among other institutions spanning from national to local levels of government. In 2014, President Barack Obama signed a presidential memorandum to create a federal strategy to promote the health of managed and unmanaged bees by increasing the area, and improving the quality of pollinator friendly habitat. In 2015, a "National Strategy to Promote the Health of Honey Bees and Other Pollinators" was adopted with the goal of enhancing 7 million acres along the Mississippi River basin for pollinators through 2022 (Vilsack and McCarthy 2015). As part of the Conservation Reserve Program, the United States of America Department of Agriculture Farm Service Agency provides incentives such as cost share payments to cover 50% of the cost of establishing pollinator friendly practices. This has led to the planting of 120,000 acres of pollinator friendly habitat (Williams et al. 2015). Importantly, there is strong evidence that the addition of pollinator habitat into agricultural landscapes can increase bee diversity and abundance (Sutter et al. 2017), but the effect of floral enhancements on bee communities is greatest in simplified landscapes as opposed to complex landscapes. This is because complex landscapes may already provide many of the additional benefits of pollinator habitat enhancements, such as increased flower availability (Kremen et al. 2002, Tscharntke et al. 2005, Isaacs et al. 2009, Williams et al. 2015). Although many acres of land have been dedicated to the restoration, conservation, and enhancement of landscapes to provide more flowering plants to bees, challenges associated with optimizing the selection of resources to use in the land management strategies still exist (Dicks et al. 2016). Specifically, there is a lack of

research on optimal plant selection for the creation or management of pollinator habitats in agricultural landscapes (Morandin and Kremen 2013, Williams et al. 2015).

Plant selection to support bees: Decision toolbox

Wildflower enhancements are typically designed to include a variety of flowering plant species that flower in sequence, providing resources that are accessible to pollinators throughout their season-long foraging activity (Garbaldi et al. 2014, Williams et al. 2015, Havens and Vitt 2016). Optimization of habitat selection for bees requires research on relative plant attractiveness to bees, species-specific plant-pollinator interactions, plant establishment, and the nutritional quality of resource plants (Issacs et al. 2009, Russo et al. 2013, Vaudo 2015, M'Gonigle et al. 2017). Historically, annual plant species, which tend to be easily grown and have readily available seeds, have dominated much of the research on plant selection to support pollinators (Fiedler et al. 2008, Isaacs et al. 2009). Additional plant evaluations have been conducted on volunteer plants blooming in the areas adjacent to crop fields (Idris and Grafius 1995, Nentwig et al. 1998). Many of the plant species that bloom in these areas are non-native weeds, and some are considered invasive by the USDA (USDA-NRCS 2008). More recently, there has been a push to include more native perennials in pollinator habitat development and conservation programs (Tuell et al. 2008, Williams et al. 2015, Isaacs et al. 2016). There are multiple reasons for why perennials may perform better than their annual counterparts. Perennial plants can have locally adapted genotypes and generally have lower water, nutrient, and pest-control requirements than annuals or non-native plant species. Unlike annuals, perennials will persist year to year, and thus

have fewer recurring costs due to their long term establishment potential. Because they can be regionally adapted, they tend to be closely associated with the local pollinator community (Isaacs et al. 2009, Isaacs et al. 2016).

The development of plant lists designed to support bees (and other beneficial insects) generally involves a direct comparison of the number of insect visits per sample for multiple plant species that range in their bloom periods, floral traits, and resource availability (Feidler and Landis 2007, Tuell et al. 2008, Garbuzov and Ratnieks 2014, Robson 2014, Garbuzuv and Ratnieks 2015). Direct comparisons generally result in clear variations in in plant attractiveness to target insect group. In a study to assess bee attractiveness to 43 different flowering plant species best suited for medium to finetextured soils in the Midwest region of the United States, Tuell et al. (2008) identified 5 plant species that were highly attractive to honey bees, 9 plant species that were highly attractive to wild bees, and determined that honey bee and wild bee populations were highly attractive to distinct plant species (Figure 1.1). In an associated study, Fiedler and Landis (2007) found that these same plant species varied considerably to natural enemies of crop pests. The results of Fiedler and Landis (2007) and Tuell et al. (2008) have been combined to inform the development of pollinator targeted plant lists developed by USDA NRCS, Xerces Society, and the Michigan State University Extension programs (e.g. Fiedler et al. 2007).

Since multiple studies demonstrate that the relationships between plant species and visitation by bees can vary among pollinating taxa (Tuell et al. 2008, Junker et al. 2013, Bruninga-Socolar et al. 2016), optimizing plant selection for floral habitat restoration likely requires a certain degree of taxa-specific information. Plant species

vary in their floral morphologies, which may differentially affect the likelihood of visitation by different bee species. For example, patterns of bumble bee visitation to perennial plant mixtures depend on tongue length of the bumblebee species (Carvell et al. 2006). Therefore, bumblebee abundance in wildflower plantings is dependent on trait complementarity between plants and bumblebees. As we build a deeper understanding of the relationships between plant species and bee species, as well as the flower traits that drive these relationship patterns, we can begin to optimize plant selection for habitat enhancements dependent on different goals or objectives. For example, land managers could strategically select plant resources with predictable bloom phenologies, flower morphologies, and resource availability to support common crop pollinators, to promote the greatest diversity of species (Carvell et al. 2006, Isaacs et al. 2016), or to promote a combination of goals.


Figure 1.1. Average number of (A) wild bees, and (B) honey bees observed foraging on study plants during 5-minute sampling events in 2005 (Tuell et al. 2008).

Additionally, there is increasing interest in combining expert knowledge with datadriven computational software to guide pollinator habitat enhancement design. This includes both shaping habitat composition (i.e. selecting what resources to plant) and placement within the greater landscape context (Brosi et al. 2008, Lonsdorf et al. 2009, Olsson et al. 2015, M'Gonigle et al. 2017). Tools to optimize pollinator conservation through habitat enhancement should consider multiple criteria for habitat design, including network interactions between plants and pollinators, bloom periods, pollinator nesting requirements, and the cost and availability of plant resources (Lonsdorf et al. 2009, M'Gonigle et al. 2017). In order to inform expert opinion and computational software, it is necessary to understand the relative attractiveness of insectary plants to pollinators in particular regions, and to identify floral traits that influence pollinator visitation.

Currently, only 43 flowering plant species found in Michigan have been directly assessed for their relative attractiveness to bees (Figure 1.1, Tuell et al. 2008), and nearly all of these plant species are adapted for mesic soils with good water retaining capabilities. Thus, there is a serious lack of similar information on drought-tolerant plant species adapted for dry, sandy soils, which are characteristic of many of the orchard cropping systems found throughout the Great Lakes region of the United States.

Overview of thesis

In this thesis, I address the issue of plant selection for pollinator habitat enhancements in the Great Lakes region of the United States by directly comparing patterns of pollinator visitation among 54 different plant species found on sandy soils in Michigan. My first objective is to assess the establishment and relative attractiveness of study plants to bees to determine which plant species best support honey bees, wild bees, and wild bee diversity. My second objective is to identify the relationships between floral traits of plants and patterns of visitation for managed and wild pollinators, and to determine which floral traits may be useful in aiding the development of pollinator

supportive plant lists in other regions. The results of my research will directly influence pollinator habitat conservation and restoration efforts across the state of Michigan, with the potential to extrapolate to the entire Great Lakes region of the United States and beyond.

CHAPTER 2:

ESTBLISHMENT AND RELATIVE ATTRACTIVENESS OF DROUGHT-TOLERANT INSECTARY PLANTS FOR USE IN POLLINATOR CONSERVATION PROGRAMS IN MICHIGAN

Introduction

Pollination services provided by bees are essential to the stability of both wild plant communities and pollinator-dependent crops (Klein et al. 2007, Kremen et al. 2007, Potts et al. 2010). Nearly 90% of flowering plant species, including 75% of the leading food crops, depend directly on insect mediated pollination, with the majority of services attributed to managed and wild bees (Ollerton et al. 2011). In agricultural systems, the services provided by insect pollinators are estimated at over \$200 billion around the world (Gallai et al. 2008). The majority of crops that rely on pollination by bees are pollinated by managed honey bees. While honey bee colonies provide many active workers and have been shown to increase yield in multiple animal pollinated crops (Klein et al. 2007, Garibaldi et al. 2013), they may not be the most efficient pollinators for a number of crops (James and Pitts-Singer 2008). Wild bees found in landscapes surrounding cropping systems can be more efficient crop pollinators in systems where honey bees are inefficient pollinators due to their diverse life histories (Javorek et al. 2002, Greenleaf and Kremen 2006, Campbell et al. 2017), and have been shown to significantly increase yields when supplementing honey bees (Garibaldi et al. 2013). The overall contribution of wild bees to crop pollination can vary significantly depending availability of foraging and nesting resources, which are driven by farm-management practices at both the local and landscape scale (Isaacs et al. 2009, Holzschuh et al. 2012, Kennedy et al. 2013).

Increased land-use intensification in agricultural and urban landscapes reduces the availability of habitat to support managed and unmanaged bees (Kremen et al. 2002, Klein et al. 2007). Habitat reduction is considered to be a primary driver of

pollinator declines worldwide (Kearns et al. 1998, Aizen and Feinsinger 2003, Goulson et al. 2008, Brown and Paxton 2009, Winfree et al. 2009, Bartomeus et al. 2013), negatively influencing the richness and abundance of wild pollinator communities (Ricketts et al. 2008, Winfree et al. 2009, Kennedy et al. 2013). Furthermore, intensified management of honey bee colonies in agricultural landscapes subjects the colony to a myriad of different pathogens, parasites, and diseases (Roulston and Goodell 2011, Graystock et al. 2016).

Since bees obtain nearly all of their nutrition from pollen and nectar provided by flowering plants (Michener 2000), the availability of these resources within their flight range is imperative. In agricultural landscapes, crops may provide the majority of these resources, but because they lack diversity, and are in bloom for a relatively short period of time, bees can suffer from nutritional shortages from feeding only on crops (Williams and Kremen 2007, Williams et al. 2015). As interest in conserving pollinators increases, more efforts have been put forth to develop strategies to mitigate the effects of resource-limited landscapes on pollinators. This includes a variety of agri-environmental schemes in Europe, as part of the Common Agricultural Policy, that have been evaluated for their support of pollinators (Kleijn et al. 2011, Wood et al. 2015, Dicks et al. 2016) and conservation programs available for US landowners to support the implementation of pollinator friendly habitat (Williams et al. 2015, M'Gonigle et al. 2015).

One method to support managed and wild bees in agricultural landscapes is the addition of flower plantings, i.e. food in the form of nectar and pollen, which provide bees with resources necessary for reproduction and survival. (Carvell et al. 2007, Haaland et al. 2011, Russo et al. 2013, Blaauw & Isaacs 2014, M'Gonigle et al. 2015,

Williams et al. 2015). Farms producing crops that rely on pollination may be motivated to add these plantings near to crop fields, with the aim of supporting pollinators that perform pollination services necessary for crop production (Williams et al. 2015). In addition to the benefit for bee communities, these floral plantings can provide services to other types of wildlife, such as alternative food sources for natural enemies of crop pests, and habitat for threatened birds, mammals, and butterflies (Van Buskirk and Willi 2004, Fiedler et al. 2008).

With support from both the general public and the scientific community, over 140,000 acres of pollinator conservation habitat have been planted across the United States, including nearly 7,000 acres in Michigan alone, under the Michigan Diverse Grassland and Michigan Native Pollinator SAFE programs (Farm Service Agency 2015). In some instances, the addition of floral resources increases the yields of adjacent crops (Kremen et al. 2002, Carvalheiro et al. 2012, Blaauw and Isaacs 2014, Garibaldi et al. 2014, Venturini et al. 2017), primarily due to a net positive effect on the pollinating community. Importantly, landscapes depleted of native habitat for bees (both forage and nesting) are likely to reap the greatest benefit from agri-environmental schemes (Scheper et al. 2013, Dick et al. 2016). This is because simplified landscapes may lack critical requirements for some species of bees and thus limit their populations, diversity, and attributed ecosystem services, while complex landscapes may already provide many of the additional benefits of pollinator habitat enhancements, such as increased flower availability (Kremen et al. 2002, Tscharntke et al. 2005, Isaacs et al. 2009, Williams et al. 2015).

In the past, floral habitat enhancements have generally been designed using relatively few plant species that are easily grown and readily available for purchase from plant producers- many of which include primarily annual or biennial species that are non-native (Fiedler et al. 2008). More recently there has been a push to include more locally adapted native perennial plant species in these wildflower enhancement mixes (Isaacs et al. 2009), and a broader understanding of the plant traits that make native plant species suitable for habitat enhancements has developed (Tuell et al. 2008). Floral enhancement strips are now designed to include a diversity of flowering plants to ensure the availability of pollen and nectar resources throughout bee foraging periods (Williams et al. 2015).

Although many pollinator-focused seed mixes have been developed, the majority of them lack plant material suggestions grounded in empirical data, and can be improved upon by field based research to understand relative plant attractiveness in different geographical regions (Fielder and Landis 2007, Isaacs et al. 2009). The Midwest region of the United States is one area that has received little attention in terms of identifying optimal plants for pollinator habitat enhancement. The only study that has assessed the relative attractiveness of plants to bees in this region found strong variation in plant attractiveness (Tuell et al. 2008), but was limited in sample size (n=43) and only used plant species primarily adapted for mesic soils.

In this chapter, I assess the establishment, phenology, and relative attractiveness of plant species that have potential for use in wildflower plantings within regions with well-drained, sandy soils, which are characteristic to many orchard cropping systems throughout Michigan. I compare 50 native and 4 non-native plant species adapted for

coarse-textured soils, planted in 3 distinct regions of Michigan, to determine their ability to establish in common garden plantings, and their relative attractiveness to honey bees, bumblebees, and other taxa of wild bees. I then conclude this chapter by identifying which plant species best support bees, and discuss ways to optimize plant selection for pollinators.

Materials and Methods

Study sites and plant selection

During the summer of 2014, 54 plant species (Table 2.1) were selected for pollinator attractiveness screening and planted using a random complete block design at three research stations within the MSU research station network: 1) Southwest Michigan (Southwest Michigan Research and Extension Center (SWMREC), 2) Berrien County, MI; Mid-Michigan (Clarksville Research Center (CRC), Ionia County, MI; and 3) Northwest Michigan (Northwest Michigan Horticultural Research Center (NWMHRC), Leelanau County, MI (Figure 2.1). Prior to the study, the research team consulted with the Michigan Native Plant Producers Association, and the Michigan Commercial Beekeepers Association, to develop a list of plant species for pollinator attractiveness screening. Plants were selected based on their commercial availability, and ability to produce pollen and nectar resources over the entire pollinator foraging season in Michigan (May – October) on coarse-textured soils with low moisture retention. The plant species selected included 49 native herbaceous perennial forbs, one native biennial, Oenothera biennis L, two native flowering shrubs, Rosa carolina L. and Rhus copallinum L., and two non-native forbs Centaurea stoebe L. ssp Micranthos (Gugler)

and *Lotus corniculatus* L (Table 2.1). Non-native plant species, as well as the natives *Pycnanthemum pilosum* and *Pycnanthemum virginianum* were chosen with particular consideration for their attractiveness to honey bees. *Centaurea stoebe micranthos*, although valued by beekeepers for its nectar production and contribution to the honey industry, is an invasive plant species that entered the United States during the 1800s and now has nationwide distribution. It can cause significant damage to native plant communities by outcompeting them for resources, and is actively removed during the management of a variety of landscapes (Carson et al. 2015). Native plants were collected from Wildtype Design and Seeds in Mason, MI and Hidden Savanna Nursery in Kalamazoo, MI, with the exception of *P. pilosum*, which was purchased from Prairie Moon Nursery in Winona, MN. The non-native plants were obtained from wild growing, local populations located on the Michigan State University Entomology Research Farm. When possible, Michigan genotypes were used during plant selection.

Site preparation

In April-May 2014, fields at SWMREC and CRC were tilled and treated with glyphosate to kill weeds (1% concentration), and then seeded with Earth Carpet Quick-2-Gro turf mix (La Crosse Seed, seeding rate of 2.44kg per 100 m²). At NWMHRC, the field selected was already a grassy lawn and so grass seeding was not necessary. A common garden research planting that consisted of a grid of $1m^2$ plots spaced 2m apart was replicated at each research station using a randomized complete block design. This resulted in 216 $1m^2$ plots (54 species x 4 reps = 216 plots per region). When grasses reached 4-6 inches in height, each $1m^2$ plot was treated with glyphosate again to control

vegetation, and all dead vegetation was removed. In June 2014, three seedling plugs of

the same species were transplanted in the center of each 1m² plot. To reduce

competition from unwanted nearby flowering plants, garden plots were regularly

maintained by hand weeding and mulching, and by mowing the grassy matrix between

plots.

Table 2.1. Plant species selected for assessment of relative attractiveness to pollinators. In 2014, plants were established as 3 individual plugs in four blocks of common garden plots at three Michigan State University research stations that span west Michigan's lower peninsula (Southwest Michigan Research and Extension Center (SWMREC), Clarksville Research Center (CRC), and Northwest Michigan Horticultural Research Center (NWMHRC)). All plant species are native with the exception of *Lotus corniculatus L.* and *Centaurea stoebe micranthos*.

Common Name

Life

Habit

Perennial

Family

Scientific Name

Achillea millefolium Yarrow Asteraceae Amorpha canescens Lead plant Fabaceae Asclepias syriaca Common milkweed Asclepiadaceae Asclepias tuberosa* Butterfly milkweed Asclepiadaceae Whorled milkweed Asclepias verticillata Asclepiadaceae Baptisia alba var. macrophylla White wild indigo Fabaceae Campanula rotundifolia Harebell Capanulaceae Ceanothus americanus New jersey tea Rhamnaceae Centaurea stoebe micranthos^ Spotted knapweed Asteraceae Chamerion angustifolium Fireweed Onagraceae Coreopsis lanceolata* Lance-leaved coreopsis Asteraceae Coreopsis palmata Prairie coreopsis Asteraceae Coreopsis tripteris Tall coreopsis Asteraceae Dasiphora fruticosa Shrubby cinquefoil Rosaceae Dalea purpurea Purple prairie clover Fabaceae Purple coneflower Echinacea purpurea Asteraceae Eryngium yuccifolium Rattlesnake master Apiaceae Helianthus occidentalis Western sunflower Asteraceae Heuchera richardsonii Prairie alumroot Saxifragaceae Helianthus strumosus Pale-leaved sunflower Asteraceae Hieracium gronovii Queendevil Asteraceae Hypericum prolificum Shrubby St. John's wort Clusiaceae Lespedeza capitata Round-headed bushclover Fabaceae Lespedeza hirta* Hairy bush clover Fabaceae Liatris aspera Rough blazing star Asteraceae Liatris cylindracea Cylindrical blazing star Asteraceae

Table 2.1 (cont'd)

Lotus corniculatus L.^	Birdsfoot trefoil	Fabaceae	Perennial
Lupinus perennis	Wild lupine	Fabaceae	Perennial
Monarda fistulosa	Wild bergamot	Lamiaceae	Perennial
Monarda punctata*	Spotted bee balm	Lamiaceae	Perennial
Oenothera biennis	Common evening primrose	Onagraceae	Perennial
Oenothera fruticosa	Sundrops	Onagraceae	Perennial
Oligoneuron rigidum	Stiff goldenrod	Asteraceae	Perennial
Penstemon digitalis	Foxglove beardtongue	Plantaginaceae	Perennial
Penstemon hirsutus*	Hairy penstemon	Plantaginaceae	Perennial
Potentilla arguta	Prairie cinquefoil	Rosaceae	Perennial
Potentilla simplex	Common cinquefoil	Rosaceae	Perennial
Pycnanthemum pilosum^	Hairy mountain mint	Lamiaceae	Perennial
Pycnanthemum virginianum^	Mountain mint	Lamiaceae	Perennial
Ratibida pinnata*	Yellow coneflower	Asteraceae	Perennial
Rhus copallinum	Winged sumac	Anacardiaceae	Shrub
Rosa carolina	Pasture rose	Rosaceae	Shrub
Rudbeckia hirta*	Black-eyed susan	Asteraceae	Perennial
Senecio obovatus	Round-leaved ragwort	Asteraceae	Perennial
Silphium integrifolium	Rosin weed	Asteraceae	Perennial
Silphium laciniatum	Compass plant	Asteraceae	Perennial
Silphium terebinthinaceum	Prairie-dock	Asteraceae	Perennial
Solidago juncea	Early goldenrod	Asteraceae	Perennial
Solidago nemoralis	Gray goldenrod	Asteraceae	Perennial
Solidago speciosa	Showy goldenrod	Asteraceae	Perennial
Symphyotrichum oolentangiense	Sky blue aster	Asteraceae	Perennial
Symphyotrichum sericeum	Silky aster	Asteraceae	Perennial
Tradescantia ohiensis	Common spiderwort	Commelinaceae	Perennial
Verbena stricta	Hoary vervain	Verbenaceae	Perennial

*- Tested in Tuell et al. (2008) ^- Beekeeper suggestion



Figure 2.1. Research design replicated at three Michigan State University research stations Michigan represented by black circles. Each plant species was established in 1m² plots separated by 2m distances. All 54 plant species were replicated in four blocks at each site.

Plant sampling

Each single species common garden planting (plot) was visited weekly to assess bloom phenology during 2015 and 2016 (late May- early October both years). An individual plot was sampled when the plant species reach adequate bloom (over 5 open flowers within the plot). Complete flower counts were conducted on each plot. In instances where plants produced thousands of individual flowers, inflorescences were counted along with an average number of total flowers per inflorescence (using 5 inflorescences). By multiplying these two numbers, an accurate estimate of the total number of flowers produced by a plant species within a plot was generated. To determine the total floral area in each plot, the width and length of 5 flowers or inflorescences was measured in millimeters for each plant species using a ruler. These measurements were first used to determine an average for each plant species, and then multiplied by the number of floral units counted for each plant species in each plot. Because plant phenologies were different at each site, collected floral data were averaged at each sites to create site specific plant phenology graphs displaying the total and peak bloom periods for each plant species assessed in this study. During the summer of 2017, each single species plot was visited once to assess the overall establishment of sown species by conducting target species stem counts.

Pollinator sampling

Pollinator samples consisted of both timed observations and specimens directly collected from study plant species, and were generally conducted on the same day as plant sampling. In some cases, pollinator sampling took place within 1-2 days of plant sampling due to inclement weather. All pollinator samples were conducted on days that had zero to low cloud cover, and wind consistently less than 5 meters/second, when pollinators are most likely to be present. A five-minute timed pollinator observation was conducted each week on plants with adequate bloom. This sample was completed in two, 2.5 minute samples once in the morning and once in the same afternoon at each plot in bloom, per week. All honey bees (*Apis mellifera*), bumblebees (genus: *Bombus*), or other wild bees (non-*Bombus*) that made contact with flowers within the sampling period were recorded. Samples of pollinators other than honey bees were collected

using a hand-held vacuum (model: 2820GA, Bioquip products Inc, Rancho Domingo, CA) with a clear extension tube that minimizes insect disturbance. Honey bees were not collected, and instead, their visits were recorded in the field. For each specimen; the site, date, block, plant species, and time of sample were recorded. Collected bee specimens were identified to the species level using on-line keys (discoverlife.org, Packer et al. 2007) and with the help of Dr. Jason Gibbs.

Data analysis

During the 2015 sampling season, plant species were still establishing and thus tended to bloom later in the season or not at all compared to the same plant species in 2016. Therefore, data in 2016 more accurately depicts the relative attractiveness of plant species used in this study. Data analysis and subsequent results will focus on data collected in 2016 (see Appendix C for 2015 relative plant attractiveness results).

For each analysis used in this experiment, normality of response data was first assessed using Shapiro-Wilk tests (R package: *stats*, version 3.4.0, p-value = 0.05). Generalized linear models with Poisson distribution (R package: *stats*, version 3.5.0, link = "log") were used to test the effect of each site on the response variables for each site independently: mean number of total pollinator visits per sample, mean number of honey bee visits per sample, mean number of bumblebee visits per sample, and the mean number of non-*Bombus* wild bee visits per sample (considered "wild bees" from here on). PERMANOVA (R package: *vegan*, function: adonis, "Bray-Curtis") was used assess differences in bee communities between sites and bloom periods. For relative plant attractiveness comparisons, data was first assessed by combining all plant data

collected at the three sites in 2016. For this comparison, study plants were assigned to one of three bloom periods based on their average bloom date in early season (late May-middle July), mid-season (middle July-Late August), and late season (late Augustearly October) so that plant attractiveness was compared when similar bee communities were active and during similar weather conditions. Response variables were measured as the number of visits to a flower received by a plant species in the full 5-minute sampling period. Differences among plant species in number of total pollinators, honey bees, bumblebees, and wild bees that visited plants per sample within each season were analyzed using a negative binomial generalized linear modeling framework (R package: glmmADMB, version 0.8.3.3). Data were first assessed using a GLM with Poisson distribution, but then switched to a negative binomial model due to overdispersion of count data. Over-dispersion was determined by assessing the ratio of residual variance/deviance to the residual degrees of freedom. On average, this ratio was greater than three for each bee group, suggesting over-dispersion of the data, and thus the use of a negative binomial model for comparison. Differences in the mean number of visits a plant received per sample were assessed using a Tukey's honest significance test (R package: *multcomp*, version 1.4-6) and a p-value of 0.05. In a series of additional analyses, this statistical framework was applied to each site independently. Due to the large number of pairwise comparisons within each bloom period, the test had reduced ability to differentiate between plant species in their relative attractiveness to study plants. Simple linear regression was used to determine the relationship between the average wild bee abundance and bee species richness for each plant species plant species, combined across sites.

Plant lists containing the most attractive plant species to honey bees,

bumblebees, and wild bees were determined for each site. Each list was determined by selecting the five plant species in each bloom period that had the greatest abundance of each bee group per sample. The resulting lists contain both plants that are statistically more attractive than alternative co-blooming plants, and plants that received more bee visits per sample and thus biologically superior in their attraction, but not statistically more attractive.

Results

Plant establishment

Plant establishment and phenology was assessed at each site. Although the majority of plant species increased in abundance over the course of this study, they varied in establishment after 3 years ($F_{52,550} = 14.57$, p<0.001). Across sites, *Coreopsis palmata* (stems = 154.3 ± 25.1), *Monarda fistulosa* (stems= 135.3 ± 29.4), *Pycnanthemum virginianum* (stems = 120.5 ± 19.5), *Helianthus occidentalis* (stems = 106 ± 17.5), and *Pycnanthemum pilosum* (stems = 90.5 ± 22.95) had the greatest average number of stems per plot. *Hieracium gronovii* (stems = 0.1 ± 0.1), *Chamerion angustifolium* (stems = 1.2 ± 0.4), *Lespedeza hirta* (stems = 2.27 ± 0.7), *Baptisa alba var. macrophylla* (stems = 2.5 ± 0.8), and *Oenothera biennis* (stems = 3 ± 1.8) had the lowest average number of stems per plot (Table 2.2). Not all plant species assessed in this study established well enough to be used in the relative attractiveness analysis at each site. Plant species that did not establish sufficiently are marked with an asterisk

above their associated pollinator per sample measurement in relative attractiveness

figures.

Table 2.2. Stem counts of plant species assessed in common garden plots at three Michigan State University research stations that span west Michigan's lower peninsula in 2017 (Southwest Michigan Research and Extension Center, Clarksville Research Center, and Northwest Michigan Horticultural Research Center). N is the number of plots where the species established out of a total of 12 possible plots. The number of stems is the average number of stems in meter square plots for each plant species. Each plat started as a set of three seedling plugs in July of 2014.

Bloom period	Plant species	N	Number of stems	<u>± SE</u>
early	Potentilla simplex	12	103.1	19.2
early	Coreopsis lanceolata	12	57.3	14.4
early	Achillea millefolium	12	50.8	13.0
early	Lotus corniculatus L.	12	46.0	15.5
early	Tradescantia ohiensis	12	26.4	3.8
early	Senecio obovatus	12	26.1	5.6
early	Penstemon hirsutus	11	23.0	4.4
early	Asclepias tuberosa	12	22.2	3.6
early	Penstemon digitalis	10	16.6	3.4
early	Asclepias syriaca	12	13.1	1.8
early	Oenothera fruticosa	11	12.0	3.4
early	Rosa carolina	12	9.9	0.9
early	Lupinus perennis	10	9.8	3.9
early	Potentilla arguta	11	7.0	2.4
early	Amorpha canescens	12	6.7	1.4
early	Ceanothus americanus	12	5.6	1.2
early	Baptisia alba var. macrophylla	11	2.5	0.8
middle	Coreopsis palmata	11	154.3	25.1
middle	Monarda fistulosa	12	135.3	29.4
middle	Pycnanthemum virginianum	12	120.5	19.5
middle	Helianthus occidentalis	10	106.0	17.5
middle	Pycnanthemum pilosum	13	90.5	23.0
middle	Solidago nemoralis	11	64.6	13.1
middle	Ratibida pinnata	12	28.6	5.5
middle	Asclepias verticillata	11	21.3	4.7
middle	Centaurea stoebe micranthos	12	21.1	2.5
middle	Campanula rotundifolia	8	18.9	8.9
middle	Echinacea purpurea	12	17.3	4.6
middle	Rudbeckia hirta	12	10.4	3.2

Table 2.2 (cont'd)

middle	Monarda punctata	11	10.1	3.2
middle	Eryngium yuccifolium	12	9.1	1.4
middle	Dasiphora fruticosa	10	7.0	1.8
middle	Verbena stricta	12	6.7	2.8
middle	Silphium laciniatum	11	5.9	0.7
middle	Liatris cylindracea	12	5.3	1.4
middle	Hypericum prolificum	12	3.1	0.4
middle	Chamerion angustifolium	11	1.2	0.4
middle	Hieracium gronovii	9	0.1	0.1
late	Solidago juncea	11	75.0	9.3
late	Coreopsis tripteris	11	56.6	7.1
late	Silphium integrifolium	11	41.9	6.2
late	Symphyotrichum sericeum	11	36.2	6.1
late	Helianthus strumosus	12	35.9	10.4
late	Oligoneuron rigidum	12	27.2	4.5
late	Dalea purpurea	10	15.0	3.2
late	Solidago speciosa	12	14.5	3.6
late	Symphyotrichum oolentangiense	11	12.0	3.5
late	Lespedeza capitata	11	6.5	1.9
late	Silphium terebinthinaceum	12	4.3	0.5
late	Liatris aspera	12	4.2	0.7
late	Rhus copallinum	12	3.3	0.3
late	Oenothera biennis	12	3.0	1.8
late	Lespedeza hirta	11	2.3	0.7

Overall trends

A total of 2034, 1509, and 1467 bees were observed visiting study plants at SWMREC, CRC, and NWMHRC, respectively. Honey bees (*Apis mellifera*) represented 40% of total observations (n = 1986), bumblebees (genus: *Bombus*) represented 16% of total observations (n = 807), and wild bees represented 44% of observations (n = 2212). Sites differed in the number of honey bees per sample, bumble bees per sample, and non-*Bombus* wild bees per sample, (df = 2, p<0.001, for all comparisions, Figure 2.2).



Figure 2.2. The average number of honey bees, bumblebees, and wild bees visiting wildflower plots at each site in 2016. Values represent the average number of visits a mono-specific plot received at a site. Bars within a bee type with the same letter are not significantly different (Tukey's HSD at alpha = 0.05).

When sites were combined, there was general increase in both the average number of pollinators observed per bloom period and the total floral area available for pollinator foraging (Figure 2.3). The relationship between pollinator abundance and bloom date was significant (df = 52, z = 5.846, p<0.001). There was an average of 2.83 \pm 0.20, 3.24 \pm 0.23, 5.05 \pm 0.41 pollinators and an average of 676.21 \pm 41.53, 593.64 \pm 44.39, and 809.79 \pm 71.46 cm² of floral area per sample during early bloom, middle bloom, and late bloom, respectively.



Figure 2.3. Average pollinators per sample (mean number of bees collected during each bloom period) and total floral area (total area of flowers measured in cm² during each bloom period). Samples are grouped by bloom periods: early bloom (late May-mid July), middle bloom (middle July-late August), late bloom (late August-early October).

Across all sites, (non-Apis) Apidae and Halictidae were the two most commonly

collected wild bee families. The most abundant wild bee genera include Halictus (n =

746), Bombus (n = 744), Lasioglossum (n = 536), Mellisodes (n = 229), Ceratina (n =

225), Agapostemon (n = 194), and Megachile (n = 125). Results from ordination

analysis demonstrate that wild bee community composition varied between the three

sites (PERMANOVA: df = 2, F = 4.79, p = 0.01) and between bloom periods

(PERMANOVA: df = 2, F = 2.53, p = 0.02).

Comparison of plant attractiveness- All sites combined

During 2016, plant species bloomed from late May until early October, encompassing the majority of the pollinator activity timeframe. Although data were assessed for the three-week period of peak bloom for each plant species, the majority of plants had bloom periods that were longer than 3 weeks. In many instances, pollinator groups had dissimilar patterns of visitation to study plants.

There was a significant effect of plant species on the mean number of pollinator visits during peak bloom for each bloom period, indicating that plant species vary in their attractiveness to pollinators (early: $F_{15,45} = 12.95$, p<0.001; middle: $F_{18,534} = 13.92$, p<0.001, late: F_{12.388} = 13.38, p<0.001). When sites were combined, Asclepias syriaca (mean visits \pm SE = 8.5 \pm 1.51) and Asclepias tuberosa (mean visits \pm SE = 8.3 \pm 1.65) received the greatest number of visits per sample during the early bloom period. During the middle bloom period, *Pycnanthemum pilosum* (mean visits \pm SE = 10.3 \pm 2.4), Monarda fistulosa (mean visits \pm SE = 10 \pm 1.41), Hypericum prolificum (mean visits \pm SE = 7.3 ± 1.14), and Solidago nemoralis (mean visits \pm SE = $4.5 \pm .78$) received the greatest number of visits per sample. Solidago speciosa (mean visits \pm SE = 22.01 \pm 3.88), Oligoneuron rigidum (mean visits \pm SE = 10.6 \pm 3.07), Coreopsis tripteris (mean visits \pm SE = 7.9 \pm 1.2) received the greatest number of visits during the late bloom period (Figure 2.4). Although these plant species were in the highest statistical ranking level (Tukey's HSD, p = 0.05), they did, in some cases, overlap with lesser attractive plant species.



Figure 2.4. Comparison of the number of wild bees, bumblebees, and honey bees visiting different insectary plants 2016. Plants are arranged within bloom period by the total number of bees observed per 5-minute sample, in decreasing order. Mean differences in the total number of bees per sample determined using Tukey's HSD test. Plant species sharing the same letter are not significantly different from each other at α = 0.05. Due to low establishment, *Potentilla arguta* (early), *Silphium laciniatum* (middle), *Chamerion angustifolium* (middle), and *Lespedeza capitata* (late) were removed from analysis.

Comparison of plant attractiveness- Individual sites

The relative attractiveness of study plants, in terms of total bees per sample, is summarized for each plant species at SWMREC (Figure 2.5), CRC (Figure 2.6), and NWMHRC (Figure 2.7). All but a small subset of flowering plant species assessed received at least one bee visit during sampling events. At SWMREC, *Chamerion angustifolium* and *Rhus copallinum* did not receive any bee visits. At CRC, *Oenothera biennis* did not receive any pollinator visits, and at NWMHRC, *Hieracium gronovii, Lespedeza hirta, Lespedeza capitata, Chamerion angustifolium*, and *Monarda punctata* did not receive any bee visits. Most of the plant species assessed were visited at low frequencies by bees, while a relatively small number of plant species were visited by a much greater number of bees. The plant families that were found to be most attractive to pollinators at each site include *Asteraceae, Asclepiadaceae, Commelinaceae, Fabaceae*, and *Plantaginaceae*.

During the early bloom period, bee visitation per sample was highest on Asclepias syriaca and Asclepias tuberosa at both SWMREC (A. syriaca: mean visits \pm SE = 10.4 \pm 4.1, A. tuberosa: mean visits \pm SE = 9.9 \pm 3.13), and NWMHRC (A. tuberosa: mean visits \pm SE = 12.8 \pm 4.3, A. syriaca: mean visits \pm SE = 5.8 \pm 1.7). At CRC, bee visitation was highest on Asclepias syriaca (mean visits \pm SE = 9.8 \pm 2.3) and Achillea millefolium (mean visits \pm SE = 4.1 \pm 1.5). In the middle bloom period, Monarda fistulosa received the greatest number of bee visits per sample at CRC (mean visits \pm SE = 12.7 \pm 1.6) and NWMHRC (mean visits \pm SE = 8.1 \pm 2.8), while at SWMREC, Pycnanthemum pilosum (mean visits \pm SE = 17.6 \pm 3.4) received more bee visits per sample than other co-blooming plant species. Hypericum prolificum received the second

most visits per sample at SWMREC (mean visits \pm SE = 12.1 \pm 2.3) and NWMHRC (mean visits \pm SE = 4.3 \pm 1.2). In the late bloom period, *Solidago speciosa* was visited frequently by bees all sites (SWMREC: mean visits \pm SE = 14 \pm 3, CRC: mean visits \pm SE = 15 \pm 1, NWMHRC: mean visits \pm SE = 27.5 \pm 6.5). In addition, *Coreopsis triperis* at SWMREC (mean visits \pm SE = 14 \pm 2.5), *Symphyotrichum oolentangiense* at CRC (mean visits \pm SE = 7.1 \pm 2), and *Oligoneuron rigidum* at NWMHRC (mean visits \pm SE = 21.1 \pm 7.2) also received more bee visits per sample that other plant species.

Honey bees, bumblebees, and wild bees did not always overlap in their patterns of plant selection and instead had distinct floral preferences (see Table 2.6). The relative attractiveness of study plants to honey bees, bumblebees, and wild bees at each site are shown at SWMREC (Table 2.3), CRC, (Table 2.4), and NWMHRC (Table 2.5).



Figure 2.5. Comparison of the number of wild bees, bumblebees, and honey bees visiting different insectary plants at Southwest Michigan Research and Extension Center Research Center, Benton Harbor MI (SWMREC) in 2016. Plants are arranged within bloom period by the total number of bees observed per 5-minute sample, in decreasing order. Mean differences in the total number of bees per sample was determined using Tukey's HSD test. Plant species sharing the same letter are not significantly different from each other at $\alpha = 0.05$.

Table 2.3. Peak bloom times and the average number of three bee groups visiting insectary plants in 2016 for study plants at SWMREC. Study plants are arranged in order of bloom time. Peak bloom weeks are highlighted in green with the average floral area (cm²) for the week recorded in cells. Pollinators per sample is only recorded for peak bloom periods for study plants. Horizontal lines separate plants by bloom period used for analyses. *- not included in analysis due to low replication.

		Bloom Timing														A	vera	age ni	umb	er of:			
Plant Species	Family		Мау	1		Ju	ne			Jı	ıly			Aug	gus	t	September	Honey bees		Bumblebees		Wild bees	
Early Season																							
Lupinus perennis	F	*	*	*	-	-	-	-	-									0.0	*	0.0	*	1.0	*
Potentilla simplex	R	*	*	*	-	-												0.1	b	0.0	*	0.7	b
Senecio obovatus	Α	*	*	*	-	-												0.0	*	0.0	*	3.9	а
Penstemon hirsutus	Р		-	*	*	*	-	-	-									0.0	*	0.0	*	0.8	b
Tradescantia ohiensis	С			-	*	*	*	-	-	-	-	-	-					1.1	b	0.3	а	0.4	b
Coreopsis lanceolata	Α		-	-	*	*	*	-	-	-								0.3	b	0.2	а	1.0	ab
Rosa carolina	R		-	-	-	*	*	-	-									0.1	b	0.1	а	0.4	b
Heuchera richardsonii	S			-	*	-	*	*	-									0.0	*	0.0	*	0.3	b
Penstemon digitalis	Р			-	-	*	*	*	-	-								0.0	*	0.2	а	0.7	b
Baptisia alba var. macrophylla	F			-	-	*	*	*	-	-								0.0	*	0.0	*	0.1	ab
Achillea millefolium	Α			-	-	*	*	*	-	-	-	-	-	-				0.0	*	0.1	а	0.9	ab
Asclepias syriaca	AS				-	*	*	*	-	-	-	-	-					9.2	а	0.4	а	0.8	ab
Oenothera fruticosa	0			-	-	*	*	*	-	-	-	-						0.0	*	0.2	а	0.4	b
Ceanothus americanus	RH					-	*	*	*	-								0.0	*	0.0	*	1.1	ab
Lotus corniculatus	F					-	*	*	*	-	-	-	-					0.3	b	0.1	а	1.8	ab
Asclepias tuberosa	AS				-	-	*	*	*	-	-	-	-	-	-			8.4	а	0.2	а	1.3	ab
Potentilla arguta	R					-	*	*	*	-	-	-	-	-				0.0	*	0.0	*	2.8	*
Amorpha canescens	F					-	*	*	*	-	-	-						0.3	b	0.4	а	1.0	ab
Coreopsis palmata	Α						-	*	*	-	-	-	-	-	-			0.4	b	0.0	*	2.0	ab
Rudbeckia hirta	Α						-	*	*	*	-	-	-	-	-			0.6	b	0.0	*	2.2	ab
Mid Season																							
Verbena stricta	V							-	*	*	-	-	-	-	-	-		0.0	*	0.3	*	0.7	*
																		10.					
Hypericum prolificum	CL						-	-	*	*	*	-	-	-	-	-		1	а	2.0	ac	0.0	*
Campanula rotundifolia	CA						-	-	*	*	*	-	-	-	-	-	-	0.0	*	0.0	*	0.5	*

Table Z.3 (COULU)	Table	2.3	(cont'd)
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Centaurea stoebe micranthos	А			-	*	*	*	-	-	-	-	-	-			0.4	b	0.6	bc	4.1	а
Dalea purpurea	F			-	*	*	*	-	-	-	-	-	-			0.2	b	0.3	С	1.8	ac
Monarda fistulosa	L		-	-	*	*	*	-	-	-	-	-				0.8	b	8.6	а	0.0	*
Pycnanthemum virginianum	L		-	-	*	*	*	-	-	-	-	-				1.3	b	0.2	С	0.1	С
Solidago nemoralis	А		-	-	*	*	*	-	-	-	-	-				0.2	*	0.0	*	4.5	*
Hieracium gronovii	Α			-	-	*	*	*	-	-						0.0	*	0.0	*	1.7	*
Ratibida pinnata	А		-	-	-	*	*	*	-	-	-	-	-			0.0	*	0.1	с	3.0	ab
Echinacea purpurea	А		-	-	-	-	*	*	*	-	-	-	-	-		0.3	b	0.2	с	1.7	ac
Eryngium yuccifolium	AP			-	-	-	*	*	*	-	-	-				0.1	b	0.0	*	1.2	bc
Monarda punctata	L			-	-	-	*	*	*	-	-	-	-			0.1	b	0.0	*	0.2	с
Pycnanthemum pilosum	L				-	-	*	*	*	-	-	-	-	-		12.9	а	2.8	ab	1.8	ac
Liatris cylindracea	А					-	-	*	*	-	-	-	-			0.0	*	0.1	bc	0.2	с
Late Season																					
Rhus copallinum	AN						-	-	*	-	-	-	-			0.0	*	0.0	*	0.0	*
Helianthus occidentalis	А					-	-	*	*	*	-	-	-			0.1	b	0.7	ab	3.8	ac
Solidago juncea	А					-	-	*	*	*	-	-	-			0.2	b	0.3	b	2.0	ac
Lespedeza hirta	F					-	-	-	*	*	*	-	-	-		0.0	*	0.0	*	1.0	bc
Asclepias verticillata	AS				-	-	-	-	*	*	*	-				1.6	ab	0.0	*	1.2	bc
Chamerion angustifolium	0				-	-	-	-	*	-	*	-				0.0	*	0.0	*	0.0	*
Coreopsis tripteris	А					-	-	-	*	*	*	-	-			1.7	ab	4.8	а	7.5	а
Silphium terebinthinaceum	А					-	-	-	*	*	*	-	-			0.6	ab	2.5	ab	2.2	ac
Helianthus strumosus	А							-	-	*	*	*	-	-		1.6	ab	0.6	ab	4.8	ab
Silphium integrifolium	А					-	-	-	-	*	*	*	-			2.7	ab	2.8	ab	4.0	ac
Liatris aspera	А								-	-	*	*	*	-		0.1	b	2.5	ab	0.8	С
Oenothera biennis	0						-	-	-	-	*	*	*	-		0.2	b	0.0	*	0.0	*
Oligoneuron rigidum	А						-	-	-	-	-	*	*	*	-	5.6	а	1.4	ab	3.8	ac
Dasiphora fruticosa	R			-	-	-	-	-	-	-	-	*	*	*	-	1.3	ab	0.0	*	2.4	ac
Symphyotrichum sericeum	А										-	*	*	*	-	0.3	b	0.0	*	6.2	а
Solidago speciosa	А											-	-	*	*	10.5	*	3.0	*	0.5	*
Symphyotrichum oolentangiense	А											-	-	*	*	2.1	ab	1.0	ab	3.6	ac

Codes for plant families: A = Asteraceae, AN = Anacardiaceae, AP = Apiaceae, AS = Asclepiadaceae, C = Commelinaceae, CA = Campanulaceae, CL = Clusiaceae, F = Fabacea, L = Lamiaceae, O = Onagraceae, P = Plantaginaceae, R = Rosaceae, RH = Rhamnaceae, S = Saxifragaceae, V = Verbenaceae.



Figure 2.6. Comparison of the number of wild bees, bumblebees, and honey bees visiting different insectary plants at Clarksville Research Center, Clarksville MI (CRC) in 2016. Plants are arranged within bloom period by the total number of bees observed per 5-minute sample, in decreasing order. Mean differences in the total number of bees per sample was determined using Tukey's HSD test. Plant species sharing the same letter are not significantly different from each other at $\alpha = 0.05$.

Table 2.4. Peak bloom times and the average number of three bee groups visiting insectary plants in 2016 for study plants at CRC. Study plants are arranged in order of bloom time. Peak bloom weeks are highlighted in green with the average floral area (cm²) for the week recorded in cells. Pollinators/ sample is only recorded for peak bloom periods for study plants. Horizontal lines separate plants by bloom period used for analyses. *- not included in analysis due to low replication.

									В	loc	om	Tir	nin	g				Ave	rage	numb	er o	of:	
Plant Species	Family		M	AY		JU	NE			JUI	_Y		AL	IGU	ST		SEPTEMBER	Honey bees		Bumblebees		Wild bees	
Early Season																							
Senecio obovatus	А	-	*	*	*	-												0.0	*	0.0	*	2.8	ab
Potentilla simplex	R	-	*	*	*	-												0.0	*	0.0	*	0.7	b
Heuchera richardsonii	S				-	*	*	-										0.0	*	0.0	*	0.1	b
Coreopsis lanceolata	А		-	-	*	*	*	-	-									0.0	*	0.0	*	3.1	ab
Penstemon hirsutus	Ρ			-	*	*	*	-	-									0.0	*	0.2	а	1.3	ab
Penstemon digitalis	Ρ				-	*	*	*	-	-								0.0	*	0.1	а	1.6	ab
Tradescantia ohiensis	С			-	-	*	*	*	-	-	-	-	-					0.0	*	0.0	*	1.3	ab
Baptisia alba var. macrophylla	F			-	-	-	*	*	-	-	-							0.0	*	0.0	*	0.3	*
Oenothera fruticosa	0			-	-	-	*	*	*	-	-							0.0	*	0.0	*	1.6	*
Asclepias syriaca	AS					-	*	*	*	-	-	-	-					7.0	а	0.0	*	2.8	ab
Ceanothus americanus	RH					-	-	*	-									0.0	*	0.0	*	3.0	*
Achillea millefolium	Α			-	-	-	*	*	*	-	-	-	-	-	-			0.1	b	0.0	*	4.0	а
Lotus corniculatus	F					-	*	*	*	-	-	-	-	-				0.3	b	0.3	а	2.5	ab
Asclepias tuberosa	AS				-	-	-	*	*	*	-	-	-	-	-	-		1.2	b	1.0	а	1.8	ab
Amorpha canescens	F						-	-	*	*	-	-						0.0	*	0.0	*	2.0	*
Mid Season																							
Hieracium gronovii	Α						-	-	*	*	*	-	-					0.0	*	0.0	*	0.3	*
Monarda fistulosa	L					-	-	-	*	*	*	-	-	-	-	-		0.3	а	5.8	а	6.7	ab
Rudbeckia hirta	Α						-	-	*	*	*	-	-	-	-	-		0.0	*	0.0	*	3.2	ad
Coreopsis palmata	Α							-	*	*	*	-	-	-	-	-		0.0	*	0.0	*	1.0	d
Hypericum prolificum	CL						-	-	*	*	*	-	-	-	-	-		0.2	а	2.4	а	2.1	bcd
Campanula rotundifolia	CA						-	-	-	*	*	-	-	-	-	-	-	0.0	*	0.0	*	0.3	*
Asclepias verticillata	AS					-	-	-	-	*	*	*	-	-	-	-	-	1.3	а	0.0	*	1.3	cd
Pycnanthemum virginianum	L								-	*	*	*	-	-	-	-	-	1.7	а	0.3	b	2.9	bcd
Solidago nemoralis	Α						-	-	-	*	*	*	-	-	-	-		0.0	*	0.0	*	9.6	а
Chamerion angustifolium	0							-	-	-	*	*	-	-	-	-	-	0.0	*	0.5	*	0.0	*

Potentilla arguta	R			-	-	-	*	*	-	-	-	-	-					0.0	*	0.0	*	0.5	*
Verbena stricta	V				-	-	*	*	*	-	-	-	-	-	-			0.4	а	0.0	*	1.0	cd
Liatris cylindracea	Α						-	*	*	-	-	-						0.0	*	0.0	*	0.4	*
Ratibida pinnata	Α		-	-	-	-	-	*	*	-	-	-	-	-	-			0.0	*	0.0	*	1.5	cd
Eryngium yuccifolium	AP				-	-	-	*	*	*	-	-	-					0.1	а	0.1	b	2.0	cd
Dasiphora fruticosa	R			-	-	-	-	*	*	*	-	-	-	-				0.0	*	0.0	*	3.9	ad
Helianthus occidentalis	Α				-	-	-	*	*	*	-	-	-					0.0	*	0.0	*	3.5	ad
Dalea purpurea	F				-	-	-	*	*	*	-	-	-	-				0.0	*	0.4	b	0.9	d
Solidago juncea	Α					-	-	*	*	*	-	-	-	-				0.0	*	0.1	b	4.9	ac
Late Season																							
Centaurea stoebe micranthos	Α						-	-	*	*	*	-	-	-	-			0.0	*	0.2	bd	5.3	а
Echinacea purpurea	Α		-	-	-	-	-	-	*	*	*	-	-	-	-	-		0.7	b	0.3	bd	1.8	bc
Silphium integrifolium	Α						-	-	*	*	*	-	-	-	-			1.3	b	2.3	а	2.2	ac
Coreopsis tripteris	Α						-	-	-	*	*	*	-	-	-	-		0.3	b	0.4	b	5.5	а
Silphium terebinthinaceum	Α						-	-	-	*	*	*	-	-	-	-		2.3	b	0.6	b	1.4	bc
Rhus copallinum	AN							-	-	-	*	*	-	-				0.0	*	0.0	*	0.5	*
Lespedeza capitata	F							-	-	-	*	*	-	-	-	-		0.0	*	0.1	ab	0.1	bc
Lespedeza hirta	F							-	-	-	*	*	*	-	-	-	-	0.0	*	0.1	b	0.4	с
Oenothera biennis	0							-	-	-	*	*	*	-	-	-	-	0.0	*	0.0	*	0.0	*
Helianthus strumosus	Α							-	-	-	*	*	*	-	-	-	-	0.5	b	0.2	b	2.1	ac
Monarda punctata	L			-	-	-	-	-	-	-	*	*	*	-	-	-		0.0	*	0.0	*	0.2	*
Oligoneuron rigidum	Α							-	-	-	*	*	*	-	-	-	-	0.0	*	0.0	*	0.8	с
Liatris aspera	Α									-	*	*	*	-	-	-	-	0.0	*	0.0	*	0.1	с
Symphyotrichum sericeum	Α											-	*	*	*	-	-	0.3	b	0.0	*	1.5	bc
Solidago speciosa	Α													-	*	*	*	10.7	а	3.1	а	1.1	bc
Symphyotrichum																							
oolentangiense	Α													-	*	*	*	1.1	b	2.4	а	3.6	ab

Table 2.4 (cont'd)

Codes for plant families: A = Asteraceae, AN = Anacardiaceae, AP = Apiaceae, AS = Asclepiadaceae, C = Commelinaceae, CA = Campanulaceae, CL = Clusiaceae, F = Fabacea, L = Lamiaceae, O = Onagraceae, P = Plantaginaceae, R = Rosaceae, RH = Rhamnaceae, S = Saxifragaceae, V = Verbenaceae.



Figure 2.7. Comparison of the number of wild bees, bumblebees, and honey bees visiting insectary plants at Northwest Michigan Horticulture Research Center, Traverse City, MI (NWMHRC) in 2016. Plants are arranged within bloom period by the total number of bees observed per 5-minute sample, in decreasing order. Mean differences in the total number of bees per sample was determined using Tukey's HSD test. Plant species sharing the same letter are not significantly different than each other at $\alpha = 0.05$.

Table 2.5. Peak bloom times and the average number of three bee groups visiting insectary plants in 2016 for study plants at NWMHRC. Study Plants are arranged in order of bloom time. Peak bloom weeks are highlighted in green with the average floral area (cm²) for the week recorded in cells. Pollinators per sample is only recorded for peak bloom periods for study plants. Horizontal lines separate plants by bloom period used for analyses. *- not included in analysis due to low replication.

										В	lo	om	Ti	imi	ng						Avera	ge ni	umb	er of:	
Plant Species	Family	м	ay			Ju	ne			Jı	uly			Au	gus	t		Septemb	er	Honey bees		Bumblebees		Wild bees	
Early Season																									
Potentilla simplex	R	-	*	*	*	-														0.0	*	0.0	*	0.3	а
Senecio obovatus	Α	-	*	*	*	-														0.0	*	0.0	*	1.8	а
Lupinus perennis	F		-	*	*	*	-	-												0.0	*	0.1	а	0.0	*
Heuchera richardsonii	S			-	-	*	*	*	-											0.0	*	0.1	а	0.3	а
Lotus corniculatus	F	1			-	*	*	*	-	-	-	-					1			0.2	d	0.2	а	0.5	а
Baptisia alba var. macrophylla	F			-	-	*	-	*	-	-										0.5	*	0.0	*	0.5	*
Penstemon hirsutus	Ρ			-	-	*	*	*	-											0.0	*	0.0	*	0.4	а
Coreopsis lanceolata	Α			-	-	-	*	*	*	-										0.3	d	0.1	а	1.1	а
Tradescantia ohiensis	С					-	*	*	*	-	-	-								3.7	ac	0.3	а	0.1	а
Rosa carolina	R		-	-	-	-	-	*	*	-										0.6	bcd	0.0	*	0.3	а
Penstemon digitalis	Ρ				-	-	-	*	*	*		-					1			0.1	bcd	0.0	*	0.3	а
Achillea millefolium	Α			-	-	-	-	*	*	*		-	-							0.3	d	0.0	*	0.4	а
Asclepias syriaca	AS					-	-	*	*	*		-					1			5.2	ab	0.1	а	0.6	а
Campanula rotundifolia	CA						-	*	*	*		-	-	-						0.1	cd	0.0	*	0.7	а
Oenothera fruticosa	0				-	-	-	*	*	*		-					1			0.8	bcd	0.0	*	0.7	а
Ceanothus americanus	RH					-	-	-	*	*										0.8	*	0.2	*	0.2	*
Asclepias tuberosa	AS				-	-	-	-	*	*		-	-	-						12.0	а	0.5	а	0.3	а
Mid Season													1				1								
Rudbeckia hirta	Α						-	-	*	*	*	-	-	-	-	-	-			0.4	ab	0.0	*	1.0	ab
Amorpha canescens	F						-	-	-	*	*	*	-							0.0	*	0.0	*	0.1	ab
Coreopsis palmata	Α						-	-	-	*	*	*	-	-	-		1			0.0	*	0.0	*	0.6	ab
Centaurea stoebe micranthos	Α								-	*	*	*	-	-	-	-	-			0.2	b	0.0	*	0.3	b
Chamerion angustifolium	0									*	*	*	-	-	-	-	-			0.0	*	0.0	*	0.0	*
Hypericum prolificum	CL							-	-	*	*	*	-	-	-	-				0.6	b	3.6	а	0.2	b
Monarda fistulosa	L							-	-	*	*	*	-	-	-	-	-			6.0	а	0.8	b	1.3	ab
Asclepias verticillata	AS									*	*	*	-	-	-	-	-			0.3	b	0.0	*	0.1	ab

		-																					
Pycnanthemum virginianum	L		-	-	-	*	*	*	-	-	-							2.5	ab	0.0	*	0.8	ab
Verbena stricta	V			-	-	*	*	*	-	-	-							2.2	ab	0.0	*	0.1	ab
Echinacea purpurea	Α			-	-	*	*	*	-	-	-	-	-	-	-			0.3	b	0.0	*	1.1	ab
Ratibida pinnata	Α			-	-	-	*	*	*		-	-	-	-				0.0	*	0.0	*	0.4	ab
Monarda punctata	L		-	-	-	-	*	*	*	· ·	-	-	-	-				0.0	*	0.0	*	0.0	*
Silphium integrifolium	Α		-	-	-	-	*	*	*		-	-	-					0.8	ab	0.1	b	2.8	а
Dalea purpurea	F			-	-	-	*	*	*		-	-	-					0.4	b	0.2	b	0.4	ab
Hieracium gronovii	Α			-	-	-	-	*	-	-	-							0.0	*	0.0	*	0.0	*
Silphium laciniatum	Α				-	-	-	*	-	-	-	-						0.0	*	0.0	*	3.0	*
Eryngium yuccifolium	AP			-	-	-	-	*	*	*	-	-						0.0	*	0.1	b	0.3	ab
Liatris cylindracea	Α					-	-	*	*	*	-	-	-					0.0	*	0.0	*	0.1	ab
Solidago nemoralis	Α			-	-	-	-	*	*	*	-	-	-					0.1	b	0.0	*	0.2	ab
Helianthus occidentalis	Α					-	-	*	*	*	-	-	-					0.0	*	0.0	*	1.1	ab
Pycnanthemum pilosum	L					-	-	*	*	*	-	-	-	-	-	-		2.0	ab	0.1	b	0.3	ab
Late Season																							
Silphium terebinthinaceum	Α					-	-	-	*	*	*	-	-					1.7	cd	0.3	b	1.9	ab
Solidago juncea	Α					-	-	-	*	*	*	-	-					0.0	*	0.0	*	0.4	b
Lespedeza hirta	F					-	-	-	-	-	*	*	-	-				0.0	*	0.0	*	0.0	*
Liatris aspera	Α										-	*	*	*	-			0.4	d	0.4	b	1.0	ab
Oenothera biennis	0							-	-	-	-	*	*	*	-			0.8	cd	0.1	b	0.1	ab
Lespedeza capitata	F							-	-	-	-	-	*	-	-			0.0	*	0.0	*	0.0	*
Helianthus strumosus	Α							-	-	-	-	-	*	*	*	-		2.0	cd	0.1	b	0.5	ab
Coreopsis tripteris	Α						-	-	-	-	-	-	*	*	*	-		2.3	cd	0.1	b	1.1	ab
Dasiphora fruticosa	R				-	-	-	-	-	-	-	-	*	*	*	-	-	0.2	d	0.1	b	0.5	b
Symphyotrichum sericeum	Α										-	-	*	*	*	-	-	1.1	cd	0.1	b	2.2	а
Oligoneuron rigidum	Α							-	-	-	-	-	*	*	*	-	-	17.2	ab	2.8	ab	1.1	ab
Solidago speciosa	Α												-	-	*	*	*	20.6	а	6.5	а	0.4	b
Symphyotrichum																							
oolentangiense	Α			<u> </u>				1					-	-	*	*	*	4.1	bc	0.8	b	0.5	ab

Table 2.5 (cont'd)

Codes for plant families: A = Asteraceae, AN = Anacardiaceae, AP = Apiaceae, AS = Asclepiadaceae, C = Commelinaceae, CA = Campanulaceae, CL = Clusiaceae, F = Fabacea, L = Lamiaceae, O = Onagraceae, P = Plantaginaceae, R = Rosaceae, RH = Rhamnaceae, S = Saxifragaceae, V = Verbenaceae.

Comparison of pollinator species richness

There was a general increase in bee species richness at all sites in 2016, measured as the number of unique bee species a plant received during full peak bloom periods (early bloom = 4.4 ± 0.59 pollinator species, middle bloom = 4.96 ± 0.66 pollinator species, late bloom = 5.63 ± 1.0 pollinator species). Associated with this, there was a positive linear relationship between wild bee species richness and wild bee abundance (t = 7.25, r² = 0.51, p<0.001) (Figure 2.8). Averaged wild bee species richness for each plant species is shown in Figure 2.9. During the early season, wild bee species richness was greatest on *Coreopsis lanceolata* (9.0 \pm 1.7 species), Asclepias tuberosa (7.7 \pm 3.5 species), and Asclepias syriaca (7.3 \pm .2.9 species). During the middle season, Centaurea stoebe micranthos (10.0 \pm 4.9 species) had the greatest species richness of wild bees, although the value was not much greater than that for *M. fistulosa* $(9.3 \pm 1.9 \text{ species})$ or *Helianthus occidentalis* $(8.7 \pm 3.2 \text{ species})$. During the late season, Coreopsis tripteris (15.0 ± 4.5 species), Dasipora fruticosa (10.0 \pm 4.6 species), and Solidago integrifolium (9.7 \pm 3.0 species) had the highest wild bee species richness of plants assessed.



Figure 2.8. Linear relationship between the average number of bees observed per sample and the total number of unique bee species collected from each plant species in 2016. The identity of the two outlier species is provided.


Figure 2.9. Average pollinator species richness for each plant species during 2016. Plants are arranged within bloom period by the overall average number of unique bee species that visited them during that bloom period. Plant species with an (*) next to their name represent plant species specifically chosen for their attractiveness to honey bees.

Most attractive plants for bees

The top five plants, by measurement of the mean number of visits per sample in each bloom period as well as plants that best support wild bee species richness, were determined at each site. The most attractive plant species for honey bees, bumblebees, and wild bees at SWMREC, CRC, and NWMHRC are shown in Table 2.6. Bloom periods of top five plants did not always overlap between sites. During the early bloom period, Asclepias syriaca and Asclepias tuberosa were consistently the two most frequently visited plants for honey bees, bumblebees, and wild bees. A. tuberosa and A. syriaca were also the second and third best plants to support wild bee species richness. During the middle bloom period, Monarda fistulosa was shared as a top five visited plant resource for all bee groups, except for wild bees at SWMREC. Instead, the most frequently visited plant at this site was *Centaurea stoebe micranthos*, which was also the plant that best supported species richness of wild bees. Additionally, Hypericum prolificum was also a top five plant resource for honey bees and bumblebees at most sites in the second bloom period, but not for wild bees at any of the three sites. During the late bloom period, Symphyotrichum oolentangiense was a top five resource for honey bees and bumblebees at all sites, but only for wild bees at CRC. The only plant species that was shared by wild bees at all sites during the late bloom period was Coreopsis tripteris, which received the greatest wild bee visits per sample at SWMREC and CRC, and the fourth most at NWMHRC. This plant species also supported the greatest overall species richness of wild bees, and was frequently visited by honey bees and bumblebees at all sites except for honey bees at CRC, and bumblebees at NWMHRC. Of plant species that supported the greatest bee species richness, M.

fistulosa, *C. tripteris*, and *C. stoebe micranthos* supported the greatest abundance. The bee families that were primarily associated with increased wild bee abundance and species richness were *Apidae*, and *Halictidae* (Figure 2.10, Figure 2.11).

Table 2.6. The top five plant species that supported overall abundances of honey bees, bumblebees, and wild bees at SWMREC, CRC, and NWMHRC during each bloom period in 2016. Also listed are the top five plants that supported overall wild bee species richness of all sites combined in 2016. Bolded plant species were attractive at all three sampling locations. Plant species that are marked with an (*) are within the highest statistical grouping using Tukey's HSD (p = 0.05). Species marked with an (`) are considered beekeeper's picks due to specific consideration of their attractiveness to honey bees. Species marked with an (†) were previously tested on mesic soils as part of Tuell et al. (2008).

	Honey bees			Bumblebees			Wild bees			
	SWMREC	CRC	NWMHRC	SWMREC	CRC	NWMHRC	SWMREC	CRC	NWMHRC	Species Richness
_	A. syriaca*	A. syriaca*	A. tuberosa* †	A. syriaca	A. tuberosa †	A. tuberosa †	S. obovatus	A. millefolium*	S. obovatus	C. lanceolata †
y Bloon	A. tuberosa* †	A. tuberosa †	A. syriaca*	A. canescens	L. comiculatus`	T. ohiensis	R. hirta †	C. lanceolata †	C. lanceolata †	A. tuberosa †
	T. ohiensis	L. comiculatus	T. ohiensis*	T. ohiensis	P. hirsutus †	L. comiculatus`	C. palmata	A. syriaca	O. fruticosa	A. syriaca
Earl	R. hirta f	A. millefolium	O. fruticosa	O. fruticosa	P. digitalis	L. perennis	L. comiculatus`	L. comiculatus`	C. rotundifolia	L comiculatus
_	C. palmata	NA	R. carolina	A. tuberosa †	NA	A. syriaca	A. tuberosa †	A. tuberosa †	A. syriaca	P. digitalis
liddle Bloom	P. pilosum*'	P. virginianum`	M. fistulosa*	M. fistulosa*	M. fistulosa*	H. prolificum*	C. micranthos*`	S. nemoralis*	S. integrifolium*	C. micranthos
	H. prolificum*	A. verticillata	P. virginianum`	P. pilosum`	H. prolificum*	M. fistulosa	R. pinnata †	M. fistulosa	M. fistulosa	M. fistulosa
	M. fistulosa	V. stricta	V. stricta	H. prolificum	D. purpurea	D. purpurea	P. pilosum`	S. juncea	E. purpurea	H. occidentalis
	C. micranthos`	M. fistulosa	P. pilosum	C. micranthos'	P. virginianum`	E. yuccifolium	D. purpurea	D. fruticosa	H. occidentalis	E. purpurea
~	E. purpurea	H. prolificum	S. integrifolium	D. purpurea	S. juncea	P. pilosum`	E. purpurea	H. occidentalis	R. hirta †	P. pilosum`
Bloom	O. rigidum*	S. speciosa*	S. speciosa*	C. tripteris*	S. speciosa*	S. speciosa*	C. tripteris*	C. tripteris*	S. sericeum*	C. tripteris
	S. integrifolium	S. terebinthinaceum	O. rigidum	S. integrifolium	S. oolentangiense*	O. rigidum	S. sericeum*	C. micranthos*	S. terebinthinaceum	D. fruticosa
	S.oolentangiense	S. integrifolium	S.oolentangiense	L. aspera	S. integrifolium*	S. oolentangiense	H. strumosus	S. oolentangiense	O. rigidum	S. integrifolium
Late	C. tripteris	S.oolentangiense	C. tripteris	S. terebinthinaceum	S. terebinthinaceum	L. aspera	S. integrifolium	S. integrifolium	C. tripteris	H. strumosus
	H. strumosus	E. purpurea	H. strumosus	S. oolentangiense	C. tripteris	S. terebinthinaceum	H. occidentalis	H. strumosus	L. aspera	S. terebinthinaceum



Figure 2.10. The total abundance of each wild bee family on insectary plants that best support wild bee abundance at SWMREC, CRC, and NWMHRC, during 2016. Only plant species that were in the top 5 plants at two or more sites are included. Plant species are arranged in order of bloom from May through September.



Figure 2.11. The total abundance of each wild bee family on the 15 insectary plants that best support wild bee species richness at SWMREC, CRC, and NWMHRC, during the early, middle, and late bloom periods in 2016. Plant species are arranged in order of bloom from May through September.

Discussion

A common theme in agroecology is to identify solutions to mitigate anthropogenic impacts on beneficial insects in agricultural landscapes (Landis et al. 2000, Losey and Vaughan 2006, Isaacs et al. 2009, Landis 2017). Accordingly, there is growing support for the conservation of pollinators in agricultural systems through the use of habitat enhancements and conservation of natural landscapes (Isaacs et al. 2016). Habitat enhancements within agricultural landscapes are generally designed to provide consistent pollen and nectar resources throughout the entire flight period of pollinator activity. They are particularly important for bees when crops are not in bloom, since they can provide abundant and diverse habitat during temporal gaps in the availability of floral resources (Matheson 1994, Tuell et al. 2008). Identifying and selecting resources, and ultimately designing landscapes to provide plant based resources that support pollinators, will be fundamental in making pollinator conservation efforts most rewarding (Tuell et al. 2008, Isaacs et al. 2009, Landis 2017).

Although habitat restoration can often be unpredictable (Dixon 2009, Sudin 2011, Brudvig 2017), it is one of the primary methods utilized to support pollinator populations (Potts et al. 2010). A working knowledge of plant establishment can help guide plant selection efforts for pollinator conservation, and result in an increased likelihood of successfully reaching desired restoration outcomes. In this study, I first assessed the establishment of insectary plants adapted for dry soils in Michigan. Plant establishment varied considerably between plant species even though plots were similarly managed for weeds. Most plant species increased in abundance over the three-year period of this study. By producing more stems per square meter than other plant species, *Potentilla*

simplex, Coreopsis palmata, Monarda fistulosa, Helianthus occidentalis,

Pycnanthemum pilosum, and *Solidago juncea* showed a high potential for successful establishment from plugs in mixed plantings as part of habitat enhancement programs. The plants used in this study have diverse life histories and may become well established without associated spreading. For example, *Hypericum prolificum* established in each of the 12 plots it was planted in, but it did not increase in overall abundance. Therefore, stem number should not be the only criteria for determining a plant species establishment success. Instead, the information should fall into a broader context of the role that each species plays in supporting some aspect of biodiversity and the services provided by insects (Fiedler and Landis 2008, Wratten et al. 2012). For developing pollinator supportive habitat specifically, identifying plant species that are both highly attractive to bees and establish relatively easily will be more rewarding than maximizing one of these aspects independently.

By assessing the relative attractiveness of 54 plant species to bees, I was able to identify attractive plants that provide consistent floral resources throughout the entire length of bee foraging activity. Of the plant species assessed in this study, a relatively small number showed high levels of attractiveness to pollinators across all pollinator groups, and across sampling regions. In general, honey bees and bumblebees had more similar floral preferences than wild bees did with either group. *Asclepias tuberosa, M. fistulosa, and Symphyotrichum oolentangiense* were in the top five attractive plants for both honey bees and bumblebees at all sites. Regional variation in plant attractiveness to honey bees was likely influenced by hive stocking densities in the landscapes surrounding each site. Although *M. fistulosa* was highly attractive to

bumblebees, this association was primarily driven by the utilization of these flowers by Bombus bimaculatus, whose long tongues are capable of reaching nectar resources at the base of *M. fistulosa*'s long tubular corollas (Cresswell 1990). The only plant species that was shared as a top resource for wild bees at all sites was *Coreopsis tripteris*. Disparities in plant attractiveness may be in part due to variation in the landscapes surrounding each site, as landscape configuration is known to influence bee community assembly (Potts et al. 2005, Brosi et al. 2008, Winfree et al. 2008, Kennedy et al. 2013). The observed significant differences in pollinator communities at each site likely represent individual species with unique life histories and resource requirements (Galen 1999). In general, wild bees can be polylectic or oligolectic, either utilizing a diversity of floral resources or showing increased affinity to particular plant genera or species (Wood 2017). Furthermore, wild bee communities are not strictly organized by the availability of foraging resources- they also need regular access to nesting resources provided by natural habitats (Kremen et al. 2002, Tscharntke et al. 2012) Therefore, differences in plant attractiveness to pollinator taxa, and between sampling locations, is likely due to a combination of both landscape and local scale effects on the pollinator communities at each site. Future wildflower selection to support bees in agricultural systems will benefit from additional knowledge on the surrounding landscape context as well as the existing pollinator community.

The results of this study are similar to previous findings that demonstrated variation in the relative attractiveness of native plants to managed and unmanaged bees (Tuell et al. 2008, Garbuzov et al. 2014) as well as other insect groups such as natural enemies (Feidler and Landis 2007). A set of plant species used in this study were

previously screened for pollinator attractiveness in Tuell et al. (2008). In both studies, *Solidago speciosa* was considered a highly attractive plant to honey bees. In Tuell et al. (2008), the authors did not identify *Asclepias tuberosa* as an attractive plant species to any of the pollinator groups assessed. In this study *A. tuberosa* was attractive to honey bees at all three sites, suggesting that there may be temporal variability in patterns of plant attractiveness, which is uncaptured in relatively short research projects such as these. *A. tuberosa* was also highly attractive to wild bees in the current study. In both studies, wild bees were attracted to *Coreopsis lanceolata*, and in this study, *C. lanceolata* was identified as the plant that best supports pollinator species richness during the early bloom period (May-Early July).

Prior to this study, a subset of plant species was chosen in collaboration with the Michigan Commercial Beekeepers Association to specifically assess plant attractiveness to honey bees. Of these, *Pycnanthemum pilosum* and *Pycnanthemum virginianum* were the only species found to be consistently attractive to honey bees. Neither *Lotus* corniculatus nor *Centaurea stoebe micranthos* were found to be attractive to honey bees at more than a single site. Instead, native alternatives attracted more honey bees per sample, and thus may be better at supporting honey bee populations as part of habitat management programs. *C. stoebe micranthos*, although listed as a noxious weed by the USDA, is commonly utilized by beekeepers as an important nectar resource for honey bees. This species can dominate landscapes and provide an abundant pulse of resources while decreasing the season long availability of native flowering plants (Carson et al. 2015). Replacing populations of *C. stoebe micranthos*

with potentially more attractive native habitat may provide a win-win situation for beekeepers and conservation land managers.

The data generated in this study can be used to aid the development of regionally specific plant mixes to support bees and other beneficial insects in agricultural landscapes across the Great Lakes region. One example of a resource that already exists is a 2015 publication by the Xerces Society for Invertebrate Conservation (Adamson et al. 2015). Of the 24 plant species included in a pollinator list developed by Xerces, 13 of them were used in this study. Only five of these were consistently found to be highly attractive to honey bees, bumblebees, or wild bees. These include *C. lanceolata, A. tuberosa, E. purpurea, M. fistulosa, S. speciosa.* The remaining plant species included in the publication and assessed in this current study were either not in the top five attractive plant species during any bloom period, or only attractive at one site and for single pollinator taxa. Incorporating the results from this study into the development of future plant lists to support pollinators will allow for the optimization of these lists to support particular pollinator groups or geographic regions.

By combining the establishment results with relative attractiveness of study plants to different bee taxa, future plant mixes can be optimized to target particular bee families, genera, or species. These optimized plant mixes could be designed to support important crop pollinators of different cropping systems, or designed to target rare pollinator species. Importantly, the current work paves the way for highly tailored plant mixes that could be adapted to fit the needs of different land management programs. Once these plant mixes have been developed, it would be useful to assess how well individual plant species establish from seed in a real world agricultural setting. In order

to generalize findings to other cropping systems, a broader understanding of the flower traits that predict pollinator visitation needs to be addressed. Although the link between plant diversity and pollinator diversity is well established (Thomas 1981, Potts et al. 2003, Williams et al. 2015), identifying these important flower traits will provide insights into plant selection in regions where plant attractiveness has not yet been assessed.

Finding ways to optimize resource integration into the context of the farm requires a coordinated approach of research, knowledge transfer, and financial support for application (Isaacs et al. 2016). A first step towards successful conservation of wild bees in farm lands will depend on determining and selecting resources that best support targeted bee communities in particularly continental regions or cropping systems. With the ultimate goal of improving the sustainability of crop pollination within intensified cropping systems, land managers and growers alike will continue to seek out new opportunities to maximize the productivity of their fields. Incorporating wildflower habitat into a larger landscape management strategy is, and will continue to prove to be an effective method. CHAPTER 3:

FLOWER TRAITS ASSOCIATED WITH FLOWER VISTATION PATTERNS OF WILD AND MANAGED POLLINATORS

Introduction

Land-use intensification in many agricultural landscapes reduces the availability and diversity of floral resources necessary to support pollinator fitness (Kremen et al. 2007, Winfree et al. 2009, Garibaldi et al. 2011, Kennedy et al. 2013, Williams et al. 2015). With growing concern surrounding pollinator declines (Potts et al. 2010, Goulson et al. 2015), and the implications for the stability of yields from insect pollinated food crops, increased attention has been paid to developing and implementing environmental strategies that support the pollination services provided by bees (Isaacs et al. 2009, Williams et al. 2015, Isaacs et al. 2016). One conservation strategy that supports bees is habitat management, which can include the incorporation of flowering habitat into agricultural landscapes, thus providing bees with a variety of pollen and nectar sources (Isaacs et al. 2016, Landis 2017). These nutritional resources are often scarce in agricultural landscapes, or are only abundant during a short time period of crop bloom. As pollen and nectar provide bees' primary dietary requirements, their availability in the environment is crucial to the long term stability of bee populations (Michener 2000, Brodschneider and Crailsheim 2010). Similarly, the ability to attract bees and other pollinators is essential for plants that depend on insect visitors for pollination (Conner and Rush 1995). This mutual benefit of reproduction has led to a diversity of pollinator syndromes, including both generalization and specialization in plant-pollinator interactions (Johnson and Steiner 2000, Fenster et al. 2004).

Foraging pollinators rely on the presence of plant based cues to guide themselves to plant resources. Multiple flower traits are known to influence visitation patterns by bees (Mitchell et al. 2004, Brunet et al. 2015). Floral area has generally

been considered the strongest and most consistent predictor of bee abundance and species richness, operating from the plant to the landscape level (Conner and Rush 1995, Potts et al. 2003, Westphal et al. 2003, Tuell et al. 2008, Blaauw and Issacs 2012, Kennedy et al. 2013). Additional traits can influence bee attraction, such as flower color or hue (Gumbert 2000, Reverte et al. 2016, Russell et al. 2016, Bauer et al. 2017), scent (Pike 2015, Junker and Parachnowitsch 2015), and the availability/quality of pollen and nectar resources (Potts et al. 2003, Nicholls and Hemple de Ibarra 2016, Vaudo et al. 2016, Russell et al. 2017). The influence of pollen and nectar on bee visitation has become a hot topic within pollinator conservation planning recently, due to increased understanding of the effects of pollen/nectar nutritional quality on bee health (Roulston and Cane 2000, Roulston and Cane 2002, Vaudo et al. 2015), and the foraging behaviors of bees (Potts et al. 2003, Cook et al. 2003, Vaudo et al. 2014). Quite often, bees forage for pollen and nectar strategically to maximize nutritional intake for themselves and their offspring (Cnaani et al. 2006, Nicolson 2011, Vaudo et al. 2015, Somme et al. 2015, Vaudo et al. 2016).

Instead of working independently to attract pollinators, flower traits can often synergize to communicate resource availability (Leonard and Masek 2014). Plant species that share particular traits can either overlap in the pollinator community that they attract (Bosch et al. 1997, Anderson and Johnson 2009), or attract unique pollinators (Bauer et al. 2017), suggesting that the importance of particular plant traits for influencing pollinator response may be system or taxa dependent. Although plant species can vary greatly in phenotypes, chemistry, and timing of resource availability, flower traits on an individual plant can be inherently correlated (Junker and

Parachnowitsch 2015). For example, multiple studies have found relationships between floral morphology and pollen production. Stanton and Preston (1988) found that pollen production is correlated with corolla size in wild radish (*Raphanus sativus*), and Hicks et al. (2016) determined that pollen volume can be predicted by floral morphology in some species in *Asteraceae*. These results suggest that flowering plants may primarily use visual cues to indicate the presence of nutritional resources to foraging bees.

Because there is wide variation among plant species in their floral morphology and resource quality, they vary significantly in their attractiveness to pollinators (Memmott 1999). A few studies have compared different flowering plant species for their attractiveness to bees and other pollinators (Frankie et al. 2005, Tuell et al. 2008, Garbuzov et al. 2014, Robson 2014). In these studies, comparisons of plant attractiveness, measured as the number of flower visits by bees and other pollinators, demonstrates variation in plant attractiveness among co-blooming plant species. For example, out of 46 screened plant species, Tuell et al. (2008) identified a total of six plant species highly attractive to honey bees and nine plant species highly attractive to wild bees, where total bee abundance varied between plant species by as much as 250 visits during 5 minute samples. In a similar study, I assessed the relative attractiveness of 54 plant species adapted to coarse-textured soils in Michigan, and found that patterns of bee visitation varied considerably among plant species (Chapter 2). Furthermore, bee taxa differed in their "preferred" plant species, providing further evidence that the relationships between pollinator taxa and plant traits are taxa specific.

Importantly, studies that evaluate relative plant attractiveness to pollinators generate valuable lists of pollinator supportive plant species that are then widely

distributed and often referenced, as land managers develop and implement pollinator friendly habitats (e.g. Fiedler et al. 2007, Adamson et al. 2015). However, because they are restricted in geographic applicability and tend to include a relatively small number of studied plant species, it is still challenging for conservation planners to apply scientific findings to new geographic locations where a different suite of plant/pollinator species dominate, and weather, soil, and temperature patterns vary. Additionally, these studies do not assess the underlying mechanisms that are responsible for the observed variation in plant attractiveness, such as variability in flower trait characteristics. This information would be useful for plant selection as part of similar studies in other regions of the world. In order to generalize these findings for application to a broader audience, it may be more appropriate to measure the flower traits that influence visitation patterns of bees.

In this chapter, I build on Chapter 2 by analyzing whether flower traits can be used as indicators of pollinator abundance. I do this by determining the relationships between plant trait characteristics and the abundance of different pollinator taxa measured at mono-specific plantings of different plant species. Specifically, I ask: 1) are observable flower traits correlated at the plant level, 2) do pollinator groups show variation in patterns of visitation to plants, 3) do pollinator family level taxa respond independently to observed flower traits, and 4) what role does pollen availability play in the structuring of the pollinator community?

Materials and Methods

In June 2014, 54 plant species (Table 3.1) were planted in a grid pattern using a randomized complete block design at three locations within the MSU research station network: 1) Southwest Michigan (Southwest Michigan Research and Extension Center (SWMREC), Berrien County, MI; 2) Mid-Michigan (Clarksville Research Center (CRC), lonia County, MI; and 3) Northwest Michigan (Northwest Michigan Horticultural Research Center (NWMHRC), Leelanau County, MI. Each plant species was planted as a set of three individual plugs in a single meter square plot and there were four replicate blocks per research location. All plants used in this study were obtained from Wildtype Design or Seeds in Mason, MI and Hidden Savanna Nursery in Kalamazoo, MI. To reduce the influence of weeds on data collection, the plots were regularly maintained by removing weeds from within each meter square plot, and by mowing the grassy matrix between plots.

Table 3.1 . Plant species used in study to assess the relationships between flower traits
and pollinator visitation. Each species was planted at SWMREC, CRC, and NWMHRC.
Sites consisted of 4 replicated blocks of 1m ² common garden plantings. Data
measurements were taken from each plant species for a 3-week period of peak bloom.

Scientific Name	Common Name	<u>Family</u>	Native	<u>Life Habit</u>
Achillea millefolium	Yarrow	Asteraceae	Yes	Perennial
Amorpha canescens	Lead plant	Fabaceae	Yes	Perennial
Asclepias syriaca	Common milkweed	Asclepiadaceae	Yes	Perennial
Asclepias tuberosa	Butterfly milkweed	Asclepiadaceae	Yes	Perennial
Asclepias verticillata	Whorled milkweed	Asclepiadaceae	Yes	Perennial
Baptisia alba var. macrophylla	White wild indigo	Fabaceae	Yes	Perennial
Campanula rotundifolia	Harebell	Capanulaceae	Yes	Perennial
Ceanothus americanus	New jersey tea	Rhamnaceae	Yes	Perennial
Centaurea stoebe micranthos	Spotted knapweed	Asteraceae	No	Perennial
Chamerion angustifolium	Fireweed	Onagraceae	Yes	Perennial
Coreopsis lanceolata	Lance-leaved coreopsis	Asteraceae	Yes	Perennial

Table 3.1 (cont'd)

Coreopsis palmata Coreopsis tripteris Dasiphora fruticosa Dalea purpurea Echinacea purpurea Eryngium yuccifolium Helianthus occidentalis Heuchera richardsonii Helianthus strumosus Hieracium gronovii Hypericum prolificum Lespedeza capitata Lespedeza hirta Liatris aspera Liatris cylindracea Lotus corniculatus L. Lupinus perennis Monarda fistulosa Monarda punctata Oenothera biennis Oenothera fruticosa Oligoneuron rigidum Penstemon digitalis Penstemon hirsutus Potentilla arguta Potentilla simplex Pycnanthemum pilosum Pycnanthemum virginianum Ratibida pinnata Rhus copallinum Rosa carolina Rudbeckia hirta Senecio obovatus Silphium integrifolium Silphium laciniatum Silphium terebinthinaceum Solidago juncea Solidago nemoralis Solidago speciosa Symphyotrichum oolentangiense Symphyotrichum sericeum Tradescantia ohiensis Verbena stricta

Prairie coreopsis Tall coreopsis Shrubby cinquefoil Purple prairie clover Purple coneflower Rattlesnake master Western sunflower Prairie alumroot Pale-leaved sunflower Queendevil Shrubby St. John's wort Round-headed bushclover Hairy bush clover Rough blazing star Cylindrical blazing star Birdsfoot trefoil Wild lupine Wild bergamot Spotted bee balm Common evening primrose Sundrops Stiff goldenrod Foxglove beardtongue Hairy penstemon Prairie cinquefoil Common cinquefoil Hairy mountain mint Mountain mint Yellow coneflower Winged sumac Pasture rose Black-eyed susan Round-leaved ragwort Rosin weed Compass plant Prairie-dock Early goldenrod Gray goldenrod Showy goldenrod Sky blue aster Silky aster Common spiderwort Hoary vervain

Asteraceae Yes Perennial Perennial Asteraceae Yes Perennial Rosaceae Yes Fabaceae Yes Perennial Asteraceae Yes Perennial Apiaceae Yes Perennial Asteraceae Yes Perennial Saxifragaceae Yes Perennial Asteraceae Yes Perennial Asteraceae Yes Perennial Clusiaceae Yes Perennial Fabaceae Yes Perennial Fabaceae Perennial Yes Asteraceae Yes Perennial Asteraceae Yes Perennial Fabaceae No Perennial Fabaceae Yes Perennial Lamiaceae Yes Perennial Lamiaceae Yes Perennial Perennial Onagraceae Yes Onagraceae Yes Perennial Perennial Asteraceae Yes Plantaginaceae Yes Perennial Plantaginaceae Yes Perennial Perennial Rosaceae Yes Rosaceae Yes Perennial Yes Perennial Lamiaceae Lamiaceae Yes Perennial Asteraceae Yes Perennial Anacardiaceae Yes Shrub Shrub Rosaceae Yes Asteraceae Yes Perennial Yes Perennial Asteraceae Perennial Asteraceae Yes Yes Perennial Asteraceae Asteraceae Yes Perennial Yes Perennial Asteraceae Asteraceae Yes Perennial Asteraceae Yes Perennial Asteraceae Yes Perennial Asteraceae Yes Perennial Perennial Commelinaceae Yes Verbenaceae Yes Perennial

Plant data collection

In 2015 and 2016, each meter square plot across all three sites was visited weekly to assess plant phenology and flower production. When a plant species reached peak bloom (defined as the three-week period of peak flower production averaged across the 4 representative plots at each site), flower trait measurements were conducted. The number of flowers, floral area per meter square, height of the tallest flower, and corolla width were determined at each site for each plant species evaluated. Photos were taken with a ruler placed adjacent to the flower(s) for reference, and at different angles. Captured photos were processed by converting flower images into white space (Knoll 2000) using Adobe Photoshop 6.0 software so that individual flower corolla width and floral area could be determined using ImageJ software (Abramoff et al. 2004). The average area of an individual flowering unit was multiplied by the number of units for each plant species to estimate total floral area within each meter square plot. In 2016 at CRC only, the quantity of pollen produced by a single flower (see below), and flower corolla chroma/hue were also estimated for all species.

To measure pollen production in the flowers of each plant species, clusters of flowers were covered using insect exclusion bags to prohibit bee visitation one day prior to insect sampling. After 24 hours, five newly opened flowers were incised and placed in a solution of 60% ethanol and water for later processing. For plant species with very small flowers (< 5mm in diameter), partial inflorescences were placed in the ethanol solution. Pollen was isolated from 5, 10, or 20 individually sampled flowers by 1) removing all stamens and placing them in a 60% ethanol solution and 2) lightly dislodging pollen from anthers using a pestle and mortar. Samples were then carefully

filtered through a mesh screen to remove plant material, centrifuged at 5000rpm for 1 minute to pelletize pollen, and decanted to remove ethanol solution from pelletized pollen sample. 50ul of a 60% ethanol solution was then added to each sample and lightly homogenized. A 5ul subsample of this mixture was placed on a slide with fuschin gel for further processing. The number of pollen grains per 5, 10, or 20 flowers for each plant species was estimated by counting total pollen on 25% of each slide and multiplying by 40 to account for the full 50ul sample. To calculate pollen per unit floral area and to extrapolate to the plot level, the resulting number was multiplied by the total number of flowers available in each meter square plot divided by the number of flowers used for the sample. Hue and chroma of field collected flowers with intact stamens were analyzed in the lab using an S2000 fiber optic spectrometer (PX2 pulsed xenon light source, Ocean Optics, Dunedin, FL), which is capable of determining floral reflectance in wavelengths 400-700 nm. All flowers were collected from CRC, with the exception of one plant species, *Pycnanthemum pilosum*, which was collected from SWMREC.

Bee data collection

At each site during peak bloom, all non-*Apis* pollinators were collected from flowers during a five-minute insect sample, conducted once per week on each meter square plot of plants in flower. Samples were collected using a modified hand-held vacuum (model: 2820GA, Bioquip products Inc, Rancho Domingo, CA) with a clear extension tube in order to minimize the disturbance to pollinators. Honey bee were not collected, and visits were counted and recorded for each sample. Specimens collected

from plots were identified to species level using online keys (Packer et al. 2007, www.discoverlife.org) and with the assistance of Dr. Jason Gibbs.

Data analysis

Individual simple linear regression models were used to determine the relationships between the average number of visits per sample of honey bees, bumblebees, wild bees, and hoverflies to study plants. Normality of response variables were first assessed using a Shapiro-Wilk Normality Test (R, version: 3.3.1, shapiro.test). Data did not fit a normal distribution so response variables were log (x + 1) transformed to meet normality assumptions. Mean values per plot were determined for the number of flowers, floral area, flower height, corolla width, flower chroma and flower hue for each plant species assessed in this study. Although chroma and hue were only collected at CRC, averaged data were assigned to plant species at each site for analysis. Pearson correlation coefficients were conducted to assess for autocorrelation among collected plant trait data using Pearson correlation tests. This information was then visualized using corrgrams (R package corrgram version 1.12). If two traits were correlated at a Pearson correlation of above 0.49 (Fiedler and Landis 2007), the trait expected to have the least biological relevance was removed from further analyses. Multiple linear regression was used to determine if the abundance of 4 main pollinator groups (honey bees, bumblebees, non-Bombus wild bees, and hoverflies) as well as bee species richness, varied with any of the floral traits collected over the two-year sampling period. A second multiple linear regression model was used to determine if bee abundance per sample of any of the five representative bee families (Andrenidae,

Apidae, *Halictidae*, *Colletidae*, and *Megachilidae*) varied with any of the plant traits measured. All abundance data were log (x+1) transformed prior to analysis to generate normally distributed response variables. Multiple linear regression models were assessed post-hoc for autocorrelation among trait data using variance inflation factors (VIFs). No single trait had a higher VIF value than 2.

A third multiple linear regression model using only data collected at CRC in 2016 was used to determine if the abundance of honey bees, bumblebees, non-*Bombus* wild bees, hoverflies, or bee species richness varied with any of the floral traits collected. Prior to analysis, Pearson correlations between plant traits were assessed using the additional plant trait data: pollen abundance per flower and pollen abundance per plot. Corolla width and pollen per flower were found to be highly correlated. Additionally, pollen per plot was correlated with total floral area, flower height, and pollen per flower. Since the purpose of this analysis was to assess the influence of plot level pollen availability on pollinator visitation, floral area, flower height, and pollen per flower were removed from the multiple linear regression analysis. Abundance data was log (x+1) transformed to generate normally distributed response variables. Again, VIFs were used post-hoc to assess variance inflation.

Principal component analysis (PCA) does not require an assumption of independence between variables, and instead creates a set of linearly uncorrelated variables based on collected data (i.e. collinear variables can be assessed together in the same model). Additionally, PCA allows for visual interpretation of how trait data might uniquely influence dissimilar components of a community. Because a subset of flower trait characteristics were found to be correlated using Pearson correlation tests,

PCA was used to assess the relationships between collected flower traits and wild bee data and included auto-correlated flower traits. In the first analysis, a biplot was created with the Bray-Curtis dissimilarity matrix based on wild bee community data collected from all sites and during 2015 and 2016 (R package vegan, version 1.12). Flower trait data was then fitted onto this plot in order to assess the relative influence of different traits on wild bee community structure and the overall abundance of five wild bee families: Megachilidae, Apidae, Andrenidae, Collectidae, and Halictidae. In general, the length and direction of each environmentally fitted arrows represent the strength and direction of pull of each flower trait. Permutational analysis of variance (PERMANOVA, function: adonis, R package vegan) was used to analyze differences in the wild bee community based on environmental fitting of collected flower traits: floral area, number of flowers, flower height, corolla width, flower chroma, and flower hue. In a second analysis, the plot level pollen abundance data collected at CRC was included in a similar PCA framework. Pollen abundance data collected at CRC in 2016 were considered to be consistent across sites for 3 reasons: 1) All plant species used in the study have identical origins, 2) sites were chosen because of their soil type (sandy soils with low moisture retention capabilities), and 3) each plot was similarly maintained in 2015-2016. After plotting bee genera data and environmental fitting of plant trait data, the three plant traits with the highest PCA loading values were selected for principal component regression analysis of the relationship between PC factor 1 and the total number of wild bees collected on each plant species at each site.

Results

Correlations among plant traits

An initial test for correlation among collected flower traits from all sites, using a Pearson correlation cutoff value of 0.49, revealed that only floral chroma and floral hue were correlated (r = 0.55) (Figure 3.1). At CRC in 2016, similar tests for correlations among flower traits were conducted, with additional flower trait measurements including the amount of pollen per flower, and the amount of pollen per plot (Figure 3.2). Again floral chroma and floral hue were highly correlated (r = 0.54). Additionally, pollen per flower was positively correlated with flower height (r = 0.52) and corolla width (r = 0.81), and pollen per plot was correlated with flower height (r = 0.55) and floral area (Figure 3.3, r = 0.69).



Figure 3.1. Corrgram of flower trait data collected on 54 potential insectary plants at SWMREC, CRC, and NWMHRC in 2015 and 2016. Pie charts indicate the strength of the correlation between the two flower traits. The numbers inside of each pie chart represents the strength of the correlation using Pearson rank correlation tests. For trait pairs with Pearson correlation values above 0.49, the least biologically relevant trait was removed from multiple linear regression analysis.



Figure 3.2. Corrgram of flower trait data collected on 54 potential insectary plants at CRC in 2016. Pie charts indicate the strength of the correlation between the two flower traits. Correlation values were determined using Pearson rank correlation tests. Only Pearson correlations significant at r = 0.49 are shown. For trait pairs with Pearson correlation values above 0.49, the least biologically relevant trait was removed from multiple linear regression analysis.



Figure 3.3. Mean total floral area versus the mean number of pollen grains estimated per plant species at CRC in 2016. Values are based on a meter square plot. The dotted line represents the best fit line between the two variables using simple linear regression.

Linear regression

The visitation rates of honey bees and bumblebees on study plants were positively correlated over the course of this study (F = 53.67, $r^2 = 0.50$, p < 0.001), as were the visitation rates of wild bees and hoverflies (F = 20.65, $r^2 = 0.27$, p < 0.001). Honey bees did not have similar visitation rates to study plants as wild bees (F = 2.64, r^2 = 0.03, p = 0.11) or hoverflies (F = 0.37, $r^2 = 0.01$, p = 0.54). Similarly, bumblebee visitation to study plants was not correlated with wild bee visitation F = 2.64, $r^2 = 0.03$, p = 0.11), or hoverfly visitation F = 0.47, $r^2 = 0.01$, p = 0.49) (Figure 3.4).



Figure 3.4. Comparison of $(\log x+1)$ visitation rates of pollinator groups on study plant species. Each point represents a single plant species and the average number of pollinators visiting that plant species for each pollinator group assessed.

flower trait correlation assessments were used to inform parameter selection for multiple linear regression analysis. Results from multiple linear regression models revealed that different bee taxa have varying responses to flower traits (Table 3.2). The overall model explained 16% of the variation in honey bee abundance, 22% of bumblebee abundance, 24% of non-*Bombus* wild bee abundance, 53% of hoverfly abundance, and 28% of the variation in wild bee species richness. For these relationships, the floral area parameter was positive and significant for the abundance of all pollinator groupings except for honey bees (bumblebees: $F_{5,35} = 3.3$, p = 0.032; non-*Bombus* wild bees: $F_{5,35} = 3.6$, p = 0.007; hoverflies: $F_{5,35} = 9.5$, p = 0.002; species

richness: $F_{5,35} = 4.1$, p = 0.004; honey bees: $F_{5,35} = 2.47$, p = 0.317). Increased honey bee, bumblebee, and hoverfly abundances were predicted by floral height (honey bees: p = 0.015, bumblebees: p = 0.018, hoverflies: p = 0.03). Additionally, increased hoverfly abundance was predicted by the number of flowers on a plant (p = 0.001).

The overall model to assess the relationships between different pollinator families and flower traits demonstrated family level variation in the importance of different trait parameters (Table 3.2). The model explained 13% of the variation in *Andrenidae* abundance, 31% of the variation in non-*Apis Apidae* abundance, and 14% of the variation in *Halictidae* abundance. The floral area parameter was significant for each of these three bee families (*Andrenidae*: $F_{5,35} = 4.33$, p < 0.01; non-*Apis Apidae*: $F_{5,35} =$ 11.42, p < 0.01; *Halictidae*: $F_{5,35} = 4.61$, p < 0.01), meaning that an increase in floral area predicts an associated increase in the abundance of visiting bees. Increased abundances of *Megachilidae* and *Colletidae* were not predicted by floral area. Instead, *Colletidae* abundance was predicted by corolla width ($F_{5,35} = 2.57$, p = 0.04), and the abundance of Megachilidae was predicted by flower height ($F_{5,35} = 2.09$, p = 0.05).

A third model was used that replaced floral area with pollen availability and used data from CRC 2016 only (Table 3.3). This model explained 23% of the variation in wild bee abundance, 15% of the variation in hoverfly abundance, and 10% of the variation in wild bee species richness. None of the flower trait parameters used in the model explained the abundance of bumblebees or wild bee species richness. Flower height was a significant predictor of increased honey bee abundance ($F_{5,35} = 1.91$, p = 0.02). Pollen availability was a significant predictor of increased wild bee and hoverfly abundances (wild bees: $F_{5,35} = 4.05$, p = 0.01; hoverflies: $F_{5,35} = 2.79$, p = 0.02).

Table 3.2. Results from multiple linear regression analysis to assess the influence of five flower traits on the log transformed abundance (log x + 1) and diversity of pollinators during 2015 and 2016. Significant parameter probability values at p<0.05 are marked with an (*). Wild bee group does not include the genus *Bombus*.

	Overall Model		Flower trait parameter estimate probabilities					
Pollinator group	r²	F _{5,35}	Р	floral area	number of flowers	flower height	corolla width	hue
Honey bees	0.16	2.47	0.05	0.32	0.88	0.02*	0.17	0.90
Bumblebees	0.22	3.28	0.02*	0.03*	0.56	0.02*	0.18	0.09
Hoverflies	0.53	9.84	<0.01*	<0.01*	<0.01*	0.03*	0.43	0.85
Wild bees	0.24	3.56	0.01*	<0.01*	0.88	0.51	0.97	0.70
Andrenidae	0.13	4.33	<0.01*	<0.01*	0.55	0.90	0.09	0.07
Non-Apis Apidae	0.31	11.42	<0.01*	<0.01*	0.70	<0.01*	0.51	0.03*
Colletidae	0.06	2.57	0.03*	0.52	0.40	0.43	0.04*	0.18
Halictidae	0.14	4.61	<0.01*	<0.01*	0.49	0.96	0.35	0.84
Megachilidae	0.05	2.09	0.07	0.07	0.68	0.05*	0.42	0.12
Species richness	0.28	4.06	0.01*	<0.01*	0.25	0.95	0.66	0.48

Table 3.3. Results from multiple linear regression analysis to assess the influence of five flower traits on the log transformed abundance (log x+1) pollinator groups and diversity of wild bees during 2016 at CRC only. Significant parameter probability values at p<0.05 are marked with an (*).

	Overall Model			Flower trait parameter estimate probabilities			
Pollinator group	r²	F _{5,35}	Р	pollen availability	number of flowers	corolla width	hue
Honey bees	0.08	1.91	0.08	0.31	0.02*	0.38	0.23
Bumblebees	-0.06	0.39	0.82	0.51	0.68	0.69	0.41
Hoverflies	0.15	2.79	0.04*	0.02*	0.31	0.21	0.34
All wild bees	0.23	4.05	0.01*	0.01*	0.18	0.73	0.67
Species richness	0.09	1.93	0.13	0.48	0.21	0.07	0.78

Wild bee community response to floral traits

Principal component analyses support the results of multiple linear regressions. The two flower trait loading factors that had the strongest effect on the family level pollinator community were floral area (PC1 = 0.52) and flower height (PC1 = 0.23) (Table 3.4, Figure 3.5). In this analysis, the wild bee community varied significantly along the axes of the following traits: (floral area: $F_{1,104} = 8.06$, p = 0.01; flower height: $F_{1,104} = 2.69$, p = 0.05; corolla width: $F_{1,104} = 2.28$, p = 0.05; flower chroma: $F_{1,104} = 2.75$, p = 0.01, PERMANOVA) (Table 3.5). When including the additional flower trait, pollen abundance, the loading factors that had the strongest effects on the pollinator community were floral area (PC1 = 0.48), flower height (PC1 = 0.27), and pollen abundance (PC1 = 0.50) (Figure 3.5) (Table 3.6). Using these three components in a regression analysis, there was a significant linear relationship between PCA factor 1 and wild bee abundance (log x + 1). Therefore, wild bees respond positively to a combination of increased floral area, flower height, and pollen abundance (t=20.70, p<0.001) of plant species assessed. This relationship explained 69% of the variation in the total number of wild bees collected per plant species.



Figure 3.5. Principal component plot of PC1 and PC2 in the PCA of wild bee families collected from study plants at SWMREC, CRC, and NWMHRC. The length and direction of arrows represent that strength and direction of flower trait effect on the wild bee community. **Key to plant trait codes**: t1 = number of flowers, t2 = floral area, t3 = flower height, t4 = corolla width, t5 = flower chroma, t6 = flower hue.

Table 3.4. Principal component loading factors for flower characteristics used to assess wild bee family level response to flower traits for all sites. The magnitude and sign of each PCA loading number represent the strength of and direction of the relationship between flower traits and the wild bee community.

		PCA Loading Factor		
Trait ID	Flower trait	PC1	PC2	
t1	number of flowers	0.11	-0.06	
t2	floral area	0.52	0.13	
t3	flower height	0.23	-0.02	
t4	corolla width	0.04	0.09	
t5	flower chroma	0.10	0.05	
t6	flower hue	0.05	0.07	

Table 3.5. Results from a PERMANOVA assessing the relationship between pollinator community structure and measured flower traits at all sites in 2015 and 2016. Community structure varies significantly along axes of traits tested.

Factor	df	F-value	r²	p-value
number of flowers	1	1.75	0.01	0.08
floral area	1	8.06	0.07	0.01*
flower height	1	2.69	0.02	0.05*
corolla width	1	2.28	0.02	0.05*
flower chroma	1	2.75	0.02	0.01*
flower hue	1	1.12	0.01	0.34

Table 3.6. Principal component loading factors for flower characteristics used to assess wild bee community response to flower traits for all sites. The magnitude and sign of each PCA loading number represent the strength of and direction of the relationship between floral traits and the wild bee community. *Pollen availability was only collected at CRC.

		PCA Loading Factor	
Trait ID	Flower trait	PC1	PC2
t1	number of flowers	0.11	0.07
t2	floral area	0.48	-0.03
t3	flower height	0.27	-0.02
t4	corolla width	-0.01	-0.07
t5	flower chroma	0.16	0.26
t6	flower hue	-0.02	-0.26
t7	t7 pollen abundance		0.30



Figure 3.6. Principal component analysis of flower traits and the wild bee genera community visiting a common garden experiment of 54 plant species. Collected bee genera are represented by their genus names. The length and direction of arrows represent the strength and direction of response to flower traits by the wild bee community. **Key to plant trait codes**: t1 = number of flowers, t2 = floral area, t3 = flower height, t4 = corolla width, t5 = flower chroma, t6 = flower hue, t7 = pollen abundance.

Discussion

Flowers are complex reproductive structures that vary considerably in their phenotypes, including the timing, composition, and magnitude of resource availability (Junker and Parachnowitsch 2015). Pollinators rely on floral cues for guidance to the pollen and nectar resources provided by flowers. Independent studies have demonstrated that multiple flower traits can mediate pollinator attraction. These include floral area (Mitchell et al. 2004, Ishii et al. 2008, Tuell et al. 2008), flower color (Reverte et al. 2016), and the size of pollen rewards (Brunet et al. 2015). Fewer studies have assessed how floral traits interact at the plant level, or the relative importance of measured floral traits for attraction of different pollinator groups (Hegland et al. 2005, Hirota et al. 2015).

In this study, the relationships between collected flower traits were assessed by determining Pearson correlation coefficients for each possible pair of plant species. Flower traits showed surprising low levels of correlation. This is similar to the findings of Fiedler and Landis (2007), where similar plant characteristics measured to assess natural enemy visitation pattern to native plants were found to be un-correlated at r = 0.49. When sites were combined in the present study, the single flower trait pair that had a Pearson correlation coefficient greater than 0.49 was corolla hue and chroma, suggesting that darker colored flowers have a higher degree of saturation. When trait correlations were assessed again using data collected at CRC in 2016, both pollen per flower and total pollen abundance were correlated with multiple flower traits. At the flower level, pollen per flower was correlated with flower height and corolla width. At the
general, plants that are taller, and with larger floral displays, contain more pollen at both the flower and plant levels. These results corroborate the findings of Hicks et al. (2016), which showed that the volume of pollen retained within a flower can be predicted by flower size and morphology. For foraging bees, these traits relationships may be of particular importance due to their use of floral area as a primary mechanism for guidance to resources in their surrounding environment (Ishii et al. 2008).

In the broad level multiple linear regression analysis (Table 3.2), each taxa of pollinators showed distinct responses to flower trait parameters. Most commonly, floral area was found to be a strong predictor of wild bee species richness, as well as the abundances of all other pollinator groups except for honey bees. Honey bees, as well as bumblebees, did respond significantly to flower height. The lack of a relationship between honey bee visitation and floral area is likely attributed to the difference in life histories of honey bees compared to wild bees. Individual honey bees receive information about resources in their environment from relatives in the same hive, while wild bees depend entirely on environmental cues to locate these same resources. Because of this type of information exchange in honey bees, it is possible that foragers are searching out larger patches of floral resources within their foraging environment. Since this study was designed to assess patterns of visitation on 1m² plantings, it may have overlooked foraging decisions made concerning larger patches of floral resources in the landscapes surrounding each research site. The abundance of hoverflies (Family: Syrphidae), whose larvae are common predators of aphids and other phytophagous insects and as adults require pollen and nectar, was predicted by floral height and the number of flowers available. Interestingly, the responses of hoverflies to flower traits

was more similar to that of wild bees than other bee taxa, suggesting that plant resources to support these two pollinator groups may overlap. No broad level pollinator taxa responded to corolla width or floral hue.

Multiple linear regressions at the level of the wild bee family provided more clarity on the relationships between pollinator abundance and flower trait characteristics. Importantly, bee families showed some unique relationships with flower trait parameters. Wild bees have diverse foraging strategies, nutritional requirements, and morphological characteristics for collecting pollen and nectar (Michener 2000), which can influence the observable variation in the relationships between flower trait and bee visitation responses. The abundance of bees from Andrenidae, non-Apis Apidae, and Halictidae were all related to floral area in this study, while the abundance of Colletidae was predicted by corolla width of an individual flower and the abundance of Megachilidae was predicted by flower height. Additionally, non-Apis Apidae abundances were also predicted by flower hue. These family level differences in bee response to varying flower traits is advantageous for maintaining complexity of the plant-bee community (Schiestl and Johnson 2013). By reducing niche overlapping between bees, there is less competition for floral resources, which can allow both generalist and specialist bees to persist in the same environment (von Felton et al. 2009, Venjakob et al. 2016).

Pollen availability performed nearly as well as floral area in describing broad scale pollinator taxa visitation, being related to visitation of non-*Bombus* wild bees, and hoverflies. Pollen availability may compliment floral area, where floral area attracts pollinators via visual cues from a distance (Karron and Mitchell 2012) while pollen

availability influences associated learning and handling time of floral resources (Harder 1983, Wilmsen et al. 2017, Russel et al. 2017). Interestingly, recent evidence suggests that the predictability of flower-resource and flower-bee relationships cease to exist when examining ornamental plants as opposed to their native counterparts (Garbuzov et al. 2017). Instead, Garbuzov et al. 2017 found that ornamental plants (in which pollen availability may have been bred out of ornamental plant trait profiles) are unattractive to foraging bees regardless of their floral area. Therefore, it is likely that bees assess resource quantity and quality in addition to visual cues when making foraging decisions. Future work should further tease apart the different effects of floral area and pollen availability on pollinator visitation patterns, such as visitation frequency, handling time, and learned behaviors associated with foraging.

Increased plant diversity can benefit bee communities in terms of overall abundance and species richness (Kremen et al. 2007, Williams et al. 2010, Kennedy et al. 2013, Scheper et al. 2013, Lichtenberg et al. 2017). This can be particularly important in agricultural landscapes where crops rely on the pollination services of bees (Klein et al. 2007, Winfree et al. 2011, Garibaldi et al. 2013, Garibaldi et al. 2016). Importantly, the link between bee diversity within agricultural landscapes and increased crop production is becoming more apparent, and work to assess the added effects of diverse flower plantings on both bee community dynamics and crop yields is increasing (Blaauw and Isaacs 2014, Williams et al. 2015). Incorporating an understanding of this information into pollinator focused conservation strategies may be useful in the future development of floral-rich habitat to support these, and other, beneficial insects.

Generally, diverse plantings contain flowering plants of varying heights, colors, floral displays, and resource availability. The results of this study demonstrate that variation in the flower traits of these plantings help structure the wild bee community. Four of the six flower traits assessed in the family level principal component analysis significantly influenced wild bee community structure, with the two most important traits being floral area, and flower height. When pollen was included in a similar analysis, pollen availability was more closely linked with a subset of the wild bee community. While the majority of the wild bee community was influenced by floral area, abundances of Andrena, Nomada, and Sphecodes were influenced primarily by pollen abundance, while Lasioglossum, Agapostemon, and Bombus were influenced by flower height. The effect of pollen abundance on the Andrena bee genus may be in part due to Andrena being active primarily as spring foragers, when less flowers are available. Therefore, this genus may more actively choose flowers based on resource availability as opposed to floral area. Alternatively, it is also possible that there are fewer plants with high levels of floral area at this time of the year. More research is needed to determine how plant traits might independently influence different components of the wild bee community.

My results demonstrate that pollinator taxa vary in their responses to flower trait characteristics, and that broad level assessments of the flower traits to predict pollinator visitation may be better suited for common species as opposed to rare species. Similarly, results from single species studies should not be applied to the entire wild bee community. The lack of an influence of pollen availability on wild bee species richness may be in part due to differences in the resource requirements of varying bee species. Future development of habitat to support pollinators should take into consideration the

importance of plant trait diversity, with plant selection including species that differ in morphology, floral displays, timing of bloom, while maximizing resource availability. Research in distinct regions, using readily available native and non-native plant species, should assess the relationships between plant traits and pollinator visitation to determine in similar patterns exist across spatial boundaries of plant and pollinator populations. Importantly, this type of work can inform both plant selection for the practical purpose of supporting pollinators in cropping systems, as well as aide in the identification of plant resources for more intensive plant attractiveness surveys. CHAPTER 4:

CONCLUSIONS AND FUTURE DIRECTIONS

Habitat loss is a primary driver of bee declines worldwide (Potts et al. 2010). Landscape complexity (i.e. the proportion of natural habitat), landscape configuration, and a number of anthropogenic disturbances can influence how bee communities' respond to their environment (Winfree et al. 2009, Koh et al. 2016). In general, agricultural landscapes that have experienced a reduction in landscape complexity support fewer individuals or have less diverse bee communities than more heterogeneous agricultural landscapes (Carvell et al. 2006, Garibaldi et al. 2011, Kennedy et al. 2013, Lichtenberg et al. 2017). This is primarily because these landscapes are depleted of diverse flowering resources, or resources are available only during short bursts of crop bloom (Isaacs et al. 2008, Sutter et al. 2017).

Multiple research programs have demonstrated a net benefit of increased wildflower availability on pollinator communities within the agricultural landscape (Kennedy et al. 2013, Blaauw and Isaacs 2014, Williams et al. 2015, Lichtenberg et al. 2017), along with increases in pollination services to target crops (Winfree et al. 2008, Carvalheiro et al. 2011). In some instances, increased pollination services attributed to wild bees leads to increases in crop yields (Carvalheiro et al. 2012, Blaauw and Isaacs 2014). Bees respond positively to wildflower plantings because wildflowers provide bees with their primary dietary requirements: pollen and nectar (Michener et al. 2000, Vaudo et al. 2015). Therefore, the availability of foraging resources provided by wildflowers is crucial to the long term stability of bee communities (Williams and Kremen 2007). In order to maximize bee fitness within agricultural landscapes, it is necessary to identify the key pollen and nectar resources that best support bees, and re-integrate them into the agricultural landscape (Isaacs et al. 2009, Landis 2017).

With this research, I had two main objectives. First, I measured the visitation rates of different pollinator taxa to insectary plants adapted to coarse-textured soils in Michigan in order to identify a set of plant species best suited to support bees in these environments. Secondly, I assessed the relationships between observable plant traits and the visitation patterns of different bee taxa in order to identify which plant traits are most closely associated with bee visitation. The results of this research demonstrate that co-blooming plant species vary considerably in their attractiveness to bees, and that plant selection to best support bees is dependent on the bee taxa of interest. Furthermore, a subset of plant traits best predicts visitation patterns of bees, but again these relationships are taxa dependent and cannot be applied to the entire bee community.

In this study, there was little overlap in the plant species most frequently visited by dissimilar bee taxa, which is likely due to differences in the nutritional requirements of bees (Michener 2000, Leonhardt and Blüthgen 2012, Vanderplanck et al. 2014, Vaudo et al. 2015). Honey bees and bumblebees shared more similarities in plant resource selection than non-*Bombus* wild bees. Both *Asclepias syriaca* and *A. tuberosa* were consistently attractive to honey bees and bumble bees across sites. Plants in the genus *Asclepias* are also the host plants of monarch butterflies (*Danaus plexippus*), which in 2014 was petitioned for consideration for protection under the Endangered Species Act (Monarch ESA Petition 2014). Additional plant species used in this study likely provide resources for natural enemies of crop pests (Fiedler and Landis 2007), or habitat for nesting and reproduction of birds and small mammals (Van Buskirk and Willi 2004, Wratten et al. 2012).

Surprisingly, relatively few research studies have directly compared flowering plant species for their relative attractiveness to pollinators (Tuell et al. 2008, Garbuzov et al. 2014) yet habitat management to support pollinators, primarily bees, has been encouraged by both federal and state agencies, and has resulted in tens of thousands of acres of pollinator friendly habitat throughout the United States alone (Dicks et al. 2016, Farm Service Agency 2015). Many of the plant species that are used in these programs are not rooted in empirically collected data, or are non-native to the region in which they are being used (Fiedler and Landis 2007). As a consequence, plant lists that are generated for these programs likely include a number of plant species that are less attractive, or establish at lower rates, than alternatively available species of plants. Habitat programs in the United States could be improved upon by utilizing data similar to the data collected in this study. More research that directly tests the relative attractiveness of potential insectary plants to pollinators is needed to improve plant selection for pollinator conservation in different geographic regions (Isaacs et al. 2009, Garbuzov et al. 2014). In Michigan, this work can be combined with previous studies that assessed relative plant attractiveness to bees (Tuell et al. 2008) in order to develop site specific, or pollinator taxa specific seed mixes.

Similarities in plant selection by bees at each sites are likely driven by the abundance of common bee species as opposed to rare species. Six bee species accounted for nearly 50% of all bees collected during this study (*Bombus bimaculatus*, *Bombus impatiens*, *Ceratina calcarata*, *Agapostemon virescens*, *Halictus ligatus*, and *Lasioglossum leucocomum*). Future habitat enhancement programs to support bee populations will require an initial consideration of habitat enhancement goals. For

example, a habitat to enhance bee abundance may utilize different set of plant species than a habitat to enhance bee species richness (M'Gonigle et al. 2016). Furthermore, to develop habitats that support crop pollinators in a pollinator dependent crop, future work will likely need to identify the common crop pollinators of that crop, and design the habitat enhancement specifically to boost their populations (Kleijn et al. 2016).

One useful byproduct of studies that assess relative plant attractiveness to pollinators is a rich dataset containing abundant visitation data. With some additional plant specific information, such as observable plant traits, these datasets can be used to develop an understanding of the underlying mechanisms that drive plant attraction to pollinators (Tuell et al. 2008). In this study, I confirmed an earlier finding that floral area is a strong predictor of visitation by wild bees, and that plants producing greater floral area will likely increase bee diversity (Tuell et al. 2008). In addition, I demonstrated that the relationships between various floral traits and bee visitation can be specific to different pollinator families. Furthermore, other plant traits, such as flower height and pollen abundance can increase pollinator abundance, but primarily affect a subset of the bee community that responds to floral area. This is particularly important as it demonstrates a degree of niche partitioning in the wild bee community, suggesting that plant trait diversity may be a better predictor of wild bee visitation that plant diversity itself (Tilman et al. 1997, Fontain et al. 2005, Sutter et al. 2017). Research that investigates the relationships between plant traits and patterns of pollinator visitation can help guide plant selection in future studies of relative plant attractiveness, or for pollinator habitat enhancements in regions lacking relative plant attractiveness comparisons.

Successful wildflower habitat enhancement begins with seed selection (Olwell and Riibe 2016) and has no clear ending, but requires regular management to maximize plant diversity, and thus bee diversity (Harmon-Threatt and Chin 2016). To date, there is very limited research that focuses on pollinator habitat restoration techniques, including both the establishment potential for different plant species in a mixed wildflower planting, and the land management techniques that result in the greatest wildflower abundance and plant species richness (Aldrich 2002, Bretzel et al. 2016). Since bee communities respond predictably to plant community structure (Carvell et al. 2006), it will be beneficial to understand the inputs that lead to a successful habitat enhancement in order to maximizes returns on effort (Kline 2005). Studies that directly test how various land management and wildflower habitat restoration strategies influence the resulting plant-pollinator community will provide land managers with valuable information that can be applied to pollinator habitat enhancement projects.

Developing strategies to help make agricultural landscapes more sustainable will be particularly important for the conservation of pollinator communities in the next few decades (Gunton et al. 2016). A promising method for supporting bees in these landscapes is through the incorporation of wildflower habitat that compliments crop bloom, and provides season long pollen and nectar resources (Isaacs et al. 2009, Williams et al .2015, Isaacs et al. 2016). I believe that an important first step in making these habitat enhancement efforts most rewarding is by identifying the plant species that best support bees and other beneficial insects, and then incorporating them into existing habitat management regimes.

APPENDICES

APPENDIX A:

GPS COORDINATES OF FIELD SITES

Table A1. GPS coordinates for common garden experiments to assess therelative plant attractiveness of Michigan wildflowers to pollinators at SWMREC,CRC, and NWMHRC.

Site	Latitude	Longitude
SWMREC	42° 5'2.19"N	86°21'12.70"W
CRC	42°52'14.44"N	85°15'23.07"W
NWMHRC	44°53'2.55"N	85°40'33.61"W

APPENDIX B:

2015 RELATIVE ATTRACTIVENESS OF MICHIGAN WILDFLOWERS



Figure B1. Comparison of the number of wild bees, bumblebees, and honey bees visiting insectary plants at Southwest Michigan Research and Extension Center in Benton Harbor, MI in 2015. Plants are arranged within bloom period by the total number of bees observed per 5-minute sample, in decreasing order. Mean differences in the total number of bees per sample was determined using Tukey's HSD test. Plant species sharing the same letter are not significantly different than each other at α =0.05.



Figure B2. Comparison of the number of wild bees, bumblebees, and honey bees visiting different insectary plants at Clarksville Research Center, Clarksville MI (CRC) in 2015. Plants are arranged within bloom period by the total number of bees observed per 5-minute sample, in decreasing order. Mean differences in the total number of bees per sample was determined using Tukey's HSD test. Plant species sharing the same letter are not significantly different from each other at α =0.05.



Figure B3. Comparison of the number of wild bees, bumblebees, and honey bees visiting insectary plants at Northwest Michigan Horticulture Research Center, Traverse City, MI (NWMHRC) in 2015. Plants are arranged within bloom period by the total number of bees observed per 5-minute sample, in decreasing order. Mean differences in the total number of bees per sample was determined using Tukey's HSD test. Plant species sharing the same letter are not significantly different than each other at α =0.05.

APPENDIX C:

WILD BEE SPECIMEN COLLECTED FROM INSECTARY PLANTS IN 2015 AND

Table C1. Complete list of bees collected during 2015-2016 at the Southwest Michigan Research and Extension Center, the Clarksville Research Center, and the Northwest Michigan Horticulture Research Center as part of "Evaluation of Wildflowers to Provide Foraging Resources for Managed and Wild Pollinators in Michigan".

site	Plant species	Bee species	number collected
SWMREC	Achillea millefolium	Andrena crataegi	1
SWMREC	Achillea millefolium	Andrena morrisonella	1
SWMREC	Achillea millefolium	Andrena wilkella	1
SWMREC	Achillea millefolium	Halictus ligatus	5
SWMREC	Achillea millefolium	Lasioglossum leucocomum	1
SWMREC	Achillea millefolium	Lasioglossum leucozonium	1
SWMREC	Achillea millefolium	Lasioglossum pectorale	1
SWMREC	Achillea millefolium	Lasioglossum pilosum	1
SWMREC	Achillea millefolium	Megachile mendica	1
SWMREC	Achillea millefolium	Melissodes subillatus	1
SWMREC	Amorpha canescens	Agapostemon virescens	1
SWMREC	Amorpha canescens	Bombus bimaculatus	1
SWMREC	Amorpha canescens	Bombus perplexus	1
SWMREC	Amorpha canescens	Bombus vagans	1
SWMREC	Amorpha canescens	Lasioglossum pilosum	1
SWMREC	Amorpha canescens	Megachile frugalis	2
SWMREC	Amorpha canescens	Megachile mendica	1
SWMREC	Amorpha canescens	Nomada valida	1
SWMREC	Amorpha canescens	Osmia lignaria	1
SWMREC	Asclepias syriaca	Bombus bimaculatus	3
SWMREC	Asclepias syriaca	Bombus griseocollis	1

SWMREC	Asclepias syriaca	Lasioglossum leucocomum	1
SWMREC	Asclepias syriaca	Megachile brevis	1
SWMREC	Asclepias syriaca	Osmia lignaria	9
SWMREC	Asclepias syriaca	Osmia pumila	4
SWMREC	Asclepias syriaca	Osmia sp.	1
SWMREC	Asclepias syriaca	Perdita octomaculata	1
SWMREC	Asclepias tuberosa	Apis mellifera	5
SWMREC	Asclepias tuberosa	Augochlorella aurata	1
SWMREC	Asclepias tuberosa	Lasioglossum leucozonium	2
SWMREC	Asclepias tuberosa	Megachile brevis	2
SWMREC	Asclepias tuberosa	Megachile mendica	1
SWMREC	Asclepias tuberosa	Megachile relativa	1
SWMREC	Asclepias tuberosa	Megachile sp.	1
SWMREC	Asclepias tuberosa	Megachile texana	1
SWMREC	Asclepias tuberosa	Osmia lignaria	2
SWMREC	Asclepias verticillata	Apis mellifera	1
SWMREC	Asclepias verticillata	Halictus 114onfuses	2
SWMREC	Asclepias verticillata	Hylaeus affinis	1
SWMREC	Asclepias verticillata	Lasioglossum ellisiae	1
SWMREC	Asclepias verticillata	Lasioglossum leucozonium	1
SWMREC	Asclepias verticillata	Lasioglossum pectorale	1
SWMREC	Asclepias verticillata	Lasioglossum pilosum	5
SWMREC	Asclepias verticillata	Megachile brevis	1
SWMREC	Asclepias verticillata	Megachile texana	1
SWMREC	Asclepias verticillata	Sphecodes cressonil	1
SWMREC	Baptisia alba var. macrophylla	Lasioglossum sp.	1
SWMREC	Campanula rotundifolia	Halictus 114onfuses	1
SWMREC	Campanula rotundifolia	Lasioglossum leucocomum	2

SWMREC	Campanula rotundifolia	Lasioglossum leucozonium	1
SWMREC	Ceanothus americanus	Apis mellifera	1
SWMREC	Ceanothus americanus	Lasioglossum leucocomum	2
SWMREC	Ceanothus americanus	Lasioglossum pilosum	1
SWMREC	Ceanothus americanus	Nomada valida	1
SWMREC	Centaurea stoebe micranthos	Agapostemon texanus	1
SWMREC	Centaurea stoebe micranthos	Agapostemon virescens	12
SWMREC	Centaurea stoebe micranthos	Bombus citrinus	3
SWMREC	Centaurea stoebe micranthos	Bombus griseocollis	5
SWMREC	Centaurea stoebe micranthos	Bombus impatiens	1
SWMREC	Centaurea stoebe micranthos	Ceratina calcarata	3
SWMREC	Centaurea stoebe micranthos	Ceratina dupla	3
SWMREC	Centaurea stoebe micranthos	Ceratina mikmaqi	1
SWMREC	Centaurea stoebe micranthos	Halictus 115onfuses	1
SWMREC	Centaurea stoebe micranthos	Halictus ligatus	24
SWMREC	Centaurea stoebe micranthos	Lasioglossum admirandum	1
SWMREC	Centaurea stoebe micranthos	Lasioglossum leucocomum	1
SWMREC	Centaurea stoebe micranthos	Lasioglossum leucozonium	25
SWMREC	Centaurea stoebe micranthos	Lasioglossum paraforbesii	1
SWMREC	Centaurea stoebe micranthos	Lasioglossum pectorale	5
SWMREC	Centaurea stoebe micranthos	Lasioglossum pilosum	3
SWMREC	Centaurea stoebe micranthos	Megachile brevis	1
SWMREC	Centaurea stoebe micranthos	Megachile mendica	1
SWMREC	Centaurea stoebe micranthos	Megachile pugnata	1
SWMREC	Centaurea stoebe micranthos	Megachile relativa	2
SWMREC	Centaurea stoebe micranthos	Perdita octomaculata	1
SWMREC	Coreopsis lanceolata	Agapostemon virescens	1
SWMREC	Coreopsis lanceolata	Andrena wilkella	1

Coreopsis lanceolata	Apis mellifera	1
Coreopsis lanceolata	Bombus citrinus	1
Coreopsis lanceolata	Ceratina calcarata	5
Coreopsis lanceolata	Halictus ligatus	15
Coreopsis lanceolata	Lasioglossum pectorale	14
Coreopsis lanceolata	Lasioglossum pilosum	4
Coreopsis lanceolata	Megachile frugalis	1
Coreopsis lanceolata	Megachile mendica	2
Coreopsis lanceolata	Melissodes agilis	1
Coreopsis lanceolata	Nomada valida	1
Coreopsis palmata	Bombus impatiens	1
Coreopsis palmata	Halictus ligatus	7
Coreopsis palmata	Lasioglossum leucocomum	1
Coreopsis palmata	Lasioglossum pectorale	2
Coreopsis palmata	Megachile pugnata	1
Coreopsis palmata	Melissodes agilis	2
Coreopsis palmata	Melissodes denticulatus	1
Coreopsis palmata	Melissodes druriellus	3
Coreopsis palmata	Melissodes subillatus	1
Coreopsis tripteris	Agapostemon texanus	1
Coreopsis tripteris	Agapostemon virescens	13
Coreopsis tripteris	Apis mellifera	4
Coreopsis tripteris	Augochlorella aurata	2
Coreopsis tripteris	Bombus citrinus	4
Coreopsis tripteris	Bombus griseocollis	1
Coreopsis tripteris	Bombus impatiens	51
Coreopsis tripteris	Bombus vagans	1
Coreopsis tripteris	Ceratina calcarata	36
	Coreopsis lanceolata Coreopsis lanceolata Coreopsis lanceolata Coreopsis lanceolata Coreopsis lanceolata Coreopsis lanceolata Coreopsis lanceolata Coreopsis lanceolata Coreopsis palmata Coreopsis tripteris Coreopsis tripteris	Coreopsis lanceolataApis meiliferaCoreopsis lanceolataBombus citrinusCoreopsis lanceolataCeratina calcarataCoreopsis lanceolataLasioglossum pectoraleCoreopsis lanceolataLasioglossum pilosumCoreopsis lanceolataMegachile frugalisCoreopsis lanceolataMegachile mendicaCoreopsis lanceolataMegachile mendicaCoreopsis lanceolataMegachile mendicaCoreopsis lanceolataMegachile mendicaCoreopsis lanceolataMegachile mendicaCoreopsis lanceolataMegachile mendicaCoreopsis palmetaBombus impatiensCoreopsis palmataBombus impatiensCoreopsis palmataLasioglossum pectoraleCoreopsis palmataLasioglossum pectoraleCoreopsis palmataMelissodes agilisCoreopsis palmataLasioglossum pectoraleCoreopsis palmataMelissodes agilisCoreopsis palmataMelissodes agilisCoreopsis palmataMelissodes denticulatusCoreopsis palmataMelissodes denticulatusCoreopsis palmataMelissodes subillatusCoreopsis tripterisAgapostemon texanusCoreopsis tripterisApis melliferaCoreopsis tripterisBombus citrinusCoreopsis tripterisBombus citrinusCoreopsis tripterisBombus citrinusCoreopsis tripterisBombus citrinusCoreopsis tripterisBombus citrinusCoreopsis tripterisBombus citrinusCoreopsis tripterisBombus citrinusCoreo

SWMREC	Coreopsis tripteris	Ceratina dupla	2
SWMREC	Coreopsis tripteris	Ceratina mikmaqi	4
SWMREC	Coreopsis tripteris	Halictus 117onfuses	1
SWMREC	Coreopsis tripteris	Halictus ligatus	38
SWMREC	Coreopsis tripteris	Halictus parallelus	1
SWMREC	Coreopsis tripteris	Halictus rubicundus	3
SWMREC	Coreopsis tripteris	Lasioglossum leucozonium	21
SWMREC	Coreopsis tripteris	Lasioglossum pectorale	1
SWMREC	Coreopsis tripteris	Lasioglossum pilosum	6
SWMREC	Coreopsis tripteris	Megachile mendica	1
SWMREC	Coreopsis tripteris	Megachile pugnata	2
SWMREC	Coreopsis tripteris	Megachile rotundata	1
SWMREC	Coreopsis tripteris	Melissodes agilis	12
SWMREC	Coreopsis tripteris	Melissodes druriellus	4
SWMREC	Coreopsis tripteris	Psuedo panurgus albitarsis	1
SWMREC	Coreopsis tripteris	Triepeolus remigatus	1
SWMREC	Coreopsis tripteris	Xylocopa virginica	3
SWMREC	Dalea purpurea	Agapostemon sericeus	1
SWMREC	Dalea purpurea	Andrena placata	1
SWMREC	Dalea purpurea	Augochlorella aurata	2
SWMREC	Dalea purpurea	Ceratina calcarata	2
SWMREC	Dalea purpurea	Ceratina dupla	1
SWMREC	Dalea purpurea	Ceratina mikmaqi	1
SWMREC	Dalea purpurea	Ceratina strenua	1
SWMREC	Dalea purpurea	Halictus 117onfuses	9
SWMREC	Dalea purpurea	Halictus ligatus	1
SWMREC	Dalea purpurea	Hylaeus affinis	2
SWMREC	Dalea purpurea	Hylaeus affinis/modestus	3

Table C1 (cont	'd)		
SWMREC	Dalea purpurea	Hylaeus modestus	2
SWMREC	Dalea purpurea	Lasioglossum pectorale	7
SWMREC	Dalea purpurea	Lasioglossum pilosum	2
SWMREC	Dalea purpurea	Lasioglossum versatum	1
SWMREC	Dasiphora fruticosa	Agapostemon texanus	4
SWMREC	Dasiphora fruticosa	Agapostemon virescens	3
SWMREC	Dasiphora fruticosa	Bombus bimaculatus	1
SWMREC	Dasiphora fruticosa	Bombus fervidus	2
SWMREC	Dasiphora fruticosa	Bombus griseocollis	1
SWMREC	Dasiphora fruticosa	Hylaeus affinis	1
SWMREC	Dasiphora fruticosa	Hylaeus affinis/modestus	1
SWMREC	Dasiphora fruticosa	Lasioglossum anomalum	1
SWMREC	Dasiphora fruticosa	Lasioglossum pectorale	1
SWMREC	Dasiphora fruticosa	Lasioglossum pilosum	6
SWMREC	Dasiphora fruticosa	Megachile brevis	1
SWMREC	Dasiphora fruticosa	Megachile frugalis	1
SWMREC	Dasiphora fruticosa	Megachile latimanus	1
SWMREC	Dasiphora fruticosa	Megachile mendica	2
SWMREC	Dasiphora fruticosa	Megachile texana	2
SWMREC	Dasiphora fruticosa	Melissodes subillatus	1
SWMREC	Echinacea purpurea	Agapostemon virescens	14
SWMREC	Echinacea purpurea	Bombus bimaculatus	2
SWMREC	Echinacea purpurea	Bombus citrinus	6
SWMREC	Echinacea purpurea	Bombus griseocollis	4
SWMREC	Echinacea purpurea	Bombus impatiens	2
SWMREC	Echinacea purpurea	Bombus vagans	1
SWMREC	Echinacea purpurea	Ceratina calcarata	7
SWMREC	Echinacea purpurea	Halictus confuses	2

SWMREC	Echinacea purpurea	Halictus ligatus	4
SWMREC	Echinacea purpurea	Hylaeus affinis	1
SWMREC	Echinacea purpurea	Lasioglossum pectorale	1
SWMREC	Echinacea purpurea	Lasioglossum pilosum	2
SWMREC	Echinacea purpurea	Megachile latimanus	1
SWMREC	Echinacea purpurea	Megachile pugnata	3
SWMREC	Echinacea purpurea	Melissodes druriellus	1
SWMREC	Eryngium yuccifolium	Ceratina calcarata	2
SWMREC	Eryngium yuccifolium	Halictus ligatus	2
SWMREC	Eryngium yuccifolium	Hylaeus affinis	1
SWMREC	Eryngium yuccifolium	Hylaeus modestus	6
SWMREC	Eryngium yuccifolium	Lasioglossum leucozonium	1
SWMREC	Eryngium yuccifolium	Lasioglossum pilosum	4
SWMREC	Helianthus occidentalis	Agapostemon splendens	1
SWMREC	Helianthus occidentalis	Agapostemon texanus	1
SWMREC	Helianthus occidentalis	Agapostemon virescens	7
SWMREC	Helianthus occidentalis	Andrena helianthi	1
SWMREC	Helianthus occidentalis	Apis mellifera	1
SWMREC	Helianthus occidentalis	Augochlorella aurata	2
SWMREC	Helianthus occidentalis	Bombus citrinus	1
SWMREC	Helianthus occidentalis	Bombus griseocollis	1
SWMREC	Helianthus occidentalis	Bombus impatiens	7
SWMREC	Helianthus occidentalis	Ceratina calcarata	3
SWMREC	Helianthus occidentalis	Halictus ligatus	32
SWMREC	Helianthus occidentalis	Halictus parallelus	1
SWMREC	Helianthus occidentalis	Heriades leavitti	1
SWMREC	Helianthus occidentalis	Lasioglossum leucozonium	20
SWMREC	Helianthus occidentalis	Lasioglossum pectorale	1

SWMREC	Helianthus occidentalis	Lasioglossum pilosum	8
SWMREC	Helianthus occidentalis	Megachile latimanus	1
SWMREC	Helianthus occidentalis	Megachile mendica	1
SWMREC	Helianthus occidentalis	Megachile pugnata	1
SWMREC	Helianthus occidentalis	Megachile relativa	1
SWMREC	Helianthus occidentalis	Melissodes agilis	3
SWMREC	Helianthus occidentalis	Melissodes druriellus	1
SWMREC	Helianthus occidentalis	Psuedo panurgus albitarsis	1
SWMREC	Helianthus strumosus	Agapostemon texanus	1
SWMREC	Helianthus strumosus	Agapostemon virescens	19
SWMREC	Helianthus strumosus	Andrena aliciae	1
SWMREC	Helianthus strumosus	Apis mellifera	3
SWMREC	Helianthus strumosus	Augochlorella aurata	1
SWMREC	Helianthus strumosus	Bombus citrinus	3
SWMREC	Helianthus strumosus	Bombus impatiens	7
SWMREC	Helianthus strumosus	Bombus vagans	3
SWMREC	Helianthus strumosus	Ceratina calcarata	32
SWMREC	Helianthus strumosus	Ceratina dupla	1
SWMREC	Helianthus strumosus	Ceratina mikmaqi	1
SWMREC	Helianthus strumosus	Halictus ligatus	6
SWMREC	Helianthus strumosus	Lasioglossum coriaceum	1
SWMREC	Helianthus strumosus	Lasioglossum leucozonium	10
SWMREC	Helianthus strumosus	Lasioglossum pectorale	1
SWMREC	Helianthus strumosus	Lasioglossum pilosum	3
SWMREC	Helianthus strumosus	Megachile relativa	1
SWMREC	Helianthus strumosus	Melissodes agilis	7
SWMREC	Helianthus strumosus	Melissodes druriellus	5
SWMREC	Helianthus strumosus	Melissodes melissodes	3

SWMREC	Hieracium gronovii	Agapostemon texanus	1
SWMREC	Hieracium gronovii	Lasioglossum leucocomum	1
SWMREC	Hieracium gronovii	Lasioglossum pilosum	1
SWMREC	Hypericum prolificum	Bombus bimaculatus	12
SWMREC	Hypericum prolificum	Bombus griseocollis	1
SWMREC	Hypericum prolificum	Bombus impatiens	12
SWMREC	Lespedeza capitata	Anthidium oblongatum	1
SWMREC	Lespedeza capitata	Bombus impatiens	1
SWMREC	Lespedeza capitata	Lasioglossum leucozonium	1
SWMREC	Lespedeza hirta	Agapostemon texanus	1
SWMREC	Lespedeza hirta	Agapostemon virescens	1
SWMREC	Lespedeza hirta	Anthidiellum notatum	2
SWMREC	Lespedeza hirta	Anthidium oblongatum	1
SWMREC	Lespedeza hirta	Bombus impatiens	1
SWMREC	Lespedeza hirta	Ceratina calcarata	1
SWMREC	Lespedeza hirta	Coelioxys octodentata	1
SWMREC	Lespedeza hirta	Lasioglossum pilosum	1
SWMREC	Lespedeza hirta	Megachile mendica	2
SWMREC	Lespedeza hirta	Megachile texana	2
SWMREC	Liatris aspera	Agapostemon virescens	6
SWMREC	Liatris aspera	Augochlora pura	1
SWMREC	Liatris aspera	Bombus citrinus	3
SWMREC	Liatris aspera	Bombus fervidus	3
SWMREC	Liatris aspera	Bombus griseocollis	4
SWMREC	Liatris aspera	Bombus impatiens	12
SWMREC	Liatris aspera	Bombus perplexus	1
SWMREC	Liatris aspera	Ceratina calcarata	6
SWMREC	Liatris aspera	Ceratina mikmaqi	1

SWMREC	Liatris aspera	Ceratina strenua	1
SWMREC	Liatris aspera	Hoplitis producta	1
SWMREC	Liatris aspera	Lasioglossum pilosum	2
SWMREC	Liatris aspera	Melissodes druriellus	2
SWMREC	Liatris cylindracea	Bombus fervidus	1
SWMREC	Liatris cylindracea	Lasioglossum pectorale	1
SWMREC	Liatris cylindracea	Lasioglossum pilosum	3
SWMREC	Lotus corniculatus L.	Andrena wilkella	17
SWMREC	Lotus corniculatus L.	Apis mellifera	1
SWMREC	Lotus corniculatus L.	Augochlorella aurata	1
SWMREC	Lotus corniculatus L.	Bombus bimaculatus	2
SWMREC	Lotus corniculatus L.	Ceratina calcarata	1
SWMREC	Lotus corniculatus L.	Lasioglossum hitchensi	1
SWMREC	Lotus corniculatus L.	Lasioglossum leucocomum	1
SWMREC	Lotus corniculatus L.	Megachile frugalis	1
SWMREC	Lotus corniculatus L.	Megachile latimanus	1
SWMREC	Lotus corniculatus L.	Megachile mendica	1
SWMREC	Lotus corniculatus L.	Megachile relativa	1
SWMREC	Lotus corniculatus L.	Nomada superba	1
SWMREC	Lupinus perennis	Lasioglossum leucocomum	4
SWMREC	Lupinus perennis	Lasioglossum pilosum	1
SWMREC	Monarda fistulosa	Bombus bimaculatus	94
SWMREC	Monarda fistulosa	Bombus citrinus	2
SWMREC	Monarda fistulosa	Bombus griseocollis	46
SWMREC	Monarda fistulosa	Bombus impatiens	31
SWMREC	Monarda fistulosa	Bombus perplexus	3
SWMREC	Monarda fistulosa	Bombus vagans	14
SWMREC	Monarda fistulosa	Ceratina dupla	1

SWMREC	Monarda fistulosa
SWMREC	Monarda fistulosa
SWMREC	Monarda punctata
SWMREC	Oenothera biennis
SWMREC	Oenothera biennis
SWMREC	Oenothera fruticosa

С	eratina mikmaqi	1
Н	alictus ligatus	2
Lä	asioglossum imitatum	1
Lä	asioglossum pilosum	1
Μ	egachile pugnata	1
A	pis mellifera	1
B	ombus impatiens	5
Lä	asioglossum ellisiae	1
La	asioglossum leucozonium	1
La	asioglossum paradmirandum	1
La	asioglossum pilosum	2
Lá	asioglossum vierecki	3
X	ylocopa virginica	2
A	gapostemon virescens	1
Lä	asioglossum pectorale	1
A	gapostemon virescens	2
B	ombus impatiens	1
С	eratina mikmaqi	1
Н	alictus ligatus	1
Lä	asioglossum ellisiae	1
Lä	asioglossum leucozonium	5
Lä	asioglossum pectorale	1
La	asioglossum pilosum	3
Μ	egachile brevis	2
Μ	egachile relativa	1
Μ	elissodes druriellus	1
Р	eponapis pruinosa	1
S	phecodes mandibularis	1

SWMREC	Oligoneuron rigidum	Agapostemon virescens	2
SWMREC	Oligoneuron rigidum	Andrena canadensis	1
SWMREC	Oligoneuron rigidum	Andrena placata	32
SWMREC	Oligoneuron rigidum	Apis mellifera	3
SWMREC	Oligoneuron rigidum	Bombus citrinus	2
SWMREC	Oligoneuron rigidum	Bombus impatiens	25
SWMREC	Oligoneuron rigidum	Ceratina calcarata	12
SWMREC	Oligoneuron rigidum	Ceratina dupla	1
SWMREC	Oligoneuron rigidum	Ceratina strenua	1
SWMREC	Oligoneuron rigidum	Halictus 124onfuses	4
SWMREC	Oligoneuron rigidum	Halictus ligatus	3
SWMREC	Oligoneuron rigidum	Hylaeus affinis/modestus	1
SWMREC	Oligoneuron rigidum	Hylaeus mesillae	1
SWMREC	Oligoneuron rigidum	Lasioglossum cressonii	1
SWMREC	Oligoneuron rigidum	Lasioglossum leucozonium	12
SWMREC	Oligoneuron rigidum	Lasioglossum pectorale	1
SWMREC	Oligoneuron rigidum	Lasioglossum pilosum	5
SWMREC	Oligoneuron rigidum	Nomada placida	2
SWMREC	Oligoneuron rigidum	Perdita octomaculata	2
SWMREC	Oligoneuron rigidum	Psuedo panurgus nebrascensis	2
SWMREC	Oligoneuron rigidum	Sphecodes illinoensis	1
SWMREC	Oligoneuron rigidum	Sphecodes mandibularis	1
SWMREC	Oligoneuron rigidum	Xylocopa virginica	1
SWMREC	Penstemon digitalis	Agapostemon virescens	3
SWMREC	Penstemon digitalis	Bombus bimaculatus	2
SWMREC	Penstemon digitalis	Bombus citrinus	1
SWMREC	Penstemon digitalis	Bombus vagans	1
SWMREC	Penstemon digitalis	Ceratina dupla	3

SWMREC	Penstemon digitalis	Ceratina mikmaqi
SWMREC	Penstemon digitalis	Lasioglossum leucocomum
SWMREC	Penstemon digitalis	Lasioglossum leucozonium
SWMREC	Penstemon digitalis	Osmia distincta
SWMREC	Penstemon digitalis	Osmia lignaria
SWMREC	Penstemon digitalis	Osmia pumila
SWMREC	Penstemon hirsutus	Apis mellifera
SWMREC	Penstemon hirsutus	Bombus bimaculatus
SWMREC	Penstemon hirsutus	Ceratina dupla
SWMREC	Penstemon hirsutus	Ceratina mikmaqi
SWMREC	Penstemon hirsutus	Hoplitis pilosifrons
SWMREC	Penstemon hirsutus	Hylaeus mesillae
SWMREC	Penstemon hirsutus	Lasioglossum leucozonium
SWMREC	Penstemon hirsutus	Lasioglossum pilosum
SWMREC	Penstemon hirsutus	Osmia bucephala
SWMREC	Penstemon hirsutus	Osmia lignaria
SWMREC	Potentilla arguta	Halictus 125onfuses
SWMREC	Potentilla arguta	Halictus ligatus
SWMREC	Potentilla arguta	Lasioglossum leucocomum
SWMREC	Potentilla arguta	Lasioglossum leucozonium
SWMREC	Potentilla arguta	Lasioglossum paradmirandum
SWMREC	Potentilla arguta	Lasioglossum pilosum
SWMREC	Potentilla arguta	Lasioglossum sp.
SWMREC	Potentilla arguta	Melissodes subillatus
SWMREC	Potentilla simplex	Augochlorella aurata
SWMREC	Potentilla simplex	Lasioglossum leucozonium
SWMREC	Potentilla simplex	Nomada sp.
SWMREC	Potentilla simplex	Nomada valida

	u)		
SWMREC	Potentilla simplex	Osmia lignaria	2
SWMREC	Potentilla simplex	Osmia pumila	2
SWMREC	Pycnanthemum pilosum	Agapostemon virescens	1
SWMREC	Pycnanthemum pilosum	Apis mellifera	11
SWMREC	Pycnanthemum pilosum	Augochlorella aurata	2
SWMREC	Pycnanthemum pilosum	Bombus bimaculatus	1
SWMREC	Pycnanthemum pilosum	Bombus citrinus	72
SWMREC	Pycnanthemum pilosum	Bombus griseocollis	7
SWMREC	Pycnanthemum pilosum	Bombus impatiens	13
SWMREC	Pycnanthemum pilosum	Bombus vagans	1
SWMREC	Pycnanthemum pilosum	Ceratina calcarata	11
SWMREC	Pycnanthemum pilosum	Ceratina dupla	3
SWMREC	Pycnanthemum pilosum	Coelioxys octodentata	1
SWMREC	Pycnanthemum pilosum	Halictus 126onfuses	2
SWMREC	Pycnanthemum pilosum	Halictus ligatus	1
SWMREC	Pycnanthemum pilosum	Hylaeus affinis/modestus	1
SWMREC	Pycnanthemum pilosum	Hylaeus mesillae	1
SWMREC	Pycnanthemum pilosum	Lasioglossum leucozonium	1
SWMREC	Pycnanthemum pilosum	Lasioglossum pectorale	2
SWMREC	Pycnanthemum pilosum	Lasioglossum pilosum	3
SWMREC	Pycnanthemum pilosum	Megachile brevis	1
SWMREC	Pycnanthemum pilosum	Megachile mendica	3
SWMREC	Pycnanthemum pilosum	Triepeolus remigatus	1
SWMREC	Pycnanthemum pilosum	Xylocopa virginica	1
SWMREC	Pycnanthemum virginianum	Augochlorella aurata	1
SWMREC	Pycnanthemum virginianum	Bombus citrinus	4
SWMREC	Pycnanthemum virginianum	Bombus impatiens	2
SWMREC	Pycnanthemum virginianum	Ceratina calcarata	3

SWMREC	Pycnanthemum virginianum	Ceratina mikmaqi	1
SWMREC	Pycnanthemum virginianum	Hylaeus affinis/modestus	2
SWMREC	Pycnanthemum virginianum	Lasioglossum leucozonium	2
SWMREC	Pycnanthemum virginianum	Lasioglossum pectorale	2
SWMREC	Pycnanthemum virginianum	Lasioglossum pilosum	4
SWMREC	Pycnanthemum virginianum	Lasioglossum tegulare	1
SWMREC	Ratibida pinnata	Agapostemon splendens	1
SWMREC	Ratibida pinnata	Bombus griseocollis	9
SWMREC	Ratibida pinnata	Bombus impatiens	2
SWMREC	Ratibida pinnata	Ceratina calcarata	5
SWMREC	Ratibida pinnata	Halictus ligatus	36
SWMREC	Ratibida pinnata	Halictus parallelus	1
SWMREC	Ratibida pinnata	Lasioglossum pectorale	2
SWMREC	Ratibida pinnata	Lasioglossum pilosum	4
SWMREC	Ratibida pinnata	Lasioglossum sp.	1
SWMREC	Ratibida pinnata	Melissodes agilis	1
SWMREC	Ratibida pinnata	Xylocopa virginica	1
SWMREC	Rhus copallinum	Megachile mendica	1
SWMREC	Rosa carolina	Hylaeus affinis	1
SWMREC	Rudbeckia hirta	Agapostemon virescens	1
SWMREC	Rudbeckia hirta	Apis mellifera	1
SWMREC	Rudbeckia hirta	Ceratina mikmaqi	1
SWMREC	Rudbeckia hirta	Halictus ligatus	25
SWMREC	Rudbeckia hirta	Lasioglossum leucozonium	1
SWMREC	Rudbeckia hirta	Lasioglossum lineatulum	1
SWMREC	Rudbeckia hirta	Lasioglossum pectorale	9
SWMREC	Rudbeckia hirta	Lasioglossum pilosum	11
SWMREC	Rudbeckia hirta	Melissodes agilis	3

SWMREC	Rudbeckia hirta	Melissodes druriellus	3
SWMREC	Rudbeckia hirta	Melissodes sp.	1
SWMREC	Rudbeckia hirta	Melissodes subillatus	1
SWMREC	Rudbeckia hirta	Melissodes tinctus	1
SWMREC	Rudbeckia hirta	Nomada articulata	1
SWMREC	Senecio obovatus	Augochlorella aurata	1
SWMREC	Senecio obovatus	Halictus ligatus	22
SWMREC	Senecio obovatus	Lasioglossum leucocomum	1
SWMREC	Senecio obovatus	Lasioglossum pectorale	6
SWMREC	Senecio obovatus	Lasioglossum pilosum	2
SWMREC	Senecio obovatus	Lasioglossum sp.	1
SWMREC	Senecio obovatus	Osmia lignaria	3
SWMREC	Senecio obovatus	Osmia pumila	2
SWMREC	Silphium integrifolium	Agapostemon virescens	41
SWMREC	Silphium integrifolium	Bombus bimaculatus	2
SWMREC	Silphium integrifolium	Bombus citrinus	5
SWMREC	Silphium integrifolium	Bombus impatiens	24
SWMREC	Silphium integrifolium	Bombus perplexus	1
SWMREC	Silphium integrifolium	Bombus vagans	6
SWMREC	Silphium integrifolium	Ceratina calcarata	2
SWMREC	Silphium integrifolium	Ceratina mikmaqi	1
SWMREC	Silphium integrifolium	Halictus ligatus	1
SWMREC	Silphium integrifolium	Megachile pugnata	4
SWMREC	Silphium integrifolium	Melissodes agilis	9
SWMREC	Silphium integrifolium	Melissodes druriellus	2
SWMREC	Silphium integrifolium	Melissodes melissodes	2
SWMREC	Silphium terebinthinaceum	Agapostemon virescens	16
SWMREC	Silphium terebinthinaceum	Bombus citrinus	7

SWMREC	Silphium terebinthinaceum	Bombus griseocollis	2
SWMREC	Silphium terebinthinaceum	Bombus impatiens	12
SWMREC	Silphium terebinthinaceum	Bombus vagans	2
SWMREC	Silphium terebinthinaceum	Melissodes agilis	4
SWMREC	Silphium terebinthinaceum	Melissodes melissodes	1
SWMREC	Silphium terebinthinaceum	Xylocopa virginica	1
SWMREC	Solidago juncea	Andrena placata	10
SWMREC	Solidago juncea	Apis mellifera	1
SWMREC	Solidago juncea	Augochlora pura	1
SWMREC	Solidago juncea	Bombus impatiens	3
SWMREC	Solidago juncea	Ceratina calcarata	6
SWMREC	Solidago juncea	Colletes simulans armatus	1
SWMREC	Solidago juncea	Halictus ligatus	12
SWMREC	Solidago juncea	Nomada placida	2
SWMREC	Solidago juncea	Perdita octomaculata	2
SWMREC	Solidago juncea	Sphecodes illinoensis	2
SWMREC	Solidago juncea	Sphecodes mandibularis	1
SWMREC	Solidago juncea	Triepeolus pectoralis	1
SWMREC	Solidago nemoralis	Ceratina calcarata	9
SWMREC	Solidago nemoralis	Ceratina dupla	2
SWMREC	Solidago nemoralis	Halictus ligatus	40
SWMREC	Solidago nemoralis	Hylaeus affinis/modestus	1
SWMREC	Solidago nemoralis	Lasioglossum anomalum	1
SWMREC	Solidago nemoralis	Lasioglossum leucozonium	1
SWMREC	Solidago nemoralis	Melissodes agilis	1
SWMREC	Solidago nemoralis	Sphecodes mandibularis	1
SWMREC	Solidago nemoralis	Sphecodes pimpinellae	1
SWMREC	Solidago speciosa	Apis mellifera	1
SWMREC	Solidago speciosa	Bombus citrinus	3
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SWMREC	Solidago speciosa	Bombus impatiens	32
SWMREC	Solidago speciosa	Bombus vagans	1
SWMREC	Solidago speciosa	Ceratina calcarata	3
SWMREC	Solidago speciosa	Ceratina dupla	1
SWMREC	Solidago speciosa	Halictus ligatus	2
SWMREC	Solidago speciosa	Lasioglossum imitatum	1
SWMREC	Solidago speciosa	Lasioglossum leucozonium	6
SWMREC	Solidago speciosa	Lasioglossum pilosum	7
SWMREC	Solidago speciosa	Megachile mendica	1
SWMREC	Solidago speciosa	Sphecodes cressonil	1
SWMREC	Solidago speciosa	Xylocopa virginica	4
SWMREC	Symphyotrichum oolentangiense	Agapostemon sericeus	3
SWMREC	Symphyotrichum oolentangiense	Agapostemon texanus	9
SWMREC	Symphyotrichum oolentangiense	Agapostemon virescens	13
SWMREC	Symphyotrichum oolentangiense	Andrena canadensis	1
SWMREC	Symphyotrichum oolentangiense	Apis mellifera	2
SWMREC	Symphyotrichum oolentangiense	Augochlorella aurata	1
SWMREC	Symphyotrichum oolentangiense	Bombus citrinus	1
SWMREC	Symphyotrichum oolentangiense	Bombus impatiens	8
SWMREC	Symphyotrichum oolentangiense	Bombus vagans	1
SWMREC	Symphyotrichum oolentangiense	Ceratina calcarata	22
SWMREC	Symphyotrichum oolentangiense	Ceratina dupla	3
SWMREC	Symphyotrichum oolentangiense	Ceratina mikmaqi	5
SWMREC	Symphyotrichum oolentangiense	Halictus 130onfuses	1
SWMREC	Symphyotrichum oolentangiense	Halictus ligatus	12
SWMREC	Symphyotrichum oolentangiense	Lasioglossum leucozonium	21
SWMREC	Symphyotrichum oolentangiense	Lasioglossum pectorale	1

SWMREC	Symphyotrichum oolentangiense	Lasioglossum pilosum
SWMREC	Symphyotrichum oolentangiense	Megachile mendica
SWMREC	Symphyotrichum oolentangiense	Megachile rotundata
SWMREC	Symphyotrichum oolentangiense	Psuedo panurgus nebrascensis
SWMREC	Symphyotrichum sericeum	Agapostemon splendens
SWMREC	Symphyotrichum sericeum	Agapostemon texanus
SWMREC	Symphyotrichum sericeum	Agapostemon virescens
SWMREC	Symphyotrichum sericeum	Andrena placata
SWMREC	Symphyotrichum sericeum	Augochlorella aurata
SWMREC	Symphyotrichum sericeum	Ceratina calcarata
SWMREC	Symphyotrichum sericeum	Ceratina dupla
SWMREC	Symphyotrichum sericeum	Ceratina mikmaqi
SWMREC	Symphyotrichum sericeum	Halictus 131onfuses
SWMREC	Symphyotrichum sericeum	Halictus ligatus
SWMREC	Symphyotrichum sericeum	Lasioglossum leucozonium
SWMREC	Symphyotrichum sericeum	Lasioglossum pilosum
SWMREC	Symphyotrichum sericeum	Megachile mendica
SWMREC	Symphyotrichum sericeum	Megachile texana
SWMREC	Symphyotrichum sericeum	Melissodes druriellus
SWMREC	Tradescantia ohiensis	Agapostemon virescens
SWMREC	Tradescantia ohiensis	Augochlorella aurata
SWMREC	Tradescantia ohiensis	Bombus bimaculatus
SWMREC	Tradescantia ohiensis	Bombus griseocollis
SWMREC	Tradescantia ohiensis	Bombus impatiens
SWMREC	Tradescantia ohiensis	Eucera hamata
SWMREC	Tradescantia ohiensis	Lasioglossum albipenne
SWMREC	Tradescantia ohiensis	Lasioglossum coriaceum
SWMREC	Tradescantia ohiensis	Lasioglossum leucozonium

SWMREC	Tradescantia ohiensis	Lasioglossum pectorale	1
SWMREC	Verbena stricta	Agapostemon texanus	1
SWMREC	Verbena stricta	Agapostemon virescens	2
SWMREC	Verbena stricta	Bombus citrinus	2
SWMREC	Verbena stricta	Bombus griseocollis	1
SWMREC	Verbena stricta	Bombus impatiens	8
SWMREC	Verbena stricta	Ceratina calcarata	3
SWMREC	Verbena stricta	Ceratina dupla	1
SWMREC	Verbena stricta	Lasioglossum leucocomum	2
SWMREC	Verbena stricta	Lasioglossum pilosum	1
SWMREC	Verbena stricta	Megachile brevis	1
SWMREC	Verbena stricta	Megachile mendica	3
SWMREC	Verbena stricta	Osmia simillima	1
CRC	Achillea millefolium	Andrena wilkella	1
CRC	Achillea millefolium	Augochlorella aurata	1
CRC	Achillea millefolium	Halictus ligatus	31
CRC	Achillea millefolium	Hylaeus affinis	1
CRC	Achillea millefolium	Lasioglossum albipenne	1
CRC	Achillea millefolium	Lasioglossum hitchensi	5
CRC	Achillea millefolium	Lasioglossum perpunctatum	1
CRC	Achillea millefolium	Osmia lignaria	1
CRC	Amorpha canescens	Lasioglossum albipenne	1
CRC	Amorpha canescens	Lasioglossum ellisiae	2
CRC	Amorpha canescens	Lasioglossum hitchensi	2
CRC	Amorpha canescens	Lasioglossum imitatum	1
CRC	Amorpha canescens	Lasioglossum paradmirandum	1
CRC	Amorpha canescens	Lasioglossum pruinosum	1
CRC	Amorpha canescens	Lasioglossum tegulare	1

CRC	Asclepias syriaca	Apis mellifera	1
CRC	Asclepias syriaca	Bombus bimaculatus	1
CRC	Asclepias syriaca	Halictus ligatus	8
CRC	Asclepias syriaca	Lasioglossum admirandum	1
CRC	Asclepias syriaca	Lasioglossum anomalum	2
CRC	Asclepias syriaca	Lasioglossum hitchensi	6
CRC	Asclepias syriaca	Lasioglossum paradmirandum	1
CRC	Asclepias syriaca	Lasioglossum pectorale	1
CRC	Asclepias syriaca	Lasioglossum perpunctatum	2
CRC	Asclepias syriaca	Lasioglossum platyparium	1
CRC	Asclepias syriaca	Lasioglossum tegulare	1
CRC	Asclepias syriaca	Osmia lignaria	2
CRC	Asclepias tuberosa	Augochlorella aurata	2
CRC	Asclepias tuberosa	Bombus bimaculatus	9
CRC	Asclepias tuberosa	Halictus ligatus	5
CRC	Asclepias tuberosa	Lasioglossum admirandum	2
CRC	Asclepias tuberosa	Lasioglossum albipenne	1
CRC	Asclepias tuberosa	Lasioglossum anomalum	2
CRC	Asclepias tuberosa	Lasioglossum hitchensi	7
CRC	Asclepias tuberosa	Lasioglossum lasioglossum	2
CRC	Asclepias tuberosa	Lasioglossum weemsi	1
CRC	Asclepias tuberosa	Megachile frugalis	1
CRC	Asclepias tuberosa	Melissodes communis	1
CRC	Asclepias tuberosa	Melissodes denticulatus	1
CRC	Asclepias tuberosa	Melissodes druriellus	1
CRC	Asclepias tuberosa	Melissodes subillatus	2
CRC	Asclepias tuberosa	Melissodes tinctus	1
CRC	Asclepias verticillata	Andrena wilkella	1

Table	C1	(cont'd)
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CRC	Asclepias verticillata	Bombus bimaculatus	1
CRC	Asclepias verticillata	Ceratina mikmaqi	1
CRC	Asclepias verticillata	Colletes nudus	1
CRC	Asclepias verticillata	Halictus 134onfuses	6
CRC	Asclepias verticillata	Halictus ligatus	1
CRC	Asclepias verticillata	Hylaeus affinis	2
CRC	Asclepias verticillata	Hylaeus affinis/modestus	4
CRC	Asclepias verticillata	Lasioglossum admirandum	2
CRC	Asclepias verticillata	Lasioglossum ephialtum	2
CRC	Asclepias verticillata	Lasioglossum hitchensi	18
CRC	Asclepias verticillata	Lasioglossum imitatum	2
CRC	Asclepias verticillata	Lasioglossum lasioglossum	1
CRC	Asclepias verticillata	Lasioglossum lineatulum	1
CRC	Asclepias verticillata	Lasioglossum oceanicum	1
CRC	Asclepias verticillata	Lasioglossum paradmirandum	4
CRC	Asclepias verticillata	Lasioglossum perpunctatum	1
CRC	Asclepias verticillata	Lasioglossum pilosum	2
CRC	Asclepias verticillata	Lasioglossum sp.	2
CRC	Asclepias verticillata	Lasioglossum tegulare	2
CRC	Asclepias verticillata	Lasioglossum versatum	3
CRC	Asclepias verticillata	Lasioglossum weemsi	1
CRC	Asclepias verticillata	Megachile rotundata	2
CRC	Asclepias verticillata	Protandrena cockerelli	2
CRC	Asclepias verticillata	Xylocopa virginica	1
CRC	Campanula rotundifolia	Lasioglossum leucozonium	1
CRC	Campanula rotundifolia	Lasioglossum paradmirandum	1
CRC	Ceanothus americanus	Halictus ligatus	1
CRC	Ceanothus americanus	Hylaeus affinis	1

CRC	Ceanothus americanus	Lasioglossum pilosum	1
CRC	Centaurea stoebe micranthos	Agapostemon virescens	2
CRC	Centaurea stoebe micranthos	Apis mellifera	2
CRC	Centaurea stoebe micranthos	Bombus bimaculatus	2
CRC	Centaurea stoebe micranthos	Bombus fervidus	1
CRC	Centaurea stoebe micranthos	Bombus impatiens	6
CRC	Centaurea stoebe micranthos	Bombus vagans	1
CRC	Centaurea stoebe micranthos	Ceratina calcarata	1
CRC	Centaurea stoebe micranthos	Ceratina dupla	6
CRC	Centaurea stoebe micranthos	Ceratina mikmaqi	4
CRC	Centaurea stoebe micranthos	Halictus 135onfuses	1
CRC	Centaurea stoebe micranthos	Halictus ligatus	22
CRC	Centaurea stoebe micranthos	Lasioglossum hitchensi	10
CRC	Centaurea stoebe micranthos	Lasioglossum imitatum	4
CRC	Centaurea stoebe micranthos	Lasioglossum leucocomum	1
CRC	Centaurea stoebe micranthos	Lasioglossum leucozonium	48
CRC	Centaurea stoebe micranthos	Lasioglossum paradmirandum	20
CRC	Centaurea stoebe micranthos	Lasioglossum pectorale	1
CRC	Centaurea stoebe micranthos	Lasioglossum pilosum	1
CRC	Centaurea stoebe micranthos	Lasioglossum tegulare	1
CRC	Centaurea stoebe micranthos	Lasioglossum versatum	1
CRC	Centaurea stoebe micranthos	Megachile brevis	1
CRC	Centaurea stoebe micranthos	Melissodes agilis	2
CRC	Chamerion angustifolium	Bombus bimaculatus	1
CRC	Chamerion angustifolium	Lasioglossum hitchensi	2
CRC	Coreopsis lanceolata	Agapostemon virescens	2
CRC	Coreopsis lanceolata	Andrena crataegi	1
CRC	Coreopsis lanceolata	Andrena perplexa	1

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CRC	Coreopsis lanceolata	Andrena wilkella	3
CRC	Coreopsis lanceolata	Augochlorella aurata	1
CRC	Coreopsis lanceolata	Ceratina calcarata	1
CRC	Coreopsis lanceolata	Ceratina mikmaqi	9
CRC	Coreopsis lanceolata	Halictus ligatus	26
CRC	Coreopsis lanceolata	Halictus parallelus	1
CRC	Coreopsis lanceolata	Heriades carinata	1
CRC	Coreopsis lanceolata	Lasioglossum albipenne	2
CRC	Coreopsis lanceolata	Lasioglossum hitchensi	3
CRC	Coreopsis lanceolata	Lasioglossum leucozonium	6
CRC	Coreopsis lanceolata	Lasioglossum paraforbesii	2
CRC	Coreopsis lanceolata	Lasioglossum pectorale	1
CRC	Coreopsis lanceolata	Lasioglossum sp.	1
CRC	Coreopsis lanceolata	Melissodes denticulatus	1
CRC	Coreopsis lanceolata	Melissodes illatus	1
CRC	Coreopsis lanceolata	Nomada articulata	1
CRC	Coreopsis lanceolata	Osmia pumila	1
CRC	Coreopsis palmata	Halictus ligatus	8
CRC	Coreopsis palmata	Halictus rubicundus	1
CRC	Coreopsis palmata	Lasioglossum leucozonium	1
CRC	Coreopsis palmata	Megachile pugnata	1
CRC	Coreopsis palmata	Melissodes druriellus	1
CRC	Coreopsis palmata	Melissodes subillatus	1
CRC	Coreopsis tripteris	Agapostemon sericeus	1
CRC	Coreopsis tripteris	Andrena helianthi	7
CRC	Coreopsis tripteris	Bombus impatiens	4
CRC	Coreopsis tripteris	Ceratina calcarata	3
CRC	Coreopsis tripteris	Ceratina mikmaqi	1

	Tab	le C1	(cont'd)
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CRC	Coreopsis tripteris	Halictus ligatus	46
CRC	Coreopsis tripteris	Halictus parallelus	1
CRC	Coreopsis tripteris	Lasioglossum albipenne	3
CRC	Coreopsis tripteris	Lasioglossum coriaceum	2
CRC	Coreopsis tripteris	Lasioglossum hitchensi	1
CRC	Coreopsis tripteris	Lasioglossum leucozonium	7
CRC	Coreopsis tripteris	Lasioglossum paradmirandum	2
CRC	Coreopsis tripteris	Lasioglossum pilosum	1
CRC	Coreopsis tripteris	Lasioglossum versatum	1
CRC	Coreopsis tripteris	Melissodes agilis	1
CRC	Coreopsis tripteris	Melissodes denticulatus	2
CRC	Coreopsis tripteris	Melissodes druriellus	1
CRC	Coreopsis tripteris	Melissodes melissodes	1
CRC	Coreopsis tripteris	Melissodes subillatus	1
CRC	Coreopsis tripteris	Melissodes tinctus	1
CRC	Coreopsis tripteris	Perdita bequaerti	1
CRC	Coreopsis tripteris	Xylocopa virginica	1
CRC	Dalea purpurea	Agapostemon virescens	1
CRC	Dalea purpurea	Augochlorella aurata	10
CRC	Dalea purpurea	Bombus impatiens	3
CRC	Dalea purpurea	Ceratina calcarata	1
CRC	Dalea purpurea	Ceratina dupla	1
CRC	Dalea purpurea	Ceratina mikmaqi	1
CRC	Dalea purpurea	Halictus 137onfuses	18
CRC	Dalea purpurea	Halictus ligatus	3
CRC	Dalea purpurea	Hylaeus affinis	4
CRC	Dalea purpurea	Hylaeus affinis/modestus	18
CRC	Dalea purpurea	Lasioglossum albipenne	1

CRC	Dalea purpurea	Lasioglossum anomalum	2
CRC	Dalea purpurea	Lasioglossum hitchensi	8
CRC	Dalea purpurea	Lasioglossum imitatum	2
CRC	Dalea purpurea	Lasioglossum leucozonium	1
CRC	Dalea purpurea	Lasioglossum lineatulum	1
CRC	Dalea purpurea	Lasioglossum paradmirandum	12
CRC	Dalea purpurea	Lasioglossum pectorale	1
CRC	Dalea purpurea	Lasioglossum perpunctatum	1
CRC	Dalea purpurea	Lasioglossum tegulare	6
CRC	Dalea purpurea	Lasioglossum weemsi	1
CRC	Dalea purpurea	Lasioglossum zephyrum	1
CRC	Dasiphora fruticosa	Agapostemon virescens	1
CRC	Dasiphora fruticosa	Augochlorella aurata	1
CRC	Dasiphora fruticosa	Lasioglossum albipenne	2
CRC	Echinacea purpurea	Apis mellifera	1
CRC	Echinacea purpurea	Bombus bimaculatus	1
CRC	Echinacea purpurea	Bombus griseocollis	5
CRC	Echinacea purpurea	Bombus impatiens	1
CRC	Echinacea purpurea	Ceratina mikmaqi	1
CRC	Echinacea purpurea	Halictus ligatus	15
CRC	Echinacea purpurea	Lasioglossum leucocomum	1
CRC	Echinacea purpurea	Lasioglossum pilosum	1
CRC	Echinacea purpurea	Lasioglossum tegulare	1
CRC	Echinacea purpurea	Megachile pugnata	2
CRC	Echinacea purpurea	Melissodes agilis	4
CRC	Echinacea purpurea	Melissodes bimaculatus	1
CRC	Echinacea purpurea	Melissodes druriellus	2
CRC	Eryngium yuccifolium	Agapostemon splendens	1

Table C1 (cont'd)			
CRC	Eryngium yuccifolium	Bombus impatiens	1
CRC	Eryngium yuccifolium	Ceratina calcarata	1
CRC	Eryngium yuccifolium	Halictus ligatus	3
CRC	Eryngium yuccifolium	Hylaeus affinis	1
CRC	Eryngium yuccifolium	Hylaeus affinis/modestus	7
CRC	Eryngium yuccifolium	Lasioglossum admirandum	1
CRC	Eryngium yuccifolium	Lasioglossum hitchensi	30
CRC	Eryngium yuccifolium	Lasioglossum imitatum	6
CRC	Eryngium yuccifolium	Lasioglossum lineatulum	4
CRC	Eryngium yuccifolium	Lasioglossum paradmirandum	11
CRC	Eryngium yuccifolium	Lasioglossum pectorale	2
CRC	Eryngium yuccifolium	Lasioglossum sp.	1
CRC	Eryngium yuccifolium	Lasioglossum versatum	1
CRC	Eryngium yuccifolium	Xylocopa virginica	1
CRC	Helianthus occidentalis	Ceratina dupla	2
CRC	Helianthus occidentalis	Halictus ligatus	38
CRC	Helianthus occidentalis	Lasioglossum albipenne	1
CRC	Helianthus occidentalis	Lasioglossum leucozonium	3
CRC	Helianthus occidentalis	Lasioglossum sp.	2
CRC	Helianthus occidentalis	Megachile brevis	1
CRC	Helianthus occidentalis	Melissodes agilis	3
CRC	Helianthus occidentalis	Perdita bequaerti	1
CRC	Helianthus strumosus	Andrena helianthi	3
CRC	Helianthus strumosus	Augochlorella aurata	1
CRC	Helianthus strumosus	Bombus impatiens	3
CRC	Helianthus strumosus	Ceratina mikmaqi	2
CRC	Helianthus strumosus	Halictus ligatus	5
CRC	Helianthus strumosus	Lasioglossum leucozonium	1

Table C1	(cont'd)
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CRC	Helianthus strumosus	Melissodes agilis	8
CRC	Helianthus strumosus	Melissodes druriellus	5
CRC	Hieracium gronovii	Halictus ligatus	1
CRC	Hieracium gronovii	Lasioglossum hitchensi	2
CRC	Hieracium gronovii	Lasioglossum leucozonium	4
CRC	Hypericum prolificum	Bombus bimaculatus	18
CRC	Hypericum prolificum	Bombus impatiens	3
CRC	Hypericum prolificum	Bombus vagans	1
CRC	Hypericum prolificum	Halictus ligatus	1
CRC	Hypericum prolificum	Hylaeus affinis/modestus	6
CRC	Hypericum prolificum	Hylaeus modestus	1
CRC	Hypericum prolificum	Lasioglossum hitchensi	3
CRC	Hypericum prolificum	Lasioglossum paradmirandum	5
CRC	Hypericum prolificum	Lasioglossum pilosum	2
CRC	Hypericum prolificum	Lasioglossum versatum	1
CRC	Lespedeza capitata	Bombus impatiens	1
CRC	Lespedeza hirta	Anthidium oblongatum	1
CRC	Lespedeza hirta	Lasioglossum hitchensi	1
CRC	Liatris aspera	Lasioglossum sp.	1
CRC	Liatris cylindracea	Lasioglossum leucozonium	1
CRC	Lotus corniculatus L.	Andrena commoda	1
CRC	Lotus corniculatus L.	Andrena nasonii	1
CRC	Lotus corniculatus L.	Andrena wilkella	14
CRC	Lotus corniculatus L.	Anthidium manicatum	3
CRC	Lotus corniculatus L.	Anthidium oblongatum	16
CRC	Lotus corniculatus L.	Bombus bimaculatus	3
CRC	Lotus corniculatus L.	Bombus fervidus	1
CRC	Lotus corniculatus L.	Halictus ligatus	1

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CRC	Lotus corniculatus L.	Halictus rubicundus	1
CRC	Lotus corniculatus L.	Hoplitis pilosifrons	1
CRC	Lotus corniculatus L.	Megachile mendica	1
CRC	Lotus corniculatus L.	Megachile rotundata	4
CRC	Lotus corniculatus L.	Osmia lignaria	2
CRC	Monarda fistulosa	Andrena thaspii	1
CRC	Monarda fistulosa	Augochlorella aurata	4
CRC	Monarda fistulosa	Bombus auricomus	1
CRC	Monarda fistulosa	Bombus bimaculatus	107
CRC	Monarda fistulosa	Bombus griseocollis	2
CRC	Monarda fistulosa	Bombus impatiens	11
CRC	Monarda fistulosa	Bombus perplexus	1
CRC	Monarda fistulosa	Bombus vagans	1
CRC	Monarda fistulosa	Ceratina dupla	2
CRC	Monarda fistulosa	Dufourea monardae	1
CRC	Monarda fistulosa	Heriades carinata	10
CRC	Monarda fistulosa	Lasioglossum albipenne	1
CRC	Monarda fistulosa	Lasioglossum anomalum	34
CRC	Monarda fistulosa	Lasioglossum ellisiae	1
CRC	Monarda fistulosa	Lasioglossum hitchensi	29
CRC	Monarda fistulosa	Lasioglossum imitatum	3
CRC	Monarda fistulosa	Lasioglossum leucozonium	1
CRC	Monarda fistulosa	Lasioglossum paradmirandum	7
CRC	Monarda fistulosa	Lasioglossum pectorale	1
CRC	Monarda fistulosa	Lasioglossum tegulare	1
CRC	Monarda fistulosa	Xylocopa virginica	1
CRC	Monarda punctata	Bombus impatiens	1
CRC	Monarda punctata	Lasioglossum ellisiae	1

Table C1 (c	ont'd)		
CRC	Monarda punctata	Lasioglossum hitchensi	1
CRC	Monarda punctata	Lasioglossum tegulare	1
CRC	Oenothera fruticosa	Agapostemon virescens	1
CRC	Oenothera fruticosa	Augochlorella aurata	2
CRC	Oenothera fruticosa	Ceratina dupla	1
CRC	Oenothera fruticosa	Ceratina mikmaqi	2
CRC	Oenothera fruticosa	Halictus ligatus	2
CRC	Oenothera fruticosa	Lasioglossum coriaceum	1
CRC	Oenothera fruticosa	Lasioglossum hitchensi	1
CRC	Oenothera fruticosa	Lasioglossum leucozonium	1
CRC	Oenothera fruticosa	Lasioglossum lineatulum	1
CRC	Oenothera fruticosa	Lasioglossum pectorale	2
CRC	Oenothera fruticosa	Lasioglossum versatum	1
CRC	Oenothera fruticosa	Sphecodes confertus	1
CRC	Oligoneuron rigidum	Andrena simplex	2
CRC	Oligoneuron rigidum	Bombus impatiens	1
CRC	Oligoneuron rigidum	Halictus ligatus	9
CRC	Oligoneuron rigidum	Hylaeus affinis/modestus	1
CRC	Oligoneuron rigidum	Lasioglossum hitchensi	1
CRC	Penstemon digitalis	Andrena wilkella	1
CRC	Penstemon digitalis	Augochlorella aurata	2
CRC	Penstemon digitalis	Bombus bimaculatus	8
CRC	Penstemon digitalis	Bombus fervidus	2
CRC	Penstemon digitalis	Ceratina dupla	4
CRC	Penstemon digitalis	Ceratina mikmaqi	11
CRC	Penstemon digitalis	Eucera hamata	5
CRC	Penstemon digitalis	Hoplitis pilosifrons	9
CRC	Penstemon digitalis	Lasioglossum albipenne	4

Table C1 (cont'd))
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CRC	Penstemon digitalis	Lasioglossum coriaceum	1
CRC	Penstemon digitalis	Lasioglossum hitchensi	4
CRC	Penstemon digitalis	Lasioglossum paradmirandum	3
CRC	Penstemon digitalis	Lasioglossum pilosum	1
CRC	Penstemon digitalis	Megachile mucida	2
CRC	Penstemon digitalis	Xylocopa virginica	1
CRC	Penstemon hirsutus	Bombus bimaculatus	2
CRC	Penstemon hirsutus	Ceratina dupla	3
CRC	Penstemon hirsutus	Ceratina mikmaqi	1
CRC	Penstemon hirsutus	Eucera dubitata	2
CRC	Penstemon hirsutus	Eucera hamata	5
CRC	Penstemon hirsutus	Hoplitis pilosifrons	2
CRC	Penstemon hirsutus	Lasioglossum albipenne	3
CRC	Penstemon hirsutus	Lasioglossum paradmirandum	2
CRC	Penstemon hirsutus	Lasioglossum sp.	1
CRC	Penstemon hirsutus	Xylocopa virginica	1
CRC	Potentilla simplex	Augochlorella aurata	2
CRC	Potentilla simplex	Hylaeus affinis	1
CRC	Potentilla simplex	Lasioglossum albipenne	1
CRC	Potentilla simplex	Nomada sayi	2
CRC	Potentilla simplex	Osmia lignaria	1
CRC	Pycnanthemum virginianum	Andrena wilkella	2
CRC	Pycnanthemum virginianum	Bombus bimaculatus	1
CRC	Pycnanthemum virginianum	Bombus griseocollis	1
CRC	Pycnanthemum virginianum	Bombus impatiens	2
CRC	Pycnanthemum virginianum	Ceratina dupla	3
CRC	Pycnanthemum virginianum	Ceratina mikmaqi	1
CRC	Pycnanthemum virginianum	Halictus ligatus	1

Table	C1	(cont'd)	
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CRC	Pycnanthemum virginianum	Halictus rubicundus	1
CRC	Pycnanthemum virginianum	Heriades carinata	1
CRC	Pycnanthemum virginianum	Hylaeus affinis/modestus	5
CRC	Pycnanthemum virginianum	Hylaeus mesillae	1
CRC	Pycnanthemum virginianum	Lasioglossum ephialtum	1
CRC	Pycnanthemum virginianum	Lasioglossum hitchensi	19
CRC	Pycnanthemum virginianum	Lasioglossum imitatum	1
CRC	Pycnanthemum virginianum	Lasioglossum leucozonium	1
CRC	Pycnanthemum virginianum	Lasioglossum paradmirandum	17
CRC	Pycnanthemum virginianum	Lasioglossum paraforbesii	1
CRC	Pycnanthemum virginianum	Lasioglossum pectorale	1
CRC	Pycnanthemum virginianum	Lasioglossum perpunctatum	2
CRC	Pycnanthemum virginianum	Lasioglossum tegulare	3
CRC	Pycnanthemum virginianum	Megachile rotundata	2
CRC	Pycnanthemum virginianum	Melissodes bimaculatus	1
CRC	Pycnanthemum virginianum	Melissodes communis	1
CRC	Pycnanthemum virginianum	Sphecodes confertus	1
CRC	Pycnanthemum virginianum	Sphecodes dichrous	1
CRC	Ratibida pinnata	Andrena rudbeckiae	1
CRC	Ratibida pinnata	Bombus bimaculatus	1
CRC	Ratibida pinnata	Bombus impatiens	1
CRC	Ratibida pinnata	Calliopsis andreniformis	1
CRC	Ratibida pinnata	Halictus ligatus	23
CRC	Ratibida pinnata	Hylaeus affinis/modestus	1
CRC	Ratibida pinnata	Lasioglossum hitchensi	1
CRC	Ratibida pinnata	Melissodes agilis	2
CRC	Ratibida pinnata	Melissodes druriellus	4
CRC	Rhus copallinum	Lasioglossum coriaceum	1

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CRC	Rhus copallinum	
CRC	Rosa carolina	
CRC	Rudbeckia hirta	
CRC	Senecio obovatus	

Senecio obovatus

Silphium integrifolium

Lasioglossum hitchensi
Lasioglossum paradmirandum
Lasioglossum pilosum
Halictus ligatus
Lasioglossum paradmirandum
Lasioglossum pectorale
Lasioglossum perpunctatum
Lasioglossum pilosum
Lasioglossum versatum
Melissodes druriellus
Melissodes illatus
Melissodes subillatus
Andrena nasonii
Apis mellifera
Augochlorella aurata
Halictus ligatus
Osmia pumila
Agapostemon virescens
Andrena aliciae
Andrena helianthi
Apis mellifera
Bombus bimaculatus
Bombus citrinus
Bombus griseocollis
Bombus impatiens

Megachile brevis

Hylaeus affinis

Bombus bimaculatus

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Table C1 (cont'd)

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Table C1	(conťd)
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CRC	Silphium integrifolium	Bombus vagans	2
CRC	Silphium integrifolium	Halictus ligatus	8
CRC	Silphium integrifolium	Lasioglossum hitchensi	2
CRC	Silphium integrifolium	Lasioglossum paradmirandum	1
CRC	Silphium integrifolium	Lasioglossum tegulare	1
CRC	Silphium integrifolium	Melissodes agilis	9
CRC	Silphium integrifolium	Melissodes druriellus	3
CRC	Silphium integrifolium	Melissodes melissodes	1
CRC	Silphium laciniatum	Halictus ligatus	4
CRC	Silphium laciniatum	Lasioglossum hitchensi	1
CRC	Silphium laciniatum	Lasioglossum pilosum	1
CRC	Silphium laciniatum	Melissodes agilis	4
CRC	Silphium terebinthinaceum	Agapostemon virescens	4
CRC	Silphium terebinthinaceum	Apis mellifera	1
CRC	Silphium terebinthinaceum	Bombus fervidus	1
CRC	Silphium terebinthinaceum	Bombus impatiens	5
CRC	Silphium terebinthinaceum	Ceratina mikmaqi	1
CRC	Silphium terebinthinaceum	Halictus ligatus	3
CRC	Silphium terebinthinaceum	Melissodes agilis	7
CRC	Silphium terebinthinaceum	Melissodes druriellus	1
CRC	Silphium terebinthinaceum	Perdita bequaerti	1
CRC	Silphium terebinthinaceum	Xylocopa virginica	1
CRC	Solidago juncea	Andrena placata	6
CRC	Solidago juncea	Bombus impatiens	2
CRC	Solidago juncea	Colletes simulans armatus	1
CRC	Solidago juncea	Halictus 146onfuses	1
CRC	Solidago juncea	Halictus ligatus	38
CRC	Solidago juncea	Hylaeus mesillae	4

Table C1 (cor	nťd)	
CRC	Solidago juncea	Lasioglossum albipenne
CRC	Solidago juncea	Lasioglossum hitchensi
CRC	Solidago juncea	Lasioglossum imitatum
CRC	Solidago juncea	Lasioglossum paradmirandum
CRC	Solidago juncea	Lasioglossum perpunctatum
CRC	Solidago juncea	Lasioglossum pruinosum
CRC	Solidago juncea	Lasioglossum sp.
CRC	Solidago juncea	Melissodes druriellus
CRC	Solidago nemoralis	Bombus bimaculatus
CRC	Solidago nemoralis	Bombus impatiens
CRC	Solidago nemoralis	Halictus ligatus
CRC	Solidago nemoralis	Hylaeus affinis
CRC	Solidago nemoralis	Lasioglossum albipenne
CRC	Solidago nemoralis	Lasioglossum anomalum
CRC	Solidago nemoralis	Lasioglossum hitchensi
CRC	Solidago nemoralis	Lasioglossum imitatum
CRC	Solidago nemoralis	Lasioglossum michiganense
CRC	Solidago nemoralis	Lasioglossum pectorale
CRC	Solidago nemoralis	Lasioglossum perpunctatum
CRC	Solidago nemoralis	Lasioglossum platyparium
CRC	Solidago nemoralis	Lasioglossum tegulare
CRC	Solidago speciosa	Andrena placata
CRC	Solidago speciosa	Apis mellifera
CRC	Solidago speciosa	Bombus citrinus
CRC	Solidago speciosa	Bombus impatiens
CRC	Solidago speciosa	Halictus ligatus
CRC	Solidago speciosa	Hylaeus affinis/modestus
CRC	Solidago speciosa	Lasioglossum paraforbesii

Table C1 (co	nťd)		
CRC	Solidago speciosa	Xylocopa virginica	1
CRC	Symphyotrichum oolentangiense	Agapostemon sericeus	2
CRC	Symphyotrichum oolentangiense	Agapostemon texanus	1
CRC	Symphyotrichum oolentangiense	Agapostemon virescens	1
CRC	Symphyotrichum oolentangiense	Andrena placata	2
CRC	Symphyotrichum oolentangiense	Andrena simplex	2
CRC	Symphyotrichum oolentangiense	Augochlorella aurata	2
CRC	Symphyotrichum oolentangiense	Bombus impatiens	20
CRC	Symphyotrichum oolentangiense	Ceratina calcarata	2
CRC	Symphyotrichum oolentangiense	Ceratina dupla	2
CRC	Symphyotrichum oolentangiense	Ceratina mikmaqi	4
CRC	Symphyotrichum oolentangiense	Coelioxys alternatus	1
CRC	Symphyotrichum oolentangiense	Halictus ligatus	9
CRC	Symphyotrichum oolentangiense	Lasioglossum albipenne	1
CRC	Symphyotrichum oolentangiense	Lasioglossum hitchensi	12
CRC	Symphyotrichum oolentangiense	Lasioglossum imitatum	7
CRC	Symphyotrichum oolentangiense	Lasioglossum paradmirandum	3
CRC	Symphyotrichum oolentangiense	Lasioglossum paraforbesii	1
CRC	Symphyotrichum oolentangiense	Lasioglossum pectorale	1
CRC	Symphyotrichum oolentangiense	Melissodes druriellus	1
CRC	Symphyotrichum oolentangiense	Psuedo panurgus andrenoides	1
CRC	Symphyotrichum sericeum	Agapostemon splendens	1
CRC	Symphyotrichum sericeum	Agapostemon virescens	12
CRC	Symphyotrichum sericeum	Augochlorella aurata	1
CRC	Symphyotrichum sericeum	Bombus impatiens	4
CRC	Symphyotrichum sericeum	Ceratina dupla	4
CRC	Symphyotrichum sericeum	Ceratina mikmaqi	5
CRC	Symphyotrichum sericeum	Halictus ligatus	7

Table	C1	(cont'd))
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CRC	Symphyotrichum sericeum	Lasioglossum hitchensi	3
CRC	Symphyotrichum sericeum	Lasioglossum imitatum	2
CRC	Symphyotrichum sericeum	Lasioglossum leucozonium	5
CRC	Symphyotrichum sericeum	Lasioglossum paradmirandum	1
CRC	Symphyotrichum sericeum	Megachile latimanus	2
CRC	Symphyotrichum sericeum	Melissodes druriellus	1
CRC	Tradescantia ohiensis	Augochlorella aurata	1
CRC	Tradescantia ohiensis	Halictus ligatus	1
CRC	Tradescantia ohiensis	Lasioglossum albipenne	1
CRC	Tradescantia ohiensis	Lasioglossum hitchensi	8
CRC	Tradescantia ohiensis	Lasioglossum leucozonium	2
CRC	Tradescantia ohiensis	Lasioglossum paradmirandum	3
CRC	Tradescantia ohiensis	Lasioglossum pectorale	1
CRC	Tradescantia ohiensis	Lasioglossum perpunctatum	1
CRC	Tradescantia ohiensis	Lasioglossum sp.	2
CRC	Verbena stricta	Andrena wilkella	1
CRC	Verbena stricta	Apis mellifera	1
CRC	Verbena stricta	Augochlorella aurata	1
CRC	Verbena stricta	Bombus bimaculatus	2
CRC	Verbena stricta	Bombus impatiens	1
CRC	Verbena stricta	Ceratina dupla	1
CRC	Verbena stricta	Ceratina mikmaqi	2
CRC	Verbena stricta	Megachile frugalis	1
NWMHRC	Achillea millefolium	Bombus bimaculatus	1
NWMHRC	Achillea millefolium	Halictus ligatus	2
NWMHRC	Achillea millefolium	Megachile latimanus	2
NWMHRC	Achillea millefolium	Melissodes druriellus	1
NWMHRC	Achillea millefolium	Melissodes subillatus	1

NWMHRC	Amorpha canescens	Lasioglossum pilosum	1
NWMHRC	Amorpha canescens	Megachile latimanus	3
NWMHRC	Amorpha canescens	Melissodes communis	1
NWMHRC	Asclepias syriaca	Bombus griseocollis	1
NWMHRC	Asclepias syriaca	Halictus ligatus	1
NWMHRC	Asclepias syriaca	Megachile latimanus	1
NWMHRC	Asclepias tuberosa	Augochlorella aurata	1
NWMHRC	Asclepias tuberosa	Lasioglossum leucozonium	1
NWMHRC	Asclepias tuberosa	Megachile pugnata	1
NWMHRC	Asclepias verticillata	Lasioglossum pilosum	1
NWMHRC	Baptisia alba var. macrophylla	Lasioglossum leucocomum	1
NWMHRC	Campanula rotundifolia	Melissodes agilis	3
NWMHRC	Campanula rotundifolia	Melissodes subillatus	1
NWMHRC	Ceanothus americanus	Augochlorella aurata	1
NWMHRC	Centaurea stoebe micranthos	Anthophora walshii	1
NWMHRC	Centaurea stoebe micranthos	Lasioglossum leucozonium	1
NWMHRC	Centaurea stoebe micranthos	Megachile pugnata	1
NWMHRC	Coreopsis lanceolata	Apis mellifera	1
NWMHRC	Coreopsis lanceolata	Dianthidium simile	1
NWMHRC	Coreopsis lanceolata	Halictus ligatus	8
NWMHRC	Coreopsis lanceolata	Lasioglossum paraforbesii	1
NWMHRC	Coreopsis lanceolata	Megachile latimanus	7
NWMHRC	Coreopsis lanceolata	Megachile mendica	1
NWMHRC	Coreopsis lanceolata	Megachile pugnata	5
NWMHRC	Coreopsis lanceolata	Melissodes agilis	3
NWMHRC	Coreopsis lanceolata	Melissodes druriellus	4
NWMHRC	Coreopsis lanceolata	Melissodes subillatus	1
NWMHRC	Coreopsis lanceolata	Nomada sp.	1

NWMHRC	Coreopsis palmata	Megachile pugnata	3
NWMHRC	Coreopsis palmata	Melissodes denticulatus	1
NWMHRC	Coreopsis tripteris	Agapostemon virescens	1
NWMHRC	Coreopsis tripteris	Bombus impatiens	2
NWMHRC	Coreopsis tripteris	Ceratina mikmaqi	1
NWMHRC	Coreopsis tripteris	Halictus 151onfuses	1
NWMHRC	Coreopsis tripteris	Halictus ligatus	12
NWMHRC	Coreopsis tripteris	Melissodes subillatus	1
NWMHRC	Coreopsis tripteris	Melissodes tinctus	2
NWMHRC	Dalea purpurea	Augochlorella aurata	1
NWMHRC	Dalea purpurea	Lasioglossum pilosum	1
NWMHRC	Dasiphora fruticosa	Anthophora walshii	1
NWMHRC	Echinacea purpurea	Bombus impatiens	7
NWMHRC	Echinacea purpurea	Bombus vagans	1
NWMHRC	Echinacea purpurea	Halictus ligatus	1
NWMHRC	Echinacea purpurea	Lasioglossum pilosum	1
NWMHRC	Echinacea purpurea	Megachile pugnata	8
NWMHRC	Echinacea purpurea	Melissodes druriellus	1
NWMHRC	Eryngium yuccifolium	Bombus griseocollis	1
NWMHRC	Eryngium yuccifolium	Colletes mandibularis	1
NWMHRC	Eryngium yuccifolium	Halictus ligatus	1
NWMHRC	Eryngium yuccifolium	Megachile latimanus	1
NWMHRC	Helianthus occidentalis	Bombus impatiens	1
NWMHRC	Helianthus occidentalis	Halictus ligatus	3
NWMHRC	Helianthus occidentalis	Lasioglossum leucozonium	1
NWMHRC	Helianthus occidentalis	Lasioglossum pilosum	1
NWMHRC	Helianthus occidentalis	Melissodes agilis	1
NWMHRC	Helianthus occidentalis	Melissodes denticulatus	1

NWMHRC	Helianthus occidentalis	Melissodes druriellus	1
NWMHRC	Helianthus occidentalis	Melissodes illatus	1
NWMHRC	Helianthus occidentalis	Melissodes tinctus	2
NWMHRC	Helianthus occidentalis	Perdita albipennis	2
NWMHRC	Helianthus strumosus	Agapostemon virescens	4
NWMHRC	Helianthus strumosus	Bombus impatiens	5
NWMHRC	Helianthus strumosus	Halictus ligatus	2
NWMHRC	Helianthus strumosus	Melissodes agilis	1
NWMHRC	Helianthus strumosus	Melissodes druriellus	1
NWMHRC	Helianthus strumosus	Melissodes tinctus	3
NWMHRC	Hypericum prolificum	Bombus bimaculatus	5
NWMHRC	Hypericum prolificum	Bombus griseocollis	5
NWMHRC	Hypericum prolificum	Bombus impatiens	8
NWMHRC	Hypericum prolificum	Bombus perplexus	1
NWMHRC	Hypericum prolificum	Bombus ternarius	1
NWMHRC	Lespedeza capitata	Bombus fervidus	1
NWMHRC	Lespedeza capitata	Bombus impatiens	2
NWMHRC	Liatris aspera	Agapostemon virescens	3
NWMHRC	Liatris aspera	Anthidium manicatum	1
NWMHRC	Liatris aspera	Bombus fervidus	1
NWMHRC	Liatris aspera	Bombus impatiens	2
NWMHRC	Liatris aspera	Lasioglossum pilosum	1
NWMHRC	Liatris cylindracea	Lasioglossum pilosum	1
NWMHRC	Lotus corniculatus L.	Andrena wilkella	6
NWMHRC	Lotus corniculatus L.	Anthidium manicatum	3
NWMHRC	Lotus corniculatus L.	Apis mellifera	2
NWMHRC	Lotus corniculatus L.	Bombus griseocollis	1
NWMHRC	Lotus corniculatus L.	Bombus impatiens	1

NWMHRC	Lotus corniculatus L.	Megachile latimanus	1
NWMHRC	Lotus corniculatus L.	Megachile mendica	1
NWMHRC	Lotus corniculatus L.	Osmia tersula	1
NWMHRC	Lupinus perennis	Bombus griseocollis	1
NWMHRC	Monarda fistulosa	Anthophora walshii	2
NWMHRC	Monarda fistulosa	Augochlorella aurata	1
NWMHRC	Monarda fistulosa	Bombus bimaculatus	3
NWMHRC	Monarda fistulosa	Bombus griseocollis	2
NWMHRC	Monarda fistulosa	Bombus impatiens	5
NWMHRC	Monarda fistulosa	Bombus perplexus	1
NWMHRC	Monarda fistulosa	Megachile latimanus	2
NWMHRC	Monarda fistulosa	Megachile pugnata	3
NWMHRC	Monarda fistulosa	Melissodes communis	1
NWMHRC	Monarda punctata	Anthophora walshii	1
NWMHRC	Monarda punctata	Bombus impatiens	2
NWMHRC	Monarda punctata	Colletes americanus	2
NWMHRC	Monarda punctata	Lasioglossum pilosum	1
NWMHRC	Oenothera fruticosa	Agapostemon virescens	6
NWMHRC	Oenothera fruticosa	Augochlorella aurata	1
NWMHRC	Oenothera fruticosa	Lasioglossum pilosum	1
NWMHRC	Oenothera fruticosa	Megachile brevis	1
NWMHRC	Oenothera fruticosa	Megachile latimanus	2
NWMHRC	Oenothera fruticosa	Megachile rotundata	1
NWMHRC	Oenothera fruticosa	Melissodes subillatus	3
NWMHRC	Oligoneuron rigidum	Agapostemon texanus	1
NWMHRC	Oligoneuron rigidum	Andrena placata	1
NWMHRC	Oligoneuron rigidum	Apis mellifera	1
NWMHRC	Oligoneuron rigidum	Bombus impatiens	28

NWMHRC	Oligoneuron rigidum	Colletes simulans armatus	1
NWMHRC	Oligoneuron rigidum	Halictus 154onfuses	1
NWMHRC	Oligoneuron rigidum	Halictus ligatus	3
NWMHRC	Oligoneuron rigidum	Lasioglossum pilosum	1
NWMHRC	Oligoneuron rigidum	Melissodes druriellus	1
NWMHRC	Penstemon digitalis	Agapostemon virescens	2
NWMHRC	Penstemon digitalis	Andrena wilkella	1
NWMHRC	Penstemon digitalis	Anthidium manicatum	1
NWMHRC	Penstemon digitalis	Ceratina mikmaqi	1
NWMHRC	Penstemon digitalis	Coelioxys rufitarsis	1
NWMHRC	Penstemon digitalis	Lasioglossum pilosum	1
NWMHRC	Penstemon digitalis	Melissodes subillatus	1
NWMHRC	Penstemon hirsutus	Anthidium manicatum	3
NWMHRC	Penstemon hirsutus	Apis mellifera	1
NWMHRC	Penstemon hirsutus	Bombus bimaculatus	1
NWMHRC	Penstemon hirsutus	Bombus impatiens	1
NWMHRC	Penstemon hirsutus	Ceratina mikmaqi	2
NWMHRC	Penstemon hirsutus	Hoplitis pilosifrons	1
NWMHRC	Potentilla simplex	Andrena miserabilis	1
NWMHRC	Potentilla simplex	Augochlorella aurata	1
NWMHRC	Potentilla simplex	Ceratina mikmaqi	1
NWMHRC	Potentilla simplex	Halictus ligatus	2
NWMHRC	Pycnanthemum pilosum	Andrena placata	1
NWMHRC	Pycnanthemum pilosum	Bombus impatiens	3
NWMHRC	Pycnanthemum virginianum	Anthidium manicatum	1
NWMHRC	Pycnanthemum virginianum	Megachile rotundata	2
NWMHRC	Pycnanthemum virginianum	Melissodes druriellus	1
NWMHRC	Pycnanthemum virginianum	Melissodes tinctus	1

NWMHRC	Ratibida pinnata	Halictus ligatus	4
NWMHRC	Ratibida pinnata	Lasioglossum leucozonium	1
NWMHRC	Ratibida pinnata	Megachile pugnata	2
NWMHRC	Ratibida pinnata	Melissodes agilis	1
NWMHRC	Ratibida pinnata	Melissodes druriellus	4
NWMHRC	Ratibida pinnata	Perdita albipennis	3
NWMHRC	Rosa carolina	Melissodes subillatus	2
NWMHRC	Rudbeckia hirta	Andrena wilkella	1
NWMHRC	Rudbeckia hirta	Megachile pugnata	2
NWMHRC	Rudbeckia hirta	Perdita albipennis	1
NWMHRC	Senecio obovatus	Augochlorella aurata	1
NWMHRC	Senecio obovatus	Halictus ligatus	8
NWMHRC	Silphium integrifolium	Apis mellifera	1
NWMHRC	Silphium integrifolium	Bombus impatiens	8
NWMHRC	Silphium integrifolium	Bombus vagans	1
NWMHRC	Silphium integrifolium	Megachile latimanus	1
NWMHRC	Silphium integrifolium	Megachile pugnata	9
NWMHRC	Silphium integrifolium	Melissodes agilis	6
NWMHRC	Silphium integrifolium	Melissodes denticulatus	1
NWMHRC	Silphium integrifolium	Melissodes druriellus	2
NWMHRC	Silphium laciniatum	Bombus impatiens	1
NWMHRC	Silphium laciniatum	Halictus ligatus	1
NWMHRC	Silphium laciniatum	Melissodes agilis	2
NWMHRC	Silphium terebinthinaceum	Agapostemon virescens	2
NWMHRC	Silphium terebinthinaceum	Bombus bimaculatus	1
NWMHRC	Silphium terebinthinaceum	Bombus impatiens	5
NWMHRC	Silphium terebinthinaceum	Ceratina calcarata	1
NWMHRC	Silphium terebinthinaceum	Halictus ligatus	1

Table C1 (cont'd) NWMHRC Silphium terebinthinaceum Melissodes agilis **NWMHRC** Melissodes druriellus Silphium terebinthinaceum NWMHRC Silphium terebinthinaceum Melissodes tinctus NWMHRC Solidago juncea Augochlorella aurata Solidago juncea NWMHRC Colletes simulans armatus Halictus 156onfuses Solidago juncea NWMHRC NWMHRC Solidago juncea Melissodes druriellus NWMHRC Solidago nemoralis Andrena placata Solidago speciosa NWMHRC Andrena hirticincta NWMHRC Solidago speciosa Apis mellifera NWMHRC Solidago speciosa Augochlorella aurata NWMHRC Solidago speciosa Bombus bimaculatus NWMHRC Solidago speciosa Bombus impatiens NWMHRC Solidago speciosa Bombus perplexus NWMHRC Solidago speciosa Bombus vagans NWMHRC Solidago speciosa Sphecodes davisii Bombus impatiens NWMHRC Symphyotrichum oolentangiense NWMHRC Symphyotrichum oolentangiense Halictus ligatus **NWMHRC** Symphyotrichum oolentangiense Lasioglossum leucozonium Lasioglossum oceanicum NWMHRC Symphyotrichum oolentangiense NWMHRC Symphyotrichum oolentangiense Lasioglossum paraforbesii NWMHRC Symphyotrichum oolentangiense Lasioglossum sp. NWMHRC Symphyotrichum oolentangiense Megachile mendica NWMHRC Symphyotrichum sericeum Agapostemon virescens Augochlorella aurata NWMHRC Symphyotrichum sericeum NWMHRC Symphyotrichum sericeum Bombus impatiens **NWMHRC** Symphyotrichum sericeum Ceratina calcarata NWMHRC Symphyotrichum sericeum Ceratina mikmagi

7 2

5

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2

1

2

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1

3

1

1 90

1

3

5

8

1

1

1

21

1

2

1 2

NWMHRC	Symphyotrichum sericeum
NWMHRC	Symphyotrichum sericeum
NWMHRC	Tradescantia ohiensis
NWMHRC	Verbena stricta

Halictus ligatus	6
Lasioglossum leucozonium	3
Agapostemon virescens	1
Bombus impatiens	3
Bombus perplexus	1
Lasioglossum pilosum	1
Melissodes agilis	1

APPENDIX D:

RECORD OF DEPOSITION OF VOUCHER SPECIMEN

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: 2017-09

Author and Title of thesis:

Logan Rowe, "Evaluation of Wildflowers to Provide Foraging Resources for Managed and Wild Pollinators in Michigan"

Museum(s) where deposited:

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

Table D1. List of voucher specimen. Each record represents a pinned adult specimen collected during 2015-2016. Identifications were made by Jason Gibbs (JG), Logan Rowe (LR), Michael Killewald (MK), and Tom Wood (TW).

					ID
Unique_ID	Family	Genus-species	quantity	sex	by
SARE_6302	Halictidae	Agapostemon sericeus	1	f	LR
SARE_5022	Halictidae	Agapostemon splendens	1	f	LR
SARE_6652	Halictidae	Agapostemon texanus	1	m	LR
SARE_6357	Halictidae	Agapostemon virescens	1	m	LR
SARE_6066	Andrenidae	Andrena aliciae	1	f	JG
SARE_6347	Andrenidae	Andrena canadensis	1	f	JG
SARE_0396	Andrenidae	Andrena crataegi	1	f	JG
SARE_2371	Andrenidae	Andrena helianthi	1	f	JG
SARE_6969	Andrenidae	Andrena hirticincta	1	m	JG
SARE_4182	Andrenidae	Andrena miserabilis	1	f	JG
SARE_0074	Andrenidae	Andrena nasonii	1	f	JG
SARE_3439	Andrenidae	Andrena perplexa	1	f	JG
SARE_2109	Andrenidae	Andrena placata	1	f	JG
SARE_4759	Andrenidae	Andrena rudbeckiae	1	f	JG
SARE_2743	Andrenidae	Andrena simplex	1	f	JG
SARE_1099	Andrenidae	Andrena thaspii	1	f	JG

SARE_0613	Andrenidae	Andrena wilkella	1	f	JG
SARE_2064	Megachilidae	Anthidiellum notatum	1	f	JG
SARE_0439	Megachilidae	Anthidium manicatum	1	m	LR
SARE_3548	Andrenidae	Andrena morrisonella	1	f	JG
SARE_2195	Megachilidae	Anthidium oblongatum	1	m	LR
SARE_6812	Apidae	Anthophora walshii	1	f	JG
SARE_0030	Andrenidae	Apis mellifera	1	f	LR
SARE_2331	Halictidae	Augochlora pura	1	m	LR
SARE_2479	Halictidae	Augochlorella aurata	1	m	LR
SARE_4094	Apidae	Bombus auricomus	1	f	LR
SARE_0916	Apidae	Bombus bimaculatus	1	f	LR
SARE_1271	Apidae	Bombus citrinus	1	m	LR
SARE_1895	Apidae	Bombus fervidus	1	m	LR
SARE_4507	Apidae	Bombus griseocollis	1	m	LR
SARE_0195	Apidae	Bombus impatiens	1	m	LR
SARE_5713	Apidae	Bombus perplexus	1	m	LR
SARE_3926	Apidae	Bombus vagans	1	f	LR
SARE_6780	Apidae	Bombus ternarius	1	f	LR
SARE_1402	Andrenidae	Calliopsis andreniformis	1	f	JG
SARE_3198	Apidae	Ceratina calcarata	1	f	LR
SARE_1621	Apidae	Ceratina dupla	1	f	LR
SARE_2576	Apidae	Ceratina mikmaqi	1	f	LR
SARE_6771	Megachilidae	Coelioxys alternatus	1	f	JG
SARE_5011	Megachilidae	Coelioxys octodentata	1	f	JG
SARE_0559	megachilidae	Coelioxys rufitarsis	1	f	JG
SARE_3062	Colletidae	Colletes americanus	1	f	JG
SARE_6819	Colletidae	Colletes mandibularis	1	f	JG
SARE_1569	Colletidae	Colletes nudus	1	f	JG
SARE_6582	Colletidae	Colletes simulans armatus	1	f	JG
Sare_0622	Megachilidae	Dianthidium simile	1	f	JG
SARE_0791	Halictidae	Dufourea monardae	1	f	JG
SARE_0369	Apidae	Eucera dubitata	1	f	LR
SARE_0048	Apidae	Eucera hamata	1	f	LR
SARE_3973	Halictidae	Halictus 160onfuses	1	f	JG
SARE_0233	Halictidae	Halictus ligatus	1	f	JG
SARE_5848	Halictidae	Halictus parallelus	1	f	LR
SARE_0962	Halictidae	Halictus rubicundus	1	m	JG
SARE_1024	Megachilidae	Heriades carinata	1	f	JG
SARE_2533	Megachilidae	Heriades leavitti	1	f	JG
SARE_0225	Megachilidae	Hoplitis pilosifrons	1	f	JG

SARE_1378	Colletidae	Hylaeus affinis	1	f	JG
SARE_1245	Colletidae	Hylaeus affinis/modestus	1	f	LR
SARE_1718	Colletidae	Hylaeus mesillae	1	f	JG
SARE_6230	Colletidae	Hylaeus modestus	1	f	JG
SARE_4223	Halictidae	Lasioglossum admirandum	1	f	JG
SARE_5774	Halictidae	Lasioglossum albipenne	1	f	JG
SARE_0986	Halictidae	Lasioglossum anomalum	1	f	JG
SARE_1949	Halictidae	Lasioglossum coriaceum	1	m	JG
SARE_2587	Halictidae	Lasioglossum cressonii	1	f	JG
SARE_5299	Halictidae	Lasioglossum ellisiae	1	f	ΤW
SARE_1961	Halictidae	Lasioglossum ephialtum	1	f	JG
SARE_4304	Halictidae	Lasioglossum hitchensi	1	f	JG
SARE_0740	Halictidae	Lasioglossum imitatum	1	f	JG
SARE_6019	Halictidae	Lasioglossum leucocomum	1	f	JG
SARE_0079	Halictidae	Lasioglossum leucozonium	1	f	JG
SARE_1449	Halictidae	Lasioglossum lineatulum	1	f	JG
SARE_0969	Halictidae	Lasioglossum michiganense	1	f	JG
SARE_3223	Halictidae	Lasioglossum oceanicum	1	f	JG
SARE_0911	Halictidae	Lasioglossum paradmirandum	1	f	JG
SARE_0769	Halictidae	Lasioglossum paraforbesii	1	f	JG
SARE_0915	Halictidae	Lasioglossum pectorale	1	f	JG
SARE_3764	Halictidae	Lasioglossum perpunctatum	1	f	JG
SARE_3920	Halictidae	Lasioglossum pilosum	1	f	JG
SARE_3824	Halictidae	Lasioglossum platyparium	1	f	JG
SARE_4135	Halictidae	Lasioglossum pruinosum	1	f	JG
SARE_5286	Halictidae	Lasioglossum tegulare	1	f	JG
SARE_6120	Halictidae	Lasioglossum versatum	1	m	JG
SARE_1325	Halictidae	Lasioglossum vierecki	1	f	JG
SARE_4020	Halictidae	Lasioglossum weemsi	1	f	ΤW
SARE_5812	Halictidae	Lasioglossum zephyrum	1	f	ΤW
SARE_1505	Megachilidae	Megachile brevis	1	Μ	LR
SARE_0867	Megachilidae	Megachile frugalis	1	f	JG
SARE_6852	Megachilidae	Megachile latimanus	1	f	LR
SARE_3682	Megachilidae	Megachile mendica	1	f	JG
SARE_1992	Megachilidae	Megachile pugnata	1	f	LR
SARE_3961	Megachilidae	Megachile relativa	1	f	LR
SARE_5127	Megachilidae	Megachile monti vaga	1	f	MK
SARE_1203	Megachilidae	Megachile texana	1	m	LR
SARE_2148	Megachilidae	Megachile rugifrons	1	f	LR
SARE_5173	Megachilidae	Melissodes agilis	1	m	LR

SARE_1539	Megachilidae	Melissodes bimaculatus	1	f	LR
SARE_1320	Megachilidae	Melissodes communis	1	f	JG
SARE_3127	Megachilidae	Melissodes denticulatus	1	f	JG
SARE_0568	Megachilidae	Melissodes druriellus	1	f	JG
SARE_4072	Megachilidae	Melissodes illatus	1	f	MK
SARE_3850	Megachilidae	Melissodes subillatus	1	f	LR
SARE_9866	Megachilidae	Melissodes tinctus	1	f	LR
SARE_0310	Apidae	Nomada articulata	1	f	JG
SARE_2034	Apidae	Nomada placida	1	m	JG
SARE_3339	Apidae	Nomada sayi	1	f	LR
SARE_0426	Apidae	Nomada superba	1	f	JG
SARE_3566	Apidae	Nomada valida	1	f	LR
SARE_0029	Megachilidae	Osmia bucephala	1	m	LR
SARE_3578	Megachilidae	Osmia distincta	1	f	JG
SARE_3330	Megachilidae	Osmia lignaria	1	f	LR
SARE_3385	Megachilidae	Osmia pumila	1	f	LR
SARE_4455	Megachilidae	Osmia simillima	1	f	JG
SARE_6713	Megachilidae	Osmia tersula	1	f	JG
SARE_0674	Apidae	Peponapis pruinosa	1	f	LR
SARE_6799	Andrenidae	Perdita albipennis	1	f	JG
SARE_5783	Andrenidae	Perdita bequaerti	1	f	JG
SARE_1645	Andrenidae	Protandrena cockerelli	1	m	JG
SARE_5183	Andrenidae	Psuedo panurgus albitarsis	1	f	JG
SARE_2970	Andrenidae	Psuedo panurgus andrenoides	1	f	JG
SARE_2835	Andrenidae	Psuedo panurgus nebrascensis	1	f	JG
SARE_0798	Halictidae	Sphecodes confertus	1	f	JG
SARE_2054	Halictidae	Sphecodes cressonil	1	f	JG
SARE_3248	Halictidae	Sphecodes davisii	1	f	JG
SARE_1434	Halictidae	Sphecodes dichrous	1	f	JG
SARE_5598	Halictidae	Sphecodes illinoensis	1	f	JG
SARE_0751	Halictidae	Sphecodes mandibularis	1	f	JG
SARE_4670	Halictidae	Sphecodes pimpinellae	1	f	JG
SARE_5525	Apidae	Triepeolus pectoralis	1	f	JG
SARE_2048	Apidae	Triepeolus remigatus	1	f	JG
SARE_6045	Apidae	Xylocopa virginica	1	f	JG

LITERATURE CITED

LITERATURE CITED

- Aizen, M. A., & Feinsinger, P. (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine'Chaco Serrano'. *Ecological applications*, 4(2), 378-392.
- Aizen, M. A., & Feinsinger, P. (2003). Bees Not to Be? Response of Insect Pollinator Faunas and Flower Pollination to Habitat Fragmentation. *Ecological Studies*, 162(2), 113–129.
- Aizen, M. A., & Harder, L. D. (2009). Report The Global Stock of Domesticated Honey Bees Is Growing Slower Than Agricultural Demand for Pollination. *Current Biology*, 19(11), 915–918.
- Aldrich, J. H. (2002). Factors and Benefits in the Establishment of Modest-Sized Wildflower Plantings: A Review. *Native Plants Journal*, *3*(1), 67–86.
- Anderson, B., & Johnson, S. D. (2009). Geographical covariation and local convergence of flower depth in a guild of fly-pollinated plants. *New Phytologist*, *182*(2), 533–540.
- Arena, M., & Sgolastra, F. (2014). A meta-analysis comparing the sensitivity of bees to pesticides. *Ecotoxicology*, *23*(3), 324–334.
- Ashman, T. L., Knight, T. M., Steets, J. A., Amarasekare, P., Burd, M., Campbell, D. R., et al. (2004). Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology*, *85*(9), 2408-2421.
- Bartomeus, I., Ascher, J. S., Gibbs, J., Danforth, B. N., Wagner, D. L., & Hedtke, S. M. (2013). Historical changes in northeastern US bee pollinators related to shared ecological traits, *110*(12), 4656–4660.
- Bauer, A. A., Clayton, M. K., & Brunet, J. (2017). Floral traits influencing plant attractiveness to three bee species: Consequences for plant reproductive success. *American Journal of Botany*, 104(5), 772–781.
- Blaauw, B. R., & Isaacs, R. (2014). Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology*, *51*(4), 890–898.
- Blaauw, B. R., & Isaacs, R. (2015). Wildflower plantings enhance the abundance of natural enemies and their services in adjacent blueberry fields. *Biological Control*, *91*, 94–103.

- Blacquière, T., Smagghe, G., Van Gestel, C. A. M., & Mommaerts, V. (2012). Neonicotinoids in bees: A review on concentrations, side-effects and risk assessment. *Ecotoxicology*, 21(4), 973–992.
- Blüthgen, N., & Klein, A. (2011). Functional complementarity and specialisation: The role of biodiversity in plant pollinator interactions. *Basic and Applied Ecology*, *12*, 282–291.
- Bosch, J., Retana, J., & Cerda, X. (1997). Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. *Oecologia*, *109*, 583–591.
- Bretzel, F., Vannucchi, F., Romano, D., Malorgio, F., Benvenuti, S., & Pezzarossa, B. (2016). Wildflowers: From conserving biodiversity to urban greening, A review. *Urban Forestry and Urban Greening*, *20*, 428–436.
- Brittain, C., & Potts, S. G. (2011). The potential impacts of insecticides on the life-history traits of bees and the consequences for pollination. *Basic and Applied Ecology*, *12*(4), 321–331.
- Brittain, C., Williams, N., Kremen, C., & Klein, A. (2013). Synergistic effects of non- Apis bees and honey bees for pollination services Synergistic effects of non- Apis bees and honey bees for pollination services. *Proceedings of the Royal Society B: Biological Sciences*, 208(1), 20122767.
- Brodschneider, R., & Carailshem, K. (2010). Nutrition and health in honey bees. *Apidologie, 41*, 278–294.
- Brosi, B. J., Armsworth, P. R., & Daily, G. C. (2008). Optimal design of agricultural landscapes for pollination services. *Conservation Letters*, 1(1), 27–36.
- Brown, M. J. F. F., & Paxton, R. J. (2009). The conservation of bees: a global perspective. *Apidologie*, *40*, 410–416.
- Bruninga-Socolar, B., Crone, E. E., & Winfree, R. (2016). The Role of Floral Density in Determining Bee Foraging Behavior: A Natural Experiment. *Natural Areas Journal*, *36*(4), 392–399.
- Brunet, J., Thairu, M. W., Henss, J. M., Link, R. I., & Kluever, J. A. (2015). The effects of flower, floral display, and reward size on bumblebee foraging behavior when pollen is the reward and plants are dichogamous. *International Journal of Plant Sciences*, 176(9), 811–819.
- Bullock, J. M., Woodcock, B. A., Heard, M. S., Jitlal, M. S., Rundl, M., Shore, R. F., et al. (2016). Replication, effect sizes and identifying the biological impacts of
pesticides on bees under field conditions. *Journal of Applied Ecology*, 53, 1358–1362.

- Button, L., & Elle, E. (2014). Wild bumble bees reduce pollination deficits in a crop mostly visited by managed honey bees. *Agriculture, Ecosystems & Environment*, *197*, 255–263.
- Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., et al. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences*, *108*(2), 662–667.
- Cameron, S. A., Lim, H. C., Lozier, J. D., Duennes, M. A., & Thorp, R. (2016). Test of the invasive pathogen hypothesis of bumble bee decline in North America. *Proceedings of the National Academy of Sciences*, *113*(16), 4386–4391.
- Campbell, A. J., Wilby, A., Sutton, P., & Wäckers, F. L. (2017). Do sown flower strips boost wild pollinator abundance and pollination services in a spring-flowering crop?
 A case study from UK cider apple orchards. *Agriculture, Ecosystems & Environment*, 239, 20–29.
- Carson B. D., Bahlai C. A., Landis D. A. (2015). Establishment, Impacts, and Current Range of Spotted Knapweed (Centaurea stoebe ssp. micranthos) Biological Control Insects in Michigan. *The Great Lakes Entomologist*, 47, 3-4.
- Carson, B. D., Bahlai, C. A., Gibbs, J., & Landis, D. A. (2016). Flowering phenology influences bee community dynamics in old fields dominated by the invasive plant Centaurea stoebe. *Basic and Applied Ecology*, *17*(6), 497–507.
- Carvalheiro, L. G., Veldtman, R., Shenkute, A. G., Tesfay, G. B., Pirk, C. W. W., Donaldson, J. S., et al. (2011). Natural and within-farmland biodiversity enhances crop productivity. *Ecology Letters*, *14*(3), 251–259.
- Carvalheiro, L. G., Seymour, C. L., Nicolson, S. W., & Veldtman, R. (2012). Creating patches of native flowers facilitates crop pollination in large agricultural fields: Mango as a case study. *Journal of Applied Ecology*, *49*(6), 1373–1383
- Carvell, C., Roy, D. B., Smart, S. M., Pywell, R. F., Preston, C. D., & Goulson, D. (2006). Declines in forage availability for bumblebees at a national scale. *Biological Conservation*, *132*(4), 481–489.
- Carvell, C., Westrich, P., Meek, W. R., Pywell, R. F., & Nowakowski, M. (2006). Assessing the value of annual and perennial forage mixtures for bumblebees by direct observations and pollen analysis. *Apidologie*, 37(3), 326-340.
- Carvell, C., Meek, W. R., Pywell, R. F., Goulson, D., & Nowakowski, M. (2007). Comparing the efficacy of agri-environment schemes to enhance bumble bee

abundance and diversity on arable field margins. *Journal of Applied Ecology*, *44*(1), 29–40.

- Cnaani, J., Thomson, J. D., & Papaj, D. R. (2006). Flower Choice and Learning in Foraging Bumblebees: Effects of Variation in Nectar Volume and Concentration, *112*, 278–285.
- Conner, J. K., Davis, R., & Rush, S. (1995). The effect of wild radish floral morphology on pollination efficiency by four taxa of pollinators. *Oecologia*, *104*(2), 234–245.
- Cook, S. M., Awmack, C. S., Murray, D. A., & Williams, I. H. (2003). Are honey bees' foraging preferences affected by pollen amino acid composition? *Ecological Entomology*, 28(5), 622-627.
- Corbet, S. A. (2007). Nectar sugar content: estimating standing crop and secretion rate in field. *Apidologie*, *34*, 1–10.
- Cresswell, J. E. (1990) How and why do nectar-foraging bumblebees initiate movements between inflorescences of wild bergamot Monarda fistulosa (Lamiaceae)? *Oecologia*, 82(4), 450-460.
- Cresswell, J. E. (2011). A meta-analysis of experiments testing the effects of a neonicotinoid insecticide (imidacloprid) on honey bees. *Ecotoxicology*, *20*(1), 149–157.
- Daily, G. C. (Ed.). (1997). Nature's services: societal dependence on natural ecosystems. Island Press.
- Delaplane, K.S., Mayer, D. R., Mayer, D. F. (2000) *Crop pollination by bees*. Cabi Publishing, New York, NY.
- Desneux, N., Decourtye, A., & Delpuech, J.-M. (2007). The Sublethal Effects of Pesticides on Beneficial Arthropods. *Annual Review of Entomology*, *52*(1), 81–106.
- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. *Ecology Letters*, *13*(8), 1030–1040.
- Dicks, L. V., Vaughan, M., & Lee-Mäder, E. (2016). Developing incentives for farmers to support pollinators. *Pollination Services to Agriculture: Sustaining and Enhancing a Key Ecosystem Service*, 216-234.
- Dickson, T. L., & Busby, W. H. (2009). Forb species establishment increases with decreased grass seeding density and with increased forb seeding density in a

Northeast Kansas, U.S.A., experimental prairie restoration. *Restoration Ecology*, *17*(5), 597–605.

- Di Pasquale, G., Salignon, M., Le Conte, Y., Belzunces, L. P., Decourtye, A., Kretzschmar, A., et al. (2013). Influence of Pollen Nutrition on Honey Bee Health: Do Pollen Quality and Diversity Matter? *PLoS ONE*, *8*(8), 1–13.
- Ebeling, A., Klein, A. M., Schumacher, J., Weisser, W. W., & Tscharntke, T. (2008). How does plant richness affect pollinator richness and temporal stability of flower visits? *Oikos*, *117*(12), 1808–1815.
- Eilenberg, J., Hajek, A., & Lomer, C. (2001). Suggestions for unifying the terminology in biological control. *BioControl*, *46*(December 2001).
- Ellis, A. M., Myers, S. S., & Ricketts, T. H. (2015). Do pollinators contribute to nutritional health? *PLoS ONE*, *10*(1), 1–17.
- Emer, C., Memmott, J., Vaughan, I. P., Montoya, D., & Tylianakis, J. M. (2016). Species roles in plant–pollinator communities are conserved across native and alien ranges. *Diversity and Distributions*, 22(8), 841–852.
- Feltham, H., Park, K., Minderman, J., & Goulson, D. (2015). Experimental evidence that wildflower strips increase pollinator visits to crops. *Ecology and Evolution*, *5*(16), 3523–3530.
- Fenster, C. B., Armbruster, W. S., Wilson, P., Dudash, M. R., & Thomson, J. D. (2004). Pollination Syndromes and Floral Specialization. *Annual Review of Ecology, Evolution, and Systematics*, 35(1), 375–403.
- Fiedler, A. K., & Landis, D. (2007). Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. *Environmental Entomology*, *36*(4), 751–765.
- Fiedler, A., Tuell, J., Isaacs, R., & Landis, D. (2007). *Attracting beneficial insects with native flowering plants*. Michigan State University, Extension Service.
- Fiedler, A. K., Landis, D. A., & Wratten, S. D. (2008). Maximizing ecosystem services from conservation biological control: The role of habitat management. *Biological Control*, *45*(2), 254–271.
- Fiedler, A. K., Landis, D. A., & Arduser, M. (2012). Rapid Shift in Pollinator Communities Following Invasive Species Removal. *Restoration Ecology*, *20*(5), 593–602.
- Fitzpatrick, Ú., Murray, T. E., Paxton, R. J., Breen, J., Cotton, D., Santorum, V., & Brown, M. J. F. (2007). Rarity and decline in bumblebees A test of causes and correlates in the Irish fauna. *Biological Conservation*, *136*(2), 185–194.

- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., et al. (2005). Global Consequences of Land Use. *Science*, *309*(5734), 570–574.
- Fontaine, C., Dajoz, I., Meriguet, J., & Loreau, M. (2006). Functional diversity of plantpollinator interaction webs enhances the persistence of plant communities. *PLoS Biology*, *4*(1), 0129–0135.
- Frankie, G. W., Thorp, R. W., Schindler, M., Hernandez, J., Ertter, B., & Rizzardi, M. (2005). Ecological Patterns of Bees and Their Host Ornamental Flowers in Two Northern California Cities. *Journal of the Kansas Entomological Society*, 78(3), 227–246.
- Glaettli, M., & Barrett, S. C. H. (2008). Pollinator responses to variation in floral display and flower size in dioecious Sagittaria latifolia (Alismataceae). *New Phytologist*, *179*, 1193–1201.
- Galen, C. (1999). Why do flowers vary? The functional ecology of variation in flower size and form within natural plant populations. *Bioscience*, 49(8), 631-640.
- Gallai, N., Salles, J., Settele, J., Vaissière, B. E., Pollinisation, L., Abeilles, E., et al. (2008). Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. *Ecological Economics*, *68*(3), 810–821.
- Garbuzov, M., & Ratnieks, F. L. W. (2014). Quantifying variation among garden plants in attractiveness to bees and other flower-visiting insects. *Functional Ecology*, *28*(2), 364–374.
- Garbuzov, M., & Ratnieks, F. L. W. (2015). Using the British national collection of asters to compare the attractiveness of 228 varieties to flower-visiting insects. *Environmental Entomology*, *44*(3), 638–646.
- Garbuzov, M., Alton, K., & Ratnieks, F. L. (2017). Most ornamental plants on sale in garden centres are unattractive to flower-visiting insects. *PeerJ*, 5, e3066.
- Garibaldi, L. A., Steffan-Dewenter, I., Kremen, C., Morales, J. M., Bommarco, R., Cunningham, S. A., et al. (2011). Stability of pollination services decreases with isolation from natural areas despite honey bee visits. *Ecology Letters*, *14*(10), 1062–1072.
- Garibaldi, L. A., Steffan-Dewenter, I., Winfree R., Aizen, M. A., Bommarco, R., Cunningham, S. A., et al. (2013) Wild Pollinators Enhance Fruit Set of Crops Regardless of Honey Bee Abundance. Science, 339(6127), 1608-1611.
- Garibaldi, L. A., Carvalheiro, L. G., Leonhardt, S. D., Aizen, M. A., Blaauw, B. R., Isaacs, R., et al. (2014). From research to action: Enhancing crop yield through wild pollinators. *Frontiers in Ecology and the Environment*, *12*(8), 439–447.

- Garibaldi, L. A., Aizen, M. A., Cunningham, S. A., Harder, L. D., & Klein, A. M. (2016). Incremental contribution of pollination and other ecosystem services to agricultural productivity. *Pollination Services to Agriculture: Sustaining and Enhancing a Key Ecosystem Service*, 33-42.
- Garnett, T., Appleby, M. C., Balmford, A., Bateman, I. J., Benton, T. G., Bloomer, P., et al. (2013). Sustainable Intensification in Agriculture: Premises and Policies. *Science*, *341*(6141), 33–34.
- Glaettli, M., & Barrett, S. C. H. (2008). Pollinator responses to variation in floral display and flower size in dioecious Sagittaria latifolia (Alismataceae). *New Phytologist*, *179(4)*, 1193–1201.
- Godfray, H. C. J., & Garnett, T. (2014). Food security and sustainable intensification. *Phil. Trans. R. Soc. B*, 369(1639), 20120273.
- González-Teuber, M., & Heil, M. (2009). Nectar chemistry is tailored for both attraction of mutualists and protection from exploiters. *Plant Signaling & Behavior*, *4*(9), 809–813.
- Goulson, D., Lye, G. C., Darvill, B., & Hymenoptera, K. W. (2008). The decline and conservation of bumblebees. *Annu. Rev. Entomol.*, 53, 191–208.
- Goulson, D., Nicholls, E., Botias, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957.
- Graystock, P., Blane, E. J., McFrederick, Q. S., Goulson, D., & Hughes, W. O. H. (2016). Do managed bees drive parasite spread and emergence in wild bees? *International Journal for Parasitology: Parasites and Wildlife*, *5*(1), 64–75.
- Greenleaf, S. S., & Kremen, C. (2006). Wild bee species increase tomato production and respond differently to surrounding land use in Northern California. *Biological Conservation*, 133(1), 81-87.
- Gumbert, A. (2000). Color choices by bumble bees (Bombus terrestris): Innate preferences and generalization after learning. *Behavioral Ecology and Sociobiology*, *48*(1), 36–43.
- Gunton, R. M., Firbank, L. G., Inman, A., & Winter, D. M. (2016). How scalable is sustainable intensification? *Nature Plants*, *2*(5), 160-165.
- Gurr, G. M. Van Emden H. F., & Wratten, S. D. (1998). Habitat manipulation and natural enemy efficiency: implications for the control of pests. *Conservation biological control*, 155-183.

- Haaland, C., Naisbit, R. E., & Bersier, L. F. (2011). Sown wildflower strips for insect conservation: A review. *Insect Conservation and Diversity*, *4*(1), 60–80.
- Hanula, J. L., & Horn, S. (2011). Removing an exotic shrub from riparian forests increases butterfly abundance and diversity. *Forest Ecology and Management*, 262(4), 674–680.
- Harmon-Threatt A., & Chin, K. (2016). Common methods for tallgrass prairie restoration and their potential effects on bee diversity. Managing Pollinators on Natural Areas, 36(4), 400-409.
- Havens, K., & Vitt, P. (2016). The Importance of Phenological Diversity in Seed Mixes for Pollinator Restoration. *Natural Areas Journal*, *36*(4), 531–537.
- Heard, M. S., Baas, J., Dorne, J. Lou, Lahive, E., Robinson, A. G., Rortais, A., et al. (2017). Comparative toxicity of pesticides and environmental contaminants in bees: Are honey bees a useful proxy for wild bee species? *Science of the Total Environment*, 578, 357–365.
- Hegland, S. J., & Totland, Ø. (2005). Relationships between species' floral traits and pollinator visitation in a temperate grassland. *Oecologia*, *145*(4), 586–594.
- Henry, M., Beguin, M., Requier, F., Rollin, O., & Odoux, J. F. (2012). A Common Pesticide Decreases Foraging Success and Survival in Honey Bees, 3, 1–4.
- Herron-sweet, C. R., Lehnhoff, E. A., Burkle, L. A., Littlefield, J. L., & Mangold, J. M. (2016). dependent impacts of an invasive plant on pollinators and pollination services to a native plant, *Ecosphere*, 7(2), e01233.
- Hicks, D. M., Ouvrard, P., Baldock, K. C. R., Baude, M., Goddard, A., Kunin, W. E., et al. (2016). Food for Pollinators: Quantifying the Nectar and Pollen Resources of Urban Flower Meadows. *PLoS ONE*, *11*(6), e0158117.
- Hines, H. M., & Hendrix, S. D. (2005). Bumble Bee (Hymenoptera: Apidae) Diversity and Abundance in Tallgrass Prairie Patches: Effects of Local and Landscape Floral Resources. *Environmental Entomology*, *34*(6), 1477–1484.
- Hirota, S. K., Nitta, K., Kim, Y., Kato, A., Kawakubo, N., Yasumoto, A. A., et al. (2012). Relative role of flower color and scent on pollinator attraction: Experimental tests using F1 and F2 hybrids of daylily and nightlily. *PLoS ONE*, 7(6).
- Holzschuh, A., Dudenhöffer, J. H., & Tscharntke, T. (2012). Landscapes with wild bee habitats enhance pollination, fruit set and yield of sweet cherry. *Biological Conservation*, *153*, 101–107.

- Hudewenz, A., Klein, A. M., Scherber, C., Stanke, L., Tscharntke, T., Vogel, A., et al. (2012). Herbivore and pollinator responses to grassland management intensity along experimental changes in plant species richness. *Biological Conservation*, 150(1), 42–52.
- Hunter, M. D. (2002). Landscape structure, habitat fragmentation, and the ecology of insects. *Agricultural and Forest Entomology*, *4*, *Sciencexpress*, 159–166.
- Idris, a B., & Grafius, E. (1995). Wildflowers as nectar sources for Diadegma insulare (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Yponomeutidae). *Environmental Entomology*, 24(6), 1726–1735.
- Isaacs, R., Tuell, J., Fiedler, A., Gardiner, M., & Landis, D. (2009). Maximizing arthropod-mediated ecosystem services in agricultural landscapes: the role of native plants. *Frontiers in Ecology and the Environment*, *7*(4), 196–203.
- Isaacs, R., Blaauw, B., Williams, N., Kwapong, P., Lee-Mäder, E., & Vaughan, M. (2016). Farm-tailored measures to sustain and enhance a pollination service. *Pollination Services to Agriculture: Sustaining and Enhancing a Key Ecosystem Service*, 113-131.
- Ishii, H. S. (2006). Floral display size influences subsequent plant choice. *Functional Ecology*, *20*, 233–238.
- Ishii, H. S., Hirabayashi, Y., Kudo, G., Ishii, H. S., Hirabayashi, Y., & Kudo, G. (2008). Combined Effects of Inflorescence Architecture, Display Size, Plant Density and Empty Flowers on Bumble Bee Behaviour: Experimental Study with Artificial Inflorescences. *Oecologia*, 156(2), 341–350.
- James, R., & Pitts-Singer, T. L. (2008). Bee Pollination in Agricultural Ecosystems. *Bee Pollination in Agricultural Ecosystems*, 1–256.
- Javorek, S. K., Mackenzie K. E., and Vander Kloet S. P. (2002) Comparative pollination effectiveness among bees (Hymenoptera: Apoidea) on lowbush blueberry (Ericaceae: Vaccinium angustifolium). *Annals of the Entomological Society of America*, 95(3), 345-351.
- Jewell, S., Ashe, D., & Krofta, D. (2014) Petition to protect the monarch butterfly (Danaus plexippus plexippus) under the endangered species act. U.S. Fish and Wildlife Service
- Johansen, C. A. (1998). Pesticides and Pollinators. *Annual Review of Entomology*, 22, 177–192.
- Johnson, S. D., & Steiner, K. E. (2000). Generalization versus specialization in plant pollination systems. *Trends in Ecology & Evolution*, 15(4), 140-143.

- Johnson, R. M., Dahlgren, L., Siegfried B. D., & Ellis, M. D. (2013). Acaricide, fungicide and drug interactions in honey bees (Apis mellifera). *PloS one*, 8(1), e54092.
- Junker, R. R., Blüthgen, N., Brehm, T., Binkenstein, J., Paulus, J., Schaefer, H. M., et al. (2013). Specialization on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Functional Ecology*, 27(2), 329–341.
- Junker, R. R., & Parachnowitsch, A. L. (2015). Working Towards a Holistic View on Flower Traits— How Floral Scents Mediate Plant–Animal Interactions in Concert with Other Floral Characters. *Journal of Indian Institute of Science*, *95*(1), 43–68.
- Kaiser-bunbury, C. N., & Müller, C. B. (2009). Indirect interactions between invasive and native plants via pollinators. *Naturwissenschaften*, *96*(3), 339–346.
- Karron, J. D., & Mitchell, R. J. (2012). Effects of floral display size on male and female reproductive success in Mimulus ringens. *Annals of Botany*, *109*(3), 563–570.
- Kearns, C. A., Inouye, D. W., & Waser, N. M. (1998). Endangered Mutualisms: The Conservation of Plant-Pollinator Interactions. *Annual Review of Ecology and Systematics*, *29*, 83–112.
- Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Taylor, H., Winfree, R., et al. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems, *Ecology Letters*, 16, 584–599.
- Kevan, P. G. (1975). Pollination and Environmental Conservation. *Environmental Conservation*, 2(4), 293.
- Kleijn, D., Rundlöf, M., Scheper, J., Smith, H. G., & Tscharntke, T. (2011). Does conservation on farmland contribute to halting the biodiversity decline? *Trends in Ecology and Evolution*, 26(9), 474–481.
- Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Sciences*, 274(1608), 303–313.
- Klein, A. M., Müller, C., Hoehn, P., & Kremen, C. (2009). Understanding the role of species richness for crop pollination services. Biodiversity, ecosystem function and human wellbeing. New York, 195-208.
- Klinkhamer, P. G. L., Jong, T. J. De, & Bruyn, G. De. (1989). Plant Size and Pollinator Visitation in Cynoglossum Officinale. *Oikos*, 201–204.

- Knauer, A. C., & Schiestl, F. P. (2015). Bees use honest floral signals as indicators of reward when visiting flowers. *Ecology letters*, 18(2), 135-143.
- Koh, I., Lonsdorf, E. V., Williams, N. M., Brittain, C., Isaacs, R., Gibbs, J., & Ricketts, T. H. (2016). Modeling the status, trends, and impacts of wild bee abundance in the United States. *Proceedings of the National Academy of Sciences*, *113*(1), 140–145.
- Kraemer, M. E., & Favi, F. D. (2014). Nesting and Pollen Preference of Osmia lignaria lignaria (Hymenoptera: Megachilidae) in Virginia and North Carolina Orchards. *Environmental Entomology*, *43*(4), 932–941.
- Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America*, 99(26), 16812–16816.
- Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., et al. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters*, *10*(4), 299–314.
- Kremen, C., & M'Gonigle, L. K. (2015). Small-scale restoration in intensive agricultural landscapes supports more specialized and less mobile pollinator species. *Journal of Applied Ecology*, *52*(3), 602–610.
- Kriesell, L., Hilpert, A., & Leonhardt, S. D. (2017). Different but the same: bumblebee species collect pollen of different plant sources but similar amino acid profiles. *Apidologie*, *48*(1), 102–116.
- Kühnholz, S., & Seeley, T. D. (1997). The control of water collection in honey bee colonies. *Behavioral Ecology and Sociobiology*, *41*(6), 407–422.
- Landis, D. A., Wratten, S. D., & Gurr, G. M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture, (45), 175–201.
- Landis, D. A. (2017). Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology*, *18*, 1–12.
- Leonard, A. S., & Masek, P. (2014). Multisensory integration of colors and scents: Insights from bees and flowers. *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 200(6), 463–474.
- Leonhardt, S. D., & Blüthgen, N. (2012). The same, but different: Pollen foraging in honeybee and bumblebee colonies. *Apidologie*, *43*(4), 449–464.
- Levine, J. M., & HilleRisLambers, J. (2009). The importance of niches for the maintenance of species diversity, *Nature*, 461(7261), 254-257.

- Lichtenberg, E. M., Kennedy, C. M., Kremen, C., Batáry, P., Berendse, F., Bommarco, R., et al. (2017). A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. *Global Change Biology*, (March).
- Lonsdorf, E., Kremen, C., Ricketts, T., Winfree, R., Williams, N., & Greenleaf, S. (2009). Modelling pollination services across agricultural landscapes. *Annals of Botany*, *103*(9), 1589–1600.
- Losey, J. E., Vaughan, M. (2006). The economic value of ecological services provided by insects. *Bioscience*, *56*(4), 311–323.
- May, E. (2015). *Wild bee community responses to farm management practices, wildflower restorations, and landscape composition.* (Master's thesis, Michigan State University).
- Mcart, S. H., Koch, H., Irwin, R. E., & Adler, L. S. (2014). Arranging the bouquet of disease: Floral traits and the transmission of plant and animal pathogens. *Ecology Letters*, *17*(5), 624–636.
- McGregor, S.E. (1976). *Insect Pollination of Cultivated Crop Plants*. Agriculture Handbook No. 496. Agriculture Research Service, USDA, Washington, D.C.
- Mclaughlin, A., & Mineau, P. (1995). The impact of agricultural practices on biodiversity. *Agriculture Ecosystems & Environment*. 55, 201–212.
- MEA. (2005). Millennium ecosystem assessment. *Ecosystems and Human Well-Being: Biodiversity*, (September).
- Memmot, J. (1999). The structure of a plant-pollinator food web. *Ecology letters*, 2(5), 276-280.
- Melhim, A., Daly, Z., & Weersink, A. (2016). Value of Pollination Services and Policy. *Pollination Services to Agriculture: Sustaining and Enhancing a Key Ecosystem Service.* 235-260.
- Menz, M. H. M., Phillips, R. D., Winfree, R., Kremen, C., Aizen, M. A., Johnson, S. D., et al. (2011). Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. *Trends in Plant Science*, *16*(1), 4–12.
- M'Gonigle, L. K., Ponisio, L. C., Cutler, K., & Kremen, C. (2015). Habitat restoration promotes pollinator persistence in intensively-managed agriculture. *Ecological Applications*, 25(6), 1557–1565.

- M'Gonigle, L. K., Williams, N. M., Lonsdorf, E., & Kremen, C. (2017). A Tool for Selecting Plants When Restoring Habitat for Pollinators. *Conservation Letters*, *10*(1), 105–111.
- Michener, C.D. (2000) *The bees of the World*. The John Hopkins University Press, Baltimore, MD.
- Mitchell, R. J., Karron, J. D., G., H. K., & Bell, J. M. (2004). The influence of Mimulus ringens floral display size on pollinator visitation patterns. *Functional Ecology*, *18*, 116–124.
- Morales, C.L., & Traveset, A. (2009). A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters*, *12*(7), 716–728.
- Morandin, L. A., & Kremen, C. (2002). Hedgerow restoration promotes pollinator populations and exports native bees to adjacent fields. *Ecological Applications*, 23.4, 829–839.
- Muller, A., Diener, S., Schnyder, S., Stutz, K., Sedivy, C., & Dorn, S. (2006). Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee – flower relationships, *130*, 604–615.
- Mullin, C. A., Frazier, M., Frazier, J. L., Ashcraft, S., Simonds, R., vanEngelsdorp, D., & Pettis, J. S. (2010). High Levels of Miticides and Agrochemicals in North American Apiaries: Implications for Honey Bee Health. *PLoS ONE*, *5*(3).
- Mussen, E. C., Lopez, J. E., & Peng, C. Y. S. (2004). Effects of selected fungicides on growth and development of larval honey bees, Apis mellifera L. (Hymenoptera: Apidae). *Environmental Entomology*, *33*(5), 1151–1154.
- Nentwig, W., Frank, T., & Lethmayer, C. (1998). Sown weed strips: artificial ecological compensation areas as an important tool in conservation biological control. *Conservation biological control*, 8, 133-153.
- Nicholls, E., & Hempel de Ibarra, N. (2017). Assessment of pollen rewards by foraging bees. *Functional Ecology*, *31*(1), 76–87.
- Nicholson S. W., Nepi, M., & Pacini, E. (2007). Nectaries and nectar. Springer, 215-250.
- Nicolson, S. W. (2011). Bee food: the chemistry and nutritional value of nectar, pollen and mixtures of the two. *African Zoology*, *46*(2), 197–204.
- Oduor, A. M. O., Leimu, R., van Kleunen, M., & Mack, R. (2016). Invasive plant species are locally adapted just as frequently and at least as strongly as native plant species. *Journal of Ecology*, *104*(4), 957–968.

- Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals? (321), 321–326.
- Olsson, O., Bolin, A., Smith, H. G., & Lonsdorf, E. V. (2015). Modeling pollinating bee visitation rates in heterogeneous landscapes from foraging theory. *Ecological Modelling*, *316*, 133–143.
- Olwell, P., & Riibe, L. (2016). National Seed Strategy: Restoring Pollinator Habitat Begins with the Right Seed in the Right Place at the Right Time. *Natural Areas Journal*, *36*(4), 363–365.
- Park, M. G., Blitzer, E. J., Gibbs, J., Losey, J. E., & Danforth, B. N. (2015). Negative effects of pesticides on wild bee communities can be buffered by landscape context. *Proceedings of the Royal Society B: Biological Sciences*, 282(1809), 20150299.
- Paxton, R. J., Klee, J., Korpela, S., & Fries, I. (2007). Nosema ceranae has infected Apis mellifera in Europe since at least 1998 and may be more virulent than Nosema apis. *Apidologie*, *38*(6), 558–565.
- Pawar, S. (2014). Why are plant-pollinator networks nested? *Science*, *345*(6195), 383–383.
- Peat, J., & Goulson, D. (2005). Effects of experience and weather on foraging rate and pollen versus nectar collection in the bumblebee, *Bombus terrestris*, *58*, 152–156.
- Pettis, J. S., & Delaplane, K. S. (2010). Coordinated responses to honey bee decline in the USA. *Apidologie*, *41*(3), 256–263.
- Pichersky, E., & Gershenzon, J. (2002). The formation and function of plant volatiles: perfumes for pollinator attraction and defense. *Current Opinion in Plant Biology*, 5.3, 237–243.
- Pyke, G. H. (1984). Optimal Foraging Theory: A Critical Review. *Annual Review of Ecology and Systematics*, (15), 523–575.
- Pimentel, D., Wilson, C., McCullum, C., Huang, R., Dwen, P., Flack, J., et al. (1997). Economic and Environmental Benefits of Biodiversity. *BioScience*, *47*(11), 747–757.
- Pimentel, D., Zuniga, R., & Morrison, D. (2005). Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, *52*(3), 273–288.

- Potts, S., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. G. (2003). Linking Bees and Flowers: How Do Floral Communities Structure Pollinator Communities? *Ecology*, *84*(10), 2628–2642.
- Potts, S. G., Vulliamy, B., Roberts, S., Toole, C. O., Dafni, A., Ne, G., et al. (2004). Nectar resource diversity organises flower-visitor community structure. *Entomologia Experimentalis et Applicata*, *113*(2), 103–107.
- Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in Ecology & Evolution*, *25*(6), 345–353.
- Reverté, S., Retana, J., Gómez, J. M., & Bosch, J. (2016). Pollinators show flower colour preferences but flowers with similar colours do not attract similar pollinators. *Annals of Botany*, *118*(2), 249–257.
- Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., et al. (2008). Landscape effects on crop pollination services: Are there general patterns? *Ecology Letters*, *11*(5), 499–515.
- Robson, D. B. (2014). Identification of plant species for crop pollinator habitat enhancement in the northern prairies. *Journal of Pollination Ecology*, 14.
- Rodriguez-Saona, C., Blaauw, B. R., & Isaacs, R. (2012). Manipulation of natural enemies in agroecosystems: habitat and semiochemicals for sustainable insect pest control. *Integrated Pest Management and Pest Control-Current and Future Tactics*. 89-126.
- Rohr, R. P., Saavedra, S., & Bascompte, J. (2014). On the structural stability of mutualistic systems. *Science*, *345*(6195), 1253497–1253497.
- Rortais, A., Arnold G., Halm, M. P., Touffet-Briens, F. (2005). Modes of honeybees exposure to systematic insecticides: estimated amounts of contaminated pollen and nectar consumed by different categories of bees. *Apidologie*, 36(1), 71-83.
- Roscher, C., Schumacher, J., Baade, J., Wilcke, W., Gleixner, G., Weisser, W. W., et al. (2004). The role of biodiversity for element cycling and trophic interactions: an experimental approach in a grassland community. *Basic and Applied Ecology*, *5*(2), 107–121.
- Roulston, T. H., & Cane H. C. (2000). The Effect of Diet Breadth and Nesting Ecology on Body Size Variation in Bees (Apiformes). *Kansas Entomological Society*, 73, (3), 129-142.
- Roulston, T. H., & Cane H. C. (2000). Pollen nutritional content and digestibility for animals. *Pollen and Pollination* (pp. 187-209). Springer Vienna.

- Roulston, T. A. H., & Cane, J. H. (2002). The effect of pollen protein concentration on body size in the sweat bee Lasioglossum zephyrum (Hymenoptera: Apiformes). *Evolutionary Ecology*, 16(1), 49-65.
- Roulston, T. H., & Goodell, K. (2011). The Role of Resources and Risks in Regulating Wild Bee Populations. *Annual Review of Entomology*, *56*(1), 293–312.
- Rundlöf, M., Bengtsson, J., & Smith, H. G. (2008). Local and landscape effects of organic farming on butterfly species richness and abundance. *Journal of Applied Ecology*, *45*(3), 813–820.
- Russel, A. L., Rebekah, A. G., Anne A. S., & Daniel, D. R. (2016). Learning of Floral Preference by Bees in the Absence of Nectar Rewards. *Integrative and Comparative Biology*, 56, E191.
- Russell, A. L., Buchmann, S. L., & Papaj, D. R. (2017). How a generalist bee achieves high efficiency of pollen collection on diverse floral resources. *Behavioral Ecology*, 0, 1–13.
- Russo, L., Debarros, N., Yang, S., Shea, K., & Mortensen, D. (2013). Supporting crop pollinators with floral resources: network- based phenological matching. *Ecology and Evolution*, *3*(9), 3125–3140.
- Russo, L., Memmott, J., Montoya, D., Shea, K., & Buckley, Y. M. (2014). Patterns of introduced species interactions affect multiple aspects of network structure in plantpollinator communities. *Ecology*, 95(10), 2593–2963.
- Russo, L., Nichol, C., & Shea, K. (2016) Pollinator floral provisioning by a plant invader: quantifying beneficial effects of detrimental species. *Diversity and Distributions*, 22(2), 189-198.
- Ruxton, G. D., & Schaefer, H. M. (2016). Floral colour change as a potential signal to pollinators. *Current Opinion in Plant Biology*, *32*, 96–100.
- Sala, O. E., Chapin III, S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., et al. (2000). Global Biodiversity Scenarios for the Year 2100. *Science*, *287*(5459), 1770–1774.
- Sánchez-Bayo, F., Goulson, D., Pennacchio, F., Nazzi, F., Goka, K., & Desneux, N. (2016). Are bee diseases linked to pesticides? A brief review. *Environment International*, 89–90, 7–11.
- Scheper, J., Holzschuh, A., Kuussaari, M., Potts, S. G., Rundlöf, M., Smith, H. G., et al. (2013). Environmental factors driving the effectiveness of European agrienvironmental measures in mitigating pollinator loss - a meta-analysis. *Ecology Letters*, 16(7), 912–920.

- Schiestl, F. P., & Johnson, S. D. (2013). Pollinator-mediated evolution of floral signals. *Trends in Ecology and Evolution*, 28(5), 307-315.
- Schweiger, O., Biesmeijer, J. C., Bommarco, R., Hickler, T., Hulme, P. E., Klotz, S., et al. (2010). Multiple stressors on biotic interactions: How climate change and alien species interact to affect pollination. *Biological Reviews*, *85*(4), 777–795.
- Scott-Dupree, C. D., Conroy, L., & Harris, C. R. (2009). Impact of currently used or potentially useful insecticides for canola agroecosystems on Bombus impatiens (Hymenoptera: Apidae), Megachile rotundata (Hymentoptera: Megachilidae), and Osmia lignaria (Hymenoptera: Megachilidae). *Journal of Economic Entomology*, 102(1), 177–182.
- Sidhu, C. S., & Joshi, N. K. (2016). Establishing Wildflower Pollinator Habitats in Agricultural Farmland to Provide Multiple Ecosystem Services, *Frontiers in Plant Science*, *7*(3), 1–5.
- Southwick, E. E., Loper, G. M., & Sadwick, S. E. (1981). Nectar production, composition, energetics and pollinator attractiveness in spring flowers of western New York. *American Journal of Botany*, 994-1002.
- Somme, L., Vanderplanck, M., Michez, D., Lombaerde, I., Moerman, R., Wathelet, B., et al. (2015). Pollen and nectar quality drive the major and minor floral choices of bumble bees. *Apidologie*, *46*(1), 92–106.
- Southwick, E. E., & Southwick Jr. L. (1992). Estimating the economic value of honey bees (Hymenoptera: Apidae) as agricultural pollinators in the United States. *Journal of Economic Entomology*, 85(3), 621-633.
- Stanton, M. L., & Preston, R. E. (1988). Ecological consequences and phenotypic correlates of petal size variation in wild radish, Raphanus sativus (Brassicaceae). *American Journal of Botany*, 528-539.
- Stout, J. C., & Morales, C. L. (2009). Ecological impacts of invasive alien species on bees. *Apidologie*, *40*(3), 388–409.
- Stout, J. C., & Tiedeken, E. J. (2017). Direct interactions between invasive plants and native pollinators: evidence, impacts and approaches. *Functional Ecology*, *31*(1), 38–46.
- Suding, K. N. (2011). Toward an Era of Restoration in Ecology: Successes, Failures, and Opportunities Ahead. *Annual Review of Ecology, Evolution, and Systematics*, *42*(1), 465–487.
- Sutter, L., Jeanneret, P., Bartual, A. M., Bocci, G., & Albrecht, M. (2017). Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant

crop-pollinating bees through complementary increase in key floral resources. *Journal of Applied Ecology*, (4).

- Swinton, S. M., Lupi, F., Robertson, G. P., & Hamilton, S. K. (2007). Ecosystem services and agriculture: Cultivating agricultural ecosystems for diverse benefits, *Ecological Economics*, 64(2), 245–252.
- Tasei, J. M. N., & Aupinel A. (2008). Original article Nutritive value of 15 single pollens and pollen mixes tested on larvae produced by bumblebee workers (Bombus terrestris, Hymenoptera: Apidae)*, *39.4*, 397–409.
- Thompson, H. M., & Hunt, L. V. (1999). Extrapolating from honeybees to bumblebees in pesticide risk assessment. *Ecotoxicology*, *8*(3), 147–166.
- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., & Siemann, E. (1997). The influence of functional diversity and composition on ecosystem processes. *Science*, 277(5330), 1300–1302.
- Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., et al. (2001). Forecasting Agriculturally Driven Global Environmental Change. *Science*, 292(5515), 281–284.
- Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity - Ecosystem service management. *Ecology Letters*, *8*(8), 857–874.
- Tscharntke, T., Tylianakis, J. M., Rand, T. A., Didham, R. K., Fahrig, L., Batáry, P., et al. (2012). Landscape moderation of biodiversity patterns and processes eight hypotheses. *Biological Reviews*, *87*(3), 661–685.
- Tuell, J. K., Fiedler, A. K., Landis, D., & Isaacs, R. (2008). Visitation by wild and managed bees (Hymenoptera: Apoidea) to eastern U.S. native plants for use in conservation programs. *Environmental Entomology*, 37(3), 707–718.
- Van Buskirk, J. and Yvonne W. (2004). Enhancement of farmland biodiversity within setaside land. *Conservation Biology*, 18(4), 987-994.
- Buskirk, J. Van, Willi, Y., Buskirk, J. V. A. N., & Willit, Y. (2016). Society for Conservation Biology Enhancement of Farmland Biodiversity within Set-Aside Land Enhancement of Farmland Biodiversity within, *18*(4), 987–994.
- Vanderplanck, M., Moerman, R., Rasmont, P., Lognay, G., Wathelet, B., Wattiez, R. et al. (2014). How does pollen chemistry impact development and feeding behaviour of polylectic bees? *PLoS ONE*, *9*(1), 1–9.

- Van der Moezel, P. G., Delfs, J. C., Pate, J. S., Loneragan, W. A., & Bell, D. T. (1987). Pollen selection by honeybees in shrublands of the Northern Sandplains of Western Australia. *Journal of Apicultural Research*, 26(4), 224-232.
- Vaudo, A. D., Patch, H. M., Mortensen, D. A., Grozinger, C. M., & Tooker, J. F. (2014). Bumble bees exhibit daily behavioral patterns in pollen foraging. *Arthropod-Plant Interactions*, 8(4), 273–283.
- Vaudo, A. D., Tooker, J. F., Grozinger, C. M., & Patch, H. M. (2015). Bee nutrition and floral resource restoration. *Current Opinion in Insect Science*, *10*, 133–141.
- Vaudo, A. D., Patch, H. M., Mortensen, D. A., Tooker, J. F., & Grozinger, C. M. (2016). Macronutrient ratios in pollen shape bumble bee (Bombus impatiens) foraging strategies and floral preferences. *Proceedings of the National Academy Sciences*, 113(28), E4035-E4042.
- Vazquez, D. P., & Aizen, M. A. (2004). Asymmetric Specialization: A pervasive Feature of Plant-Pollinator Interactions. *Ecology*, *85*(5), 1251–1257.
- Venturini, E. M., Drummond, F. A., Hoshide, A. K., Dibble, A. C., & Stack, L. B. (2016). Pollination Reservoirs for Wild Bee Habitat Enhancement in Cropping Systems: a Review. Agroecology and Sustainable Food Systems, 41(2), 101–142.
- Venjakob, C., Klein, A., Ebeling, A., Tscharntke, T., & Scherber, C. (2016). Plant diversity increases spatio-temporal niche complementarity in plant-pollinator interactions. *Ecology and Evolution*, 6(8), 2249–2261.
- Visack, T., & McCarthy, G. (2015). National strategy to promote the health of honey bees and other pollinators. *Report Issued by the White House the Pollinator Health Task Force*.
- Von Felten, S., Hector, A., Buchmann, N., Niklaus, P. A., Schmid, B., & Scherer-Lorenzen, M. (2009). Belowground nitrogen partitioning in experimental grassland plant communities of varying species richness. *Ecology*, *90*(5), 1389–1399.
- Watson, A. K., & Renney, A. J. (1974). The Biology of Canadian Weeds.: Centaurea Diffusa and C. Maculosa. Canadian Journal of Plant Science, 54(4), 687-701.
- Weiss, M. R. (1995). Floral color change: a widespread functional convergence. *American Journal of Botany*, 167-185.
- Westphal, C., Steffan-Dewenter, I., & Tscharntke, T. (2003). Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters*, 6(11), 961–965.

- Whitehorn, P. R., O'Connor, S., Wackers, F. L., & Goulson, D. (2012). Neonicotinoid Pesticide Reduces Bumble Bee Colony Growth and Queen Production. *Science*, 336(6079), 351–352.
- Williams, I. H. (1994). The dependency of crop production within the European Union on pollination by honey bees. *Agricultural Zoology Reviews (United Kingdom).*
- Williams, N.M., Minckley, R.L., and Silveira, F.A. (2001). Variation in native bee faunas and its implications for detecting community changes. *Ecology and Society*, 5, 1-21.
- Williams, N. M., & Kremen, C. (2007). Resource distributions among habitats determine solitary bee offspring production in a mosaic landscape. *Ecological Applications*, 17(3), 910–921.
- Williams, N. M., Ward, K. L., Pope, N., Isaacs, R., Wilson, J., May, E. A., et al. (2015). Native wildflower plantings support wild bee abundance and diversity in agricultural landscapes across the United States. *Ecological Applications*, 25(8), 2119–2131.
- Winfree, R., Williams, N. M., Dushoff, J., & Kremen, C. (2007). Native bees provide insurance against ongoing honey bee losses. *Ecology Letters*, *10*(11), 1105–1113.
- Winfree, R., Williams, N. M., Gaines, H., Ascher, J. S., & Kremen, C. (2008). Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. *Journal of Applied Ecology*, 45(3), 793–802.
- Winfree R., Aguilar R., Vazquez, D. P., LeBuhn, G., & Aizen, M. A. (2009). A metaanalysis of bees' responses to anthropogenic disturbance. *Ecology*, 90(8), 2068-2076.
- Winfree, R., Gross, B. J., & Kremen, C. (2011). Valuing pollination services to agriculture. *Ecological Economics*, 71, 80-88.
- Winston M. L. (1987). *The biology of the honey bee*, Harvard University Press, Cambridge.
- Wood, T. J. (2017). *The effect of agri-environment schemes on farmland bee populations*. (Doctoral dissertation, University of Sussex)
- Wratten, S. D., Gillespie, M., Decourtye, A., Mader, E., & Desneux, N. (2012). Pollinator habitat enhancement: Benefits to other ecosystem services. *Agriculture, Ecosystems and Environment*, *159*, 112–122.